Cosyne, 2007
Computational and Systems Neuroscience

Conference Program and Abstracts

22–25 February 2007

Marriot Hotel, Downtown
Salt Lake City, Utah
The annual Cosyne meeting provides a forum for the exchange of experimental and theoretical results in systems neuroscience. Presentations are arranged in a single track, so as to encourage interdisciplinary interactions.

The 2007 meeting consists of 15 invited talks selected by the Executive Committee, along with 18 talks and 291 posters selected from submitted abstracts by the Program Committee. Ten of the poster presenters will also give a 4-minute “spotlight” presentation summarizing their submitted work. Abstracts will remain available on the internet after the meeting at http://cosyne.org

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Registration/Hotel: Christina Laycock, Conference and Events Office, University of Rochester  
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Thursday, 22 February

4:00pm Registration desk opens
6:00pm Welcome reception, including cocktails and buffet
7:30pm Introductory remarks, Zach Mainen and Eero Simoncelli

7:45pm Hippocampal-neocortical interactions, up-states, and accelerated replay of neocortical memory episodes, Bruce McNaughton (invited); University of Arizona .................. p 7

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9:10am Motor learning with unstable neural representations, Uri Rokni, Andrew Richardson, Emilio Bizzi, Sebastian Seung; Massachusetts Institute of Technology ............... p 64
9:30am Sleep and learning, Daniel Margoliash (invited); University of Chicago ............... p 65

10:10am Refreshment break

10:40am Spike latencies in retinal ganglion cells encode spatial image details, Tim Gollisch, Markus Meister; Harvard University .................. p 66
11:00am Neural coding of natural signals: Theory, computation, and data, Michael Lewicki (invited); Carnegie Mellon University .................. p 67
11:40am Bayesian inference underlies contraction bias, Paymon Hosseini, Yonatan Loewenstein; Massachusetts Institute of Technology .................. p 68

12:00 Lunch break

2:00pm Dendritic arithmetic: Some new twists and curves, Bartlett Mel (invited); University of Southern California .................. p 69
2:40pm Small fields change spike timing: A functional role of local-field potentials?, Yuzhuo Su, Thomas Radman, Marom Bikson, Lucas Parra; City College of New York ........ p 70
3:00pm Cerebellar glomeruli: Can limited extracellular calcium propagate information among distant synapses, David Eagleman¹, Olivier Coenen², Vladimir Mitsner³, Thomas Bartoli³, Terrence Sejnowski³; ¹Baylor College of Medicine, ²Sony Computer Science Laboratory, Paris France, ³The Salk Institute .................. p 71

3:20pm Refreshment break
3:50pm Testing hypotheses about computation and coding in the visual system, Sheila Nirenberg (invited); Cornell University ................................................. p 72

4:30pm A model of temporal integration during electrical stimulation of the human retina, Alan Horsager¹, Scott Greenwald², Geoff Boynton³, Mark Humayun¹, Robert Greenberg², James Weiland¹, Matthew McMahon², Ione Fine¹; ¹University of Southern California; ²Second Sight Medical Products Inc; ³The Salk Institute ................................................. p 73

4:50pm Spotlight presentations:

- Learning sparse and invariant features hierarchies, Y-Lan Boureau, Marc’Aurelio Ranzato, Fu Jie Huang, Yann LeCun; New York University ....................... p 90
- Perceptual learning as improved Bayesian inference in early sensory areas, Vikranth Bejjanki, Wei Je Ma, Jeffrey Beck, Alexandre Pouget; University of Rochester .... p 120
- Are cortical networks balanced?, John Hertz; Nordita, Niels Bohr Institute ...... p 136
- Population coding of song element sequence in the songbird brain nucleus HVC, Jun Nishikawa, Masato Okada, Kazuo Okanoya; RIKEN Brain Science Institute, Japan ................................................................. p 157
- Chromatic statistics and information in natural images, Patrick Garrigan, Charles Ratliff, Peter Sterling, David Brainard, Vijay Balasubramanian; University of Pennsylvania ......................................................... p 181

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7:30-11:30pm Poster Session II .................................................. pp 74–191

Saturday, 24 February

7:30am Continental breakfast

8:30am A bottom up visual saliency map in the primary visual cortex: Theory and its experimental tests, Li Zhaoping (invited); University College London, UK ............... p 192

9:10am Equalization of ocular dominance columns by an activity dependent learning rule and inhibition, Taro Toyoizumi, Kenneth Miller; Columbia University .............. p 193

9:30am How thalamic circuits change visual signals en route from retina to cortex, Judith Hirsch (invited); University of Southern California ......................... p 194

10:10am Refreshment break
10:40am  Retinal oscillations carry visual information to cortex, Kilian Koepsell1, Xin Wang2, Yichun Wei2, Qingbo Wang2, Vishal Vaingankar2, Judith Hirsch2, Friedrich Sommer; 1University of California, Berkeley  2University of Southern California  CIF 2007  p 195

11:00am  Coding 3D by 3V: How sensor motion constrains sensory coding, Ehud Ahissar (invited); The Weizmann Institute of Science, Israel  CIF 2007  p 196

11:40am  From spikes to space: Reconstructing features of the environment from spikes alone, Vladimir Itskov1, Carina Curto2; 1Columbia University, 2Rutgers University  CIF 2007  p 197

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2:00pm  On the agnosticism of spikes: Attention, intention, and salience in the monkey lateral intraparietal area, Michael E. Goldberg (invited); Columbia University  CIF 2007  p 198

2:40pm  Medial prefrontal cortex and the temporal control of action, Mark Laubach, Nandakumar Narayanan; Yale University  CIF 2007  p 199

3:00pm  Hemodynamic correlates of a perceptual decision, Mehrdad Jazayeri, Justin Gardner, David Heeger; New York University  CIF 2007  p 200

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3:50pm  Planning and decision-making in parieto-frontal circuits, Richard Andersen (invited); California Institute of Technology  CIF 2007  p 201

4:30pm  Neural correlates of tactile detection: Combined MEG and biophysically based computational modeling study, Stephanie Jones1, Dominique Pritchett2, Steven Stufflebeam1, Matti Hämäläinen1, Christopher Moore2; 1Massachusetts General Hospital, 2Massachusetts Institute of Technology  CIF 2007  p 202

4:50pm  Spotlight presentations:

- On the origin of the cortical architecture, Dario Ringach; University of California, Los Angeles  CIF 2007  p 231

- Optimal learning: A route to depression?, Quentin Huys, Peter Dayan; The Gatsby Center, University College London, UK  CIF 2007  p 244

- Experience-dependent dynamics of spatio-temporal precision and synchrony in place cells, Sen Cheng, Loren Frank; University of California, San Francisco  CIF 2007  p 251

- Two-color, bi-directional optical voltage control of genetically-targeted neurons, Edward Boyden1, Xue Han2; 1Stanford University, 2Massachusetts Institute of Technology  CIF 2007  p 269

- Maximum entropy modeling of multi-neuron firing patterns in V1, Ifijie Ohiorhenuan, Jonathan Victor; Weill Medical College, Cornell University  CIF 2007  p 292

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9:10am  Spikes in the auditory forebrain: Surprise, not intensity, Patrick Gill, Frederic Theunissen; University of California, Berkeley ................................................................. p 321

9:30am  Spike timing-dependent plasticity and the didactic reorganization of cortical receptive fields, Joshua Young¹, Violetta Waleszczyk²,³, Chun Wang², Mike Calford⁴, Bogdan Dreher², Klaus Obermayer¹; ¹Berlin University of Technology, Germany, ²University of Sydney, Australia, ³Nencki Institute of Experimental Biology, Poland, ⁴University of Newcastle, Australia ......................................................... p 322

9:50am  Refreshment break

10:30am Unraveling fine-scale and cell-type specificity of cortical circuits, Ed Callaway (invited); The Salk Institute ................................................................. p 323

11:10am  Functional constraints do not cause observed correlations between maximal conductances in an identified neuron, Adam Taylor, Eve Marder; Brandeis University . p 324

11:30am  Synchronized excitation and inhibition during spontaneous and evoked response in the barrel cortex, Michael Okun, Ilan Lampl; Weizmann Institute of Science, Israel .. p 325

11:50am  Lunch break

2:00pm  A neural mechanism for decision-making, or how I learned to stop worrying and love the bound, Michael Shadlen (invited); University of Washington, Seattle . . . . . p 326

2:40pm  Role of serotonin in delayed reward choice in humans, Nicolas Schweighofer¹, Saori Tanaka², Kazuhiro Shishida³, Mathieu Bertin², Cheol Han¹, Yasumasa Okamoto³, Shigeto Yamawaki³, Kenji Doya²; ¹University of Southern California, ²Advanced Telecommunications Research Institute, Japan, ³Hiroshima University, Japan ....................... p 327

3:00pm  Credit assignment with Bayesian reward estimation, Constantin Rothkopf, Dana Ballard; University of Rochester ......................................................... p 328

3:20pm  Just decide: Computational studies of intertemporal choice in humans and monkeys, Paul Glimcher (invited); New York University ......................................................... p 329

4:00pm  End of conference
Hippocampal-neocortical interactions, up-states, and fast-forward replay of neocortical memory episodes

Bruce McNaughton
University of Arizona

The hippocampal output vector spans a subspace that is determined by spatial location. Within that subspace, both intrinsic neural activity (e.g., working memory, motivation, goals, behavioral set etc.) and external input (sensory cues) modify the direction of the population vector. Thus, hippocampus provides a context code to the neocortex that is jointly determined by what is happening and where it happens, with the latter factor dominant. These hippocampal context or ‘index’ codes are believed to link memory items stored in parameter specific, relatively sparsely interconnected neocortical modules by indirect association. The superficial layers of the neocortex, which receive the main hippocampal outflow, are similarly sensitive to spatial context (consistent with the need to store index codes in the neocortex at the time the memory is acquired), whereas deeper neocortex layers are relatively context independent (and thus contain the stored data in a context free form). It appears that the initially sparse hippocampal output code is ‘zipped’ for more efficient transmission in the CA1-subiculum transformation, and ‘unzipped’ to sparse form again for storage in superficial neocortex.

During slow-wave sleep and quiet wakefulness, hippocampal sharp-wave-ripple events (lasting about 50-100 msec) convey bursts of recently stored index sequences to the neocortex, and may trigger transitions from ‘down’ states to ‘up’ states, during which some form of memory reprocessing may occur. During ‘up’ states, some neocortical areas can exhibit high fidelity replay of temporal sequences of neural ensemble activity, compressed in time by a factor of about 5-7 fold. Only forward replay is observed, not reverse. The emerging picture is one in which the hippocampus, in slow-wave sleep, periodically (randomly) seeds the neocortex with snippits (100 msec) of recently stored index code sequences, which triggers more temporally extended sequence replay (500 msec) of cortically stored data, corresponding to several seconds of real time. What happens to cortical information structures as a consequence of this process is mostly still a matter of speculation, falling under the general theme of ‘systems-level memory consolidation’.

[End of text]
Role of task difficulty in modulation of neural activity

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How does attentional modulation of a neuron’s preferred feature (µ), or changing its tuning width (σ), or its response gain (g) benefit behavioral performance? We investigate this in the context of a visual search task, e.g., search for a vertical bar among horizontal bars (which becomes more difficult as the target orientation approaches horizontal). We consider $SNR$ (ratio of expected population response to the target over the distractor) as the performance metric [1]. We compute the benefit in performance per unit change in µ, σ and g. Our simulation results show that changing σ can be beneficial or not, depending on the task difficulty due to target-distractor discriminability (measured here as separation in degrees between target and distractor orientation). We find that a unit change in σ is more beneficial in difficult than easy tasks (fig 1b). A similar trend is observed for changing µ (fig 1a). However, the opposite trend is observed for gain modulation – a unit change in g is more beneficial in easy tasks than difficult tasks (fig 1c).

These results suggest that gain modulation is more likely to be observed in easy tasks, while tuning width modulation is more likely to occur in difficult tasks. We suggest that the differences in task difficulty may resolve existing conflicts in the field on whether attention modulates gains or tuning width. Indeed, previous studies reporting gain modulation have used easy tasks (target-distractor separation around 45-90° [2], or target only without any distractor [3]), while studies reporting tuning width modulation have used difficult tasks (22.5°, [4]). We conclude that task difficulty plays a critical role in determining attentional modulation.

Acknowledgments
This work was supported by HFSP, NSF (CRCNS), DARPA and ONR.

References
Bayesian Models of Dynamic Attentional Selection

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Selection amongst potentially conflicting inputs is a critical facet of many decision making tasks. According to Bayesian optimality principles, the attentional suppression of irrelevant inputs and inappropriate responses should reflect implicitly encoded prior assumptions about the statistical structure of sensory inputs. This argument has particularly interesting ramifications for experimental tasks that violate the statistics of the natural environment. Here, we provide a Bayesian formulation for dynamic attentional selection that elucidates this problem, and consider the consequences for behavioral performance. We illustrate these issues using the Eriksen flanker task, a classical paradigm that explores the effects of competing sensory inputs on response tendencies. In this task, the presence of conflicting flanker stimuli has been shown to interfere with the processing of a central target stimulus, especially on short reaction-time trials. We show how two distinct Bayesian inferential principles can explain the detrimental effects of competition in speeded decisions. The first rests on the notion that the brain may be wired, through either evolutionary adaptation or developmental learning, to encode a compatibility bias: that is, the prior belief that spatially proximate items in a visual scene tend to be featurally similar. The second emphasizes the spatial uncertainty induced by overlapping receptive fields of visual sensory processes, which can give rise to a confusion of stimulus identity early on during visual presentation. We also elaborate a simpler, approximate, inference model that formalizes previous work suggesting that different neural structures are involved in the monitoring of conflict and the detection of unexpected events. Finally, we suggest explicit experimental tests to resolve the remaining conflicts between the models.

Acknowledgments
We thank Philip Holmes, David MacKay, Sam McClure, and Liu Yuan for helpful discussions. Funding for AJY comes from an NIH NRSA institutional training grant.

References

Modulation of auditory responses by modality-specific attention in rat primary auditory cortex

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How does attention modulate sensory representations? In order to probe the underlying neural mechanisms, we established a simple rodent model of modality-specific attention. Here we describe results of experiments in freely moving rats in which we have used tetrodes to record neural responses in primary auditory cortex (area A1) while subjects performed this behavior.

Subjects were first trained to perform distinct auditory and olfactory two alternative forced-choice (2AFC) tasks. Training and testing were conducted in a custom three-poke computer-controlled behavioral apparatus. Subjects initiated trials with a center-poke, which triggered presentation of a tone (either 5 or 15 Hz), a task odor (either R(-)-2-Octanol or S(+)-2-Octanol), or both. Subjects responded moving to the left or right poke. Correct responses were rewarded with water. Auditory and olfactory blocks (of 50 trials each) were interleaved in a single session. In auditory blocks, pure tones were either presented with or without a null odor (caproic acid, n=2 and 3 respectively), and subjects were cued to perform the task based on auditory stimuli. In olfactory blocks, both task odors and pure tones were presented simultaneously, and subjects were cued to perform the task based on olfactory stimuli.

After subjects reached consistent performance on the interleaved blocks, tetrode drives were implanted in primary auditory cortex of the left hemisphere. Single unit responses to tones were heterogeneous, and included transient, sustained, and suppressed. Among 304 responsive units recorded, 19% (58 units) showed modality-specific attentional modulation of at least one of the tone-evoked responses; in most cases, the responses to a particular auditory stimulus was enhanced in the auditory block (or, equivalently, suppressed in the olfactory block). In addition, we also observed modality-specific attentional modulation of the spontaneous activity in similar proportion of units (61 units).

Our results suggest that shifting attention from audition to olfaction and back can modulate the activity of single neurons in primary auditory cortex.
Improvement of dendritic signal transfer due to non-uniform membrane property

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$^1$JSPS Research Fellow, $^2$RIKEN BSI, $^3$Tokyo Inst. of Tech., $^4$Univ. of Tokyo

In hippocampus, CA1 pyramidal neurons receive two distinct synaptic inputs: autoassociative memory inputs from CA3 and sensory inputs from entorhinal cortex (EC) (Fig. 1A). In fact, these inputs are known to be separately received in dendrites (Fig. 1B); inputs from CA3 are given to proximal dendrite, whereas inputs from the EC are to distal dendrite. Understanding manner of signal propagation and integration in dendrites of CA1 pyramidal neurons is important since CA1 is first stage of hippocampal output to neocortex.

A previous simulation study by Jarsky et al. [1] suggested that signal transfer from distal dendrite to soma is difficult and additional inputs (from CA3) to proximal dendrite are needed for somatic firing. On the other hand, experimental study by Nakazawa et al. showed that CA1 neurons of CA3-NMDAR knockout mice respond normally [2], suggesting that CA1 neuron can induce somatic firing without strong inputs to its proximal dendrite. These results [1,2] may be conflicting about possibility of somatic firing only by distal inputs. In our previous studies [3], we estimated distribution of membrane resistance in dendrite of CA1 pyramidal neurons. The estimated result was a step function (Fig.2A bottom); there is a steep decrease of membrane resistance. The estimated non-uniformity may concern behavior of dendritic signal propagation.

In this study, we investigate effects of non-uniform membrane property on dendritic signal transfer and discuss the possibility of somatic firing only by distal inputs. Assuming the estimated non-uniform distribution of membrane property [3], we analyze cable equations and perform numerical simulation of compartment models to clarify functional role of non-uniform membrane property. By analysis of cable equation, we find that when we give inputs to distal dendrite, somatic responses obtained for non-uniform model of membrane resistance were significantly stronger than those for uniform model (Fig. 2). Furthermore, using compartment models with active channels, we find that dendritic spike propagation is also improved by non-uniformity, and somatic firing can be obtained even just with distal inputs for non-uniform model. This result implies that the signal can be propagated from distal dendrite to soma without CA3 input, and may support the experimental results by Nakazawa et al. [2]. Moreover, our results suggest that the steep decrease of membrane resistance in distal dendrite realizes dendritic signal transfer from distal dendrite to soma.

![Figure 1: (A) local circuit of hippocampal formation; (B) dendrite of CA1 pyramidal neuron](image)

![Figure 2: (A) membrane response to distal inputs; (B) improvement of dendritic signal transfer](image)

References


Metabolic capacity of mammalian axons
Janos Perge, Kristin Koch, Jian Li, Vijay Balasubramanian, and Peter Sterling
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Brain is one of the body’s most metabolically expensive tissues, and a large proportion of its energy budget (an estimated 35%) goes to restore ionic balances following action potentials [1]. Despite the importance of energy metabolism to neuronal computation, we know little about the metabolic cost of spiking. Metabolic capacity can be estimated by the fraction of cytoplasm occupied by mitochondria. Thus to study the metabolic demand of spike propagation we measured the mitochondrial content of retinal ganglion cell axons.

Analyzing electron micrographs, we reconstructed the distribution and volume of mitochondria within the axons, both in the unmyelinated segments (in retina) and in the myelinated segments (in optic nerve). Conventional wisdom states that the main energy cost lies in restoring the Na⁺/K⁺ balance following action potentials. It follows that: (i) total mitochondrial volume should be proportional to axonal membrane capacitance, therefore membrane surface area; (ii) since myelination reduces membrane capacitance by several orders of magnitude, mitochondrial volume in the myelinated axon segment should thus be correspondingly smaller than in the unmyelinated segment; (iii) mitochondria might be expected to accumulate at or near the nodes of Ranvier, as they do at other regions of high ion pumping activity (e.g., the photoreceptor inner segment). Instead we found: (i) mitochondrial volume was a roughly constant fraction of axoplasmic volume (3.4 for unmyelinated and 1.6% for myelinated axons); (ii) myelination reduced mitochondrial volume by a factor of only ~2.5; (iii) mitochondria, which were 3 ±2.3 µm (mean ± SD) long did not accumulate near the nodes of Ranvier; instead they distributed randomly along the length of the axon, with an estimated mean separation between mitochondrion centers of 3.2 µm, and an average distance between mitochondria and nodal membrane of 0.4 µm.

The finding that mitochondrial volume scales with axon volume and not with axonal membrane surface area might be explained if ganglion cell firing rates scaled linearly with axon diameter, giving a power requirement that would scale as (surface area) x (diameter). Simultaneous measurements of ganglion cell firing rate and axon volume are not available. However, we do know that the cell type with the thinnest axons are ‘local-edge’, with mean firing rates to natural scenes of ~4 spikes/s and that the cell type with the thickest axons are ‘brisk-transient’ with mean firing rates of ~8 spikes/sec [2]. More generally the hypothesis predicts a match between the distribution of axon diameters and the distribution of firing rates, and this is roughly what we find. It is less clear why a cell with a higher firing rate should need a larger axon. The conventional wisdom is that by achieving a higher conduction velocity, the conduction time to the brain is shorter. Yet, the distribution of fiber diameters is conserved from mouse to man, despite a 10-fold increase in conduction distance. Alternatively, the higher firing rates, which carry more information [2], might require a larger terminal arbor with more vesicle release sites to transfer the information; thus we hypothesize that a larger axon is needed to provide greater capacity for axonal transport to supply the larger terminal arbors. This is consistent with findings in retina that neurons carrying more information have more active zones and thicker axons [3]. The reason why myelination saves so little remains unanswered.

References
Estimation of two-layer statistical model of natural images using score matching leads to complex cell properties

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We present a two-layer model of natural images that produces outputs similar to Complex Cells. Unsupervised learning using the novel method Score Matching (SM) [1] is used to estimate the model. In contrast to our previous work, both layers are freely learned from the data. The second layer has a very sparse connectivity as predicted by the Hubel and Wiesel Model of primary visual cortex, and describes local dependencies between first layer features.

Score Matching is a locally consistent estimation method for non-normalized statistical models. By making use of the Score Function (the gradient of the log-probability), an estimation without knowledge of the partition function is possible. This is in contrast to Monte Carlo methods such as Contrastice Divergence, which rely on slow random sampling, or methods based on approximations. We apply the method to a model of the form

$$\log p(x|W, V) = \sum_i \sqrt{v_i (Wx)^2} - \log Z \quad (1)$$

where $x$ is a data vector, $V$ and $W$ are weight matrices and $Z$ is the intractable partition function. The nonlinearities are applied elementwise. We can compute an objective function in terms of derivatives of the score function, which is then optimized by stochastic gradient descent.

When applied to natural image patches, the first layer converges to Gabor-type features. The second layer, however exhibits a very sparse connectivity, where each row has significant activity only for a few similar first layer features. These features that are pooled by the second layer have similar size, position and orientation, but differ in spatial frequencies. This local pooling is in contrast to similar two-layer models, in which the second layer describes more global structure. Similar results are obtained for a range of overcomplete model specifications and data dimensionalities.

Left: The matrix $V$ with white representing zero and darker colors representing stronger activation. The sparse connectivity is evident. In the non-overcomplete case the number of units in the second layer is the same as in the first layer, so several output units share a similar receptive field.

Right: The features given by rows of $W$. The features $W$ have been sorted according to subspaces as identified by $V$.

References

Tapestries of experts and a novel path to score matching

Jascha Sohl-Dickstein, Bruno Olshausen

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We present the Tapestry of Experts (TOE) model, a spatially heterogeneous generalization of the Field of Experts (FOE) [2] model in which individual experts need not be concerned with interference by spatially shifted versions of themselves. In addition we present an independent derivation of the score matching [1] objective function for performing maximum likelihood estimation on models (like FOE and TOE) which cannot be analytically normalized, and consider extensions suggested by our derivation.

The TOE model we propose has a model distribution

\[ p(x) = \frac{1}{Z(\theta)} \prod_{i=1}^{M} \prod_{j=1}^{M} \prod_{k=1}^{O} \phi(i \text{mod} N, j \text{mod} N, k) \times |0 < i_x < N, 0 < j_x < N| \]

where \( N, M \) are the widths of receptive field and image, \( O \) is the degree of overcompleteness and \( \phi_i(x) = \left( 1 + \frac{1}{2} (J_i^T x)^2 \right)^{-\alpha} \).

As in FOE the experts tile the data space, but unlike in FOE experts only recur when they will no longer overlap themselves. TOE appears better able to capture the statistics of natural scenes - as demonstrated below in an image denoising task:

An image (a) with additive Gaussian noise (\( \sigma = 0.3\sigma_{\text{image}} \)) and MAP estimates of the original image from (b) a 24x overcomplete FOE model with 5x5 receptive fields and (c) a 6x overcomplete TOE model with 5x5 receptive fields.

The \( Z(\theta) \) normalization term - the so called partition function - is intractable in both FOE and TOE models. We sidestep this difficulty by approximating the learning gradient using an expansion around the datapoints of the difference in energy gradients between data and model distributions. In contrast to traditional methods for dealing with intractable partition functions, such as mean field or renormalization group theory, this technique depends solely on local properties of the model rather than macroscopic or scale invariant properties. The derived objective function

\[ \left( \frac{1}{2} \nabla_x E(x; \theta) \cdot \nabla_x E(x; \theta) - \nabla_x \cdot \nabla_x E(x; \theta) \right)_{p(x)} \]

turns out to be precisely that derived by Hyvärinen via score matching. The derivation we present places score matching more firmly in a context with other approximate analytical solutions to the partition function problem however, and promises several extensions. It is possible for instance to include higher order terms in the derivation, increasing the size of the patches around the datapoints over which the model distribution can be approximated.

References

Detecting transitions: A probabilistic description of short-term plasticity

Nabil Bouaouli, Sophie Deneve, Group for Neural Theory, LSCP-CNRS, Paris

Many experiments have shown that synapses, instead of being static, take part actively and over a wide range of time scales in processing and transmitting information in the brain. Moreover, sensitivity to fast changing stimuli is a ubiquitous feature in the brain and is believed to be one of the roles supported by short-term depression. Here, we use a probabilistic approach and derive the dynamics of short-term plasticity one would expect for detecting, as reliably and quickly as possible, a sudden change in the environment.

In this study, we consider that the input to a synapse is a sample spike train generated by a Hidden Markov Model describing the temporal dynamics of a binary variable $x$ representing the presence ($x=1$) or absence ($x=0$) of a feature in the neuron’s receptive field. Meanwhile, the firing rate of the pre-synaptic neuron is higher when $x$ is 1. We require, then, the synapse compute the probability that a stimulus appeared within a short temporal window, given the spikes observed. Using a procedure developed in a previous work for learning the dynamic parameters of the generative model, we compute this probability online and found that, depending on the parameters set chosen, the underlying synaptic computation is an integration of EPSPs which exhibits either/both short-term facilitation or/and depression.

An isolated spike received by the synapse increases temporarily the probability of a switch having occurred (an EPSP); whereas successive spikes are integrated if they are sufficiently close. This integration, however, is not a simple sum. Initially, the amplitude of the EPSP increases (facilitation) to reflect accumulating evidence that $x$ switched to 1. While the synapse responds strongly to the spikes immediately following the state transition, the subsequent responses decay in amplitude (depression). Eventually, future spikes provide no contribution to the probability and bring it below its resting level. This resembles a phenomenon in synaptic plasticity known as Desensitization (Fig. A response to a regular input burst). In fig.B2, we show an example of detecting transitions on a hidden variable (Fig.B1). As observed experimentally, depression is stronger for smaller ISI’s (right most transition).

This result suggests that membrane potential of a post-synaptic sensory neuron may reflect transitions probabilities of hidden variables to which they are tuned. These transition probabilities would be represented by the instantaneous membrane potential deviations from resting potential. Furthermore, the amplitude of an EPSP, its duration, the presence and strength of depression, facilitation and desensitization, their time constants, and frequency dependence are all constrained by the statistics of the input to the synapse. As we have shown in a previous work, these parameters could be learned by long-term spike-time dependant plasticity rules, suggesting that short-term and long-term plasticity might collaborate to make a synapse an efficient detector of changes.
Nonlinear receptive field analysis: making kernel methods interpretable

Wolf Kienzle, Jakob H. Macke, Felix A. Wichmann, Bernhard Schölkopf, Matthias O. Franz

Max Planck Institute for Biological Cybernetics

Identification of stimulus-response functions is a central problem in systems neuroscience and related areas. Prominent examples are the estimation of receptive fields and classification images [1]. In most cases, the relationship between a high-dimensional input and the system output is modeled by a linear (first-order) or quadratic (second-order) model. Models with third or higher order dependencies are seldom used, since both parameter estimation and model interpretation can become very difficult.

Recently, Wu and Gallant [3] proposed the use of kernel methods, which have become a standard tool in machine learning during the past decade [2]. Kernel methods can capture relationships of any order, while solving the parameter estimation problem efficiently. In short, the stimuli are mapped into a high-dimensional feature space, where a standard linear method, such as linear regression or Fisher discriminant, is applied. The kernel function allows for doing this implicitly, with all computations carried out in stimulus space. As a consequence, the resulting model is nonlinear, but many desirable properties of linear methods are retained. For example, the estimation problem has no local minima, which is in contrast to other nonlinear approaches, such as neural networks [4].

Unfortunately, although kernel methods excel at modeling complex functions, the question of how to interpret the resulting models remains. In particular, it is not clear how receptive fields should be defined in this context, or how they can be visualized. To remedy this, we propose the following definition: noting that the model is linear in feature space, we define a nonlinear receptive field as a stimulus whose image in feature space maximizes the dot-product with the learned model. This can be seen as a generalization of the receptive field of a linear filter: if the feature map is the identity, the kernel method becomes linear, and our receptive field definition coincides with that of a linear filter. If it is nonlinear, we numerically invert the feature space mapping to recover the receptive field in stimulus space.

Experimental results show that receptive fields of simulated visual neurons, using natural stimuli, are correctly identified. Moreover, we use this technique to compute nonlinear receptive fields of the human fixation mechanism during free-viewing of natural images.

References


Exact Bayesian Bin Classification: 
a fast alternative to Bayesian Classification and its application to neural response analysis

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We investigate the general problem of signal classification and, in particular, that of assigning stimulus labels to neural spike trains recorded from single cortical neurons. Finding efficient ways of classifying neural responses is especially important in experiments involving rapid presentation of stimuli.

We introduce a fast, exact alternative to Bayesian classification. Instead of estimating the class-conditional densities \( p(x|y) \) (where \( x \) is a scalar function of the feature(s), \( y \) the class label) and converting them to \( P(y|x) \) via Bayes’ theorem, this probability is evaluated directly and without the need for approximations. This is achieved by integrating over all possible binnings of \( x \) with an upper limit on the number of bins. Computational time is quadratic in both the number of observed data points and the number of bins. The algorithm also allows for the computation of feedback signals, which can be used as input to subsequent stages of inference, e.g. neural network training.

Responses of single neurons from high-level visual cortex (area STSa) to rapid sequences of complex visual stimuli are analysed. Information latency and information response duration (IRD) increase non-linearly with presentation duration, suggesting that neural processing speeds adapt to presentation speeds. Moreover, IRD is longer than presentation duration if the latter is smaller than \( \approx 50\,\text{ms} \), and shorter otherwise. Thus, for longer stimuli, the visual system should be able to separate the responses to successive stimuli, because IRD is the duration of the response needed for best stimulus discrimination. This is no longer the case for the shorter presentation durations: here responses to stimuli will begin to overlap, and thus optimal classification performance can no longer be attained.

Acknowledgments
We would like to thank Dengke Xiao and David Perrett for making the data [1] available to us. We would also like to thank Mike Oram and Johannes Schindelitz for useful discussions. This work was supported by the MRC training fellowship grant XMR065.

References
Bayesian Analysis of Response Bias in Behavioral Experiments

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Accurate characterizations of behavior during learning experiments are essential for understanding the neural bases of learning. While learning experiments often require subjects to learn multiple tasks simultaneously, most analyze subject performance separately on each individual task, ignoring the true interleaved presentation order of the tasks and making it difficult to distinguish learning behavior from response preferences that may represent biases. We present a Bayesian analysis of a state-space model for characterizing simultaneous learning of multiple tasks and for assessing behavioral biases in these learning experiments. Under the Bayesian analysis the posterior probability densities of the model parameters and the learning state are computed using Monte Carlo Markov Chain methods. Measures of learning, including the learning curve, the ideal observer curve and the learning trial translated directly from our previous likelihood-based state-space model analyses \cite{1}.

We compare the Bayesian and previous likelihood-based approaches in the analysis of a simulated conditioned T-maze task and of an actual object-place association task \cite{2}. Modeling the interleaved learning feature of the experiments along with the animal's response sequences allows us to disambiguate actual learning from response biases. The implementation of the Bayesian analysis using the WinBUGS software \cite{3} provides an efficient way to test different models without developing a new algorithm for each model. The new state-space model and the Bayesian estimation procedure suggest an improved, computationally-efficient approach for accurately characterizing learning in behavioral experiments.

Acknowledgments

This work was supported by MH071847 (ENB, ACS), DA015644 (ENB, WAS), MH58847 (WAS), the McKnight Foundation (WAS) and Fondation pour la Recherche Medicale, France (SW).

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Context-dependent modulation of functional connectivity: S2 to PFC connections in two-stimulus-interval discrimination tasks

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In a complex world, processing of signals from the environment must be flexible: a sensory cue may prompt different actions in different contexts. A laboratory example of context-dependent sensory processing is the two-stimulus-interval discrimination task. In each trial, a first stimulus (f1) must be stored in short-term memory, and later compared to a second stimulus (f2), in order to come to a binary decision as the result of the comparison (was f1 > f2? Y or N). The two stimuli, applied to the very same sensory receptors, must be treated quite differently. This task thus provides a clear example of context-dependent processing.

Our laboratory recently proposed a network model of processing in the prefrontal cortex (PFC) that addresses both the short-term memory and decision-making component of such tasks [1]. But the model requires connections from sensory cortex to PFC to switch sign in between the first and the second stimulus. The sign inversion is part of how the two stimuli are treated differently and is crucial to the proposed model. Yet how it is achieved in biology is unclear.

Here we develop a biologically plausible model of the signal transformation from secondary somatosensory cortex (S2) to PFC. To ground our model in experimental neurophysiology, we use neurophysiological data recorded by R. Romo’s laboratory from both cortical area S2 and PFC in monkeys performing the task. Our main goal is to use experimentally-observed context-dependent modulations of firing rates in cortical area S2 as the basis for a model that achieves a context-dependent inversion of the sign of S2 to PFC connections [2]. This is done without requiring any changes in connectivity [3]. We (a) characterize the experimentally-observed context-dependent firing rate modulation in area S2; (b) construct a model that results in the sign transformation; (c) characterize the robustness and consequent biological plausibility of the model.

Acknowledgments
Stephanie Chow was supported by a Swartz Foundation fellowship.

References


Bayesian sensorimotor integration in recurrent networks with population codes.

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A growing body of experiments has shown that the brain integrates sensory and motor information in a nearly optimal fashion. The Bayesian approach provides a good theoretical framework to understand this integration. Several theoretical studies have investigated how probability distributions could be represented in the activity of a population of neurons. In this study, we propose how recurrent networks could build, over time, a representation of the probability distributions (PDFs) of relevant sensory and motor variables, combining information about the executed motor commands and the sensory feedback. We explore the implication of this model for neural responses in brain areas involved in sensorimotor integration and motor control.

Concretely, we propose that neurons represent the logarithm of the probability that sensory and motor variables correspond to a preferred sensorimotor state. Then, the variance of the corresponding variable is encoded in the gain of the population code. This is consistent with the experimental finding that the gain of a population code is modulated by the contrast of the stimulus. Moreover, this representation allows the neurons to perform probabilistic computations by simply summing their activities. The sensorimotor network model is a layer of units \( i \) representing various preferred combinations of sensory states and motor states \( x_i \) at various time shifts \( t_i \) relative to the actual time (time shifts can be negative, i.e. lagging compared to the true state of the system, or positive, i.e. anticipating the future state of the system). Sensory inputs, in the form of noisy population codes, and motor commands are applied on this layer. In parallel, recurrent connections within the layer predict the sensorimotor state at various time shifts, such that the connection between neuron \( i \) and \( j \) corresponds to the probability of being in state \( j \) at time \( t_j \) given that one was in state \( i \) at time \( t_i \). When \( t_j > t_i \), these connections predict the future given the current state, and implement a probabilistic forward model for the motor dynamics. When \( t_j < t_i \), the connections implement a probabilistic inverse model (which is able to compute the succession of motor commands leading from an initial state to a final desired state). The propagation of activity in this network is equivalent to the forward-backward algorithm used for inference in hidden Markov models.

Using such a network architecture, a sensorimotor area could compute the most precise estimate of the current sensorimotor state given past motor commands and sensory feedback, perform optimal trajectory planning given the motor noise, and learn the forward and inverse dynamics of the sensorimotor system with simple hebbian learning rules. We applied this approach to the control of a simplified arm, in the presence of motor noise whose standard deviation increases with the motor commands, and/or with priors on low accelerations. As reported previously, this predicts smooth bell-shaped velocity profile, as observed in human arm movements.

The model predicts that neural responses in sensorimotor areas are widely tuned to the motor effectors position, velocity and acceleration at various time shifts. Moreover, the gain of neural responses should be controlled by the global precision of the internal model estimate, which varies as a function of the movement parameters, the time in the trajectory and the context. Finally, we expect that correlations between sensory and motor variables introduced by the movement dynamics are reflected by shifts of the corresponding tuning curves, e.g shifts of the velocity tuning curves for different arm position.
Hidden Markov models applied toward the inference of neural states and the improved estimation of linear receptive fields

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Several recent experimental results suggest that neurons are associated with multiple firing regimes, or states (e.g. tonic and burst modes of LGN cells and up-and-down states in the cortex). We develop a general framework for estimating neural receptive fields (RFs) from paired spike-train and stimulus data assuming that neurons transition between several discrete hidden states. Previous approaches applied to RF estimation such as the spike-triggered average, the linear-nonlinear-Poisson (LNP) point-process model, and information theoretic techniques are predicated on the assumption that all spikes are equally informative about the stimulus. If, instead, some spikes occur while the neuron is in a stimulus-ignoring state, then including those spikes in the RF estimation will necessarily worsen the estimate. Furthermore, if the neuron moves between several states, each of which responds to different features of the stimulus, then these techniques will discover some composite RF that may differ significantly from all of the individual, state-specific RFs. By discovering the hidden state of the neuron at every point in time, each of the individual RFs can be estimated for each of the hidden states.

We have modified the traditional hidden Markov model (HMM) theoretical framework (Rabiner, 1989) to allow for point-process observables (i.e. spike-trains) and to be parameterized by $N^2$ linear filters of the time-varying stimulus (where $N$ is the number of states) rather than static, conditional probability tables. Specifically, each state is associated with its own $N$ filters: $N - 1$ of these determine the transition rates from the current state to the other states, and the remaining filter determines the firing rate for the current state. This latter filter is the canonical RF (although now there are $N$ of them, one for each state), while the former filters are “RFs” for the state dynamics, a new concept in sensory neurophysiology. The actual transition and firing rates are the result of nonlinear transformations of the dot-products of the filters and the stimulus (i.e. as in LNP models). Stimulus-dependent transition rates are required to ensure that the neuron can be prompted by the stimulus to enter a particular state needed to respond to a feature of the stimulus.

The filters are learned using expectation-maximization (EM)—specifically the Baum-Welch algorithm—to maximize the log-likelihood as with traditional HMMs. Assuming the nonlinearities used in the model conform to a certain class of functions (Paninski, 2004), the M-step of EM is concave in the parameter space with a unique solution easily found via gradient ascent. We show the results of training from a number of simulated spike-train and stimulus pairs. The linear filters recovered by our algorithm nicely match the filters used to generate the data.

References


Application of a Temporal Model of Behavior to Activity of Delay Neurons in the Medial Prefrontal Cortex and Motor Cortex in a Reaction-Time Task

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A mathematical model of timing provides good fits to many standard behavioral timing tasks [1]. The question was whether or not this model would also fit the activity of delay-modulated neurons in the medial prefrontal cortex and motor cortex [3].

Rats were trained to hold down a lever for 1000 ms at which time an auditory trigger stimulus occurred (delay period). The release of the lever within 600 ms of the trigger stimulus produced water reinforcement (Fig. 1). Approximately 1/3 of the neurons showed a delayed response pattern: on most trials the spike rate abruptly increased after a delay period. With variability in the time of transition, the mean spike rate increased gradually through the interval, as shown in the bottom panels of Figure 2. Two examples are shown in Figure 2 for one session of two neurons.

A mathematical model that was previously used for timing behavior [1, 2] was used to fit the neural spike rate. It consisted of a pattern memory and a strength memory, which, together, were used to generate behavioral responses and spike activity. A closed form solution of this model [2] was used to obtain the parameter estimates.

The conclusion is that the same mathematical models used for the analysis of behavior, such as lever pressing and head entry into a food cup, can be applied to the analysis of spike activity of delay neurons in the medial prefrontal cortex and the motor cortex of rats. This may facilitate the analysis of the relationship between the neuronal and behavior activity.

(This work was supported by funds from The John B. Pierce Laboratory and the Kavli Institute for Neuroscience at Yale to M.L. and from the Army Research Office to N.S.N., and by the National Institute of Mental Health Grant MH44234 to Brown University.)

References
Pairwise Correlations Determine the Activities of a Neuronal Network in vivo

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In studying the activities of neuronal networks, much attention has been focused on pairwise correlations between neurons. This popular analysis might overlook higher-order correlations within the neuronal population and, consequently, prevent one from understanding the network dynamics fully. By using a maximum entropy model, it has been shown recently that pairwise correlations explain most of the temporal structure of population activities in isolated retina and in cultured neuronal networks, suggesting that 2\textsuperscript{nd} order correlations alone are sufficient to characterize the behavior of these networks \cite{1}. Here we investigated whether this finding can be generalized to more complex cortical networks in vivo. We recorded the visual responses of a neuron population in area 17 of anesthetized cats. We found, similarly to the study in vitro, that the structure of network activity could be predicted successfully by considering only the 2\textsuperscript{nd} order correlations. In addition, we found that the correlated structure of cortical activity has much more capacity for representing various spatial patterns than what has been reported for retina.

Acknowledgments

The authors are thankful to Martha Nari Havenith, Julia Biederlack, Sergio Neuenschwander, and Nan-Hui Chen for their help with data acquisition and processing.

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The importance of neural diversity in complex cognitive tasks

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Our decisions are usually based on a variety of factors, not only sensory inputs and response options, but also behavioral rule in play, previous choices and their consequences. All these factors determine the context which plays a key role in our decision process. Here we propose a model for the internal representation of contexts as attractor states of a neural circuit. Every contextual attractor corresponds to a specific inner mental state, which is self-sustained and reflects a specific disposition to behavior (e.g. how to interpret a stimulus in a specific context and to react to it in order to get reward). Every externally or internally generated event induces a transition from one inner mental state to another. In principle such a dynamical system can reproduce arbitrarily complex behaviors, provided that there are enough inner mental states. Notice that in the most general case the transition to a particular context state will depend on both the previous state (i.e. the attractor which is currently activated) and on the triggering event. We show that unfortunately the fraction of transitions that can actually be implemented in a dynamical system decreases rapidly with the total number of desired transitions (see Figure). Such a limitation does not depend on the representation of the attractors or the external events. The solution that we propose is to harness the huge diversity observed in the neural responses recorded in vivo, which most likely reflects the heterogeneity of the neural cells and their connections. If we start from the neurons which have a particular selectivity (e.g. to a stimulus, or to an intended motor response), other neurons with random connections with them would exhibit mixed selectivity. We prove that if there are enough of these mixed selectivity neurons, then any scheme of attractors and transitions can be implemented in a dynamical system. The recipe that we propose to build such a system is valid for any arbitrary neural representation of the inner mental states (attractors) and the events which trigger the transitions. We then illustrate the theory by building an attractor neural network of Hopfield like neurons which reproduces the animal behavior and several features of the neural activity recorded in prefrontal cortex in an experiment in which monkeys make decisions about motor response according to one of the two possible rules, and the rule currently in effect switch without warning [1].


![Figure 1: How the performance depends on heterogeneity: the performance is measured as the fraction of neural output units which satisfy the conditions for both the attractors and the transitions (both chosen randomly). Different curves correspond to different numbers of mixed selectivity neurons, MSNs, which measures the degree of heterogeneity. The number of MSNs is expressed a fraction (0, 0.1, 0.25, 0.5, 1) multiplied by the total number of units $N = 256$. For no heterogeneity (black curve), the performance drops quickly. Even a small number of MSNs can dramatically improve the performance. The number of implementable transitions grows linearly with the number of MSNs.](image-url)
The Role of the Primate Mediofrontal Cortex in Evaluation and Integration of Gains and Losses

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Outcomes of decisions are evaluated as positive or negative, even when reward can be obtained only through a series of state transitions. Nevertheless, the neural mechanisms responsible for evaluating such state transitions are largely unknown. In this study, we recorded the activity of neurons in the dorsal anterior cingulate cortex (ACCd) and the overlying dorsomedial prefrontal cortex (DMFC) of rhesus monkeys performing an oculomotor binary decision-making task involving such multiple state transitions.

Throughout the experiment, the center of a computer screen displayed a variable number of red disks that indicated a particular state. The number of disks increased (forward state transition), decreased (backward state transition) or remained unchanged (no transition) according to the payoff matrix of a biased matching pennies game. The animal was rewarded with 6 drops of juice, when it reached the final state of 6 disks. The animal began each trial by fixating a square at the center of the screen, and two peripheral targets were presented along the horizontal meridian. When the central square was extinguished after a 0.5 s-delay period, the animal was required to shift its gaze towards one of the two targets. After a 0.5-s hold period, the outcome of the animal's choice was revealed by the color of a feedback ring presented around the chosen target. Choosing one of the targets (safe target) led to a forward or no transition, whereas the other target (risky target) led to a forward or backward transition. The forward transition occurred only when the animal selected the same target as the computer, which was programmed to simulate an opponent in the biased matching pennies game. The optimal strategy for the animal was to choose the safe target with a 2/3 probability. The safe and risky targets changed their positions unpredictably after a minimum of 40 trials.

Behavioral data from the two monkeys showed that the probability of choosing a particular target was systematically influenced by the direction of state transitions resulting from their previous choices. Neural activity during delay and feedback periods were analyzed using a multiple linear regression model, in which the spike count during the 0.5-s delay and feedback period was modeled as the function of the animal’s choices and their outcome in the current and multiple previous trials. In many neurons, the activity during the feedback period was modulated by forward state transition (80% and 76% in DMFC and ACCd, respectively), backward state transition (58% and 41% in the DMFC and ACCd), or both (42% and 35% in DMFC and ACCd), suggesting that these areas might be involved in evaluating gains and losses. Furthermore, activity of some neurons in DMFC (26%) and ACCd (20%) encoded forward and backward transitions by changing their activity in opposite directions, suggesting that they might encode outcome utilities. Activity during delay and feedback periods was also modulated by the animal’s choices and outcomes in the multiple previous trials. For example, 34%, 44% of the neurons in the DMFC and the ACCd modulated their activity for the previous gain, respectively, and 56% and 36% for the previous loss. These results suggest that the primate mediofrontal cortex might play a key role in evaluating the state transitions resulting from the animal’s actions and integrating this information across multiple trials for optimal decision-making strategy.

Acknowledgements
This study was supported by the NIMH.
Bayesian Inference With Stochastic Synapses: A Neural Model of Probabilistic Decision Making

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Recently, there have been growing behavioral evidence that the brain encodes sensory information in terms of conditional probabilities and uses this information to make decisions [1]. An open question is how the required computations are instantiated by neurons in a biophysically plausible way. To elucidate neural mechanisms underlying combination of evidence from different cues, neurophysiologists have trained monkeys to perform a task similar to the weather prediction task [2]. In this task a monkey chooses between two targets, based on evidence about possible reward by observing 4 shapes which appeared on a screen sequentially. These shapes were selected randomly from a set of 10 distinguishable shapes, each of which were allocated a unique weight of evidence (WOE) about possible reward, defined by the log likelihood ratio. It was found that the monkey is able to learn the evidence associated with each shape and its choice behavior is influenced by the sum of evidence from four presented shapes in each trial. Moreover, neurons in the posterior parietal cortex area LIP exhibit activities correlated with accumulated WOE.

Here we show that a biophysically-based model of decision-making, endowed with reward-dependent Hebbian synaptic plasticity [3], can reproduce salient experimental observations in this probabilistic categorization task. In our model, each shape stimulus activates two sets of modifiable synapses, one onto each of two competing neural pools (selective for the two targets) of a decision network. We show that, in a task in which only one shape is presented in each trial, the strength of synapses onto a decision neural pool dynamically changes to estimate the posterior probability that this alternative is the correct response. Since choice probability in our model is a sigmoid function of the difference in synaptic strengths, the model instantiates a probabilistic version of Bayesian decision rule. When the model simulates the weather prediction task in which four shapes are presented in each trial, the log of choice probability is found to be the sum of evidence from all presented shapes, as observed in the monkey experiment. This is because, in our model, the log of choice probability ratio for a given pattern (i.e. combination of four shapes) is a linear function of the sum of the difference in synaptic strengths for all shapes presented in that pattern. Moreover, the firing rate of model neurons in two target-selective pools varies with the strength of inputs through plastic synapses, thereby reflects the summated WOE as observed in LIP neurons. These results show that our neural circuit model naturally implements Bayesian inference for two alternative choice task. Testable predictions will be discussed. This work was supported by NIH grant MH073246.

References


Human decision making in a probabilistic visual task: Testing a model based on expected utility theory.

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Purpose: Researchers in decision making under risk have repeatedly found that Expected Utility Theory (EUT) cannot describe the choices humans actually make [1]. The pattern of failures in their choices suggests that subjects’ use of the explicit probability information they are given is markedly distorted [2,3]. In contrast, human performance in rapid motor decisions under risk, where uncertainty is implicit in subjects’ motor error, comes close to maximizing expected gain, consistent with EUT [4,5]. Here we studied human decision making in a visual aiming task that is stochastic (subjects can only partially control the outcome) but where probability information is implicit, based on a visual estimate of width. We apply a criterion due to Allais [2] to test whether subjects’ choices are consistent with EUT. Task: Subjects chose between two possible outcomes by shooting a noisy bullet at one of two possible target zones. The trajectory of the bullet was simulated by a random walk with fixed Gaussian noise. The width of the zone and the location of the shooter determined the probability of hitting the zone. Subjects were presented with pairs of widely-spaced target zones and could choose to shoot at one or the other but not both. The widths of the zones were adjusted so that the subject could win points $O_i$ with probability $p_i$, $i = 1,2$ by choosing to aim at zone $i$. Subjects competed for the highest score. Predictions: According to EUT, subjects should prefer the zone with the higher expected utility, 

$$EU_i = p_i U(O_i), \quad i = 1,2$$

(1)

where $U(O_i)$ is a function mapping outcomes $O_i$ to subjective utility and their estimates of probability were based on a visual estimate of the width of each target zone. When $EU_1 = EU_2$ subjects will be indifferent between the two options. That is, they are indifferent precisely when

$$\frac{p_1}{p_2} = \frac{U(O_2)}{U(O_1)}$$

(2)

In four conditions, we varied the probability $p_2$ of incurring outcome $O_2$ between 0.8, 0.6, 0.4 and 0.2 by varying the width of one of the target areas. Only two outcome values were used ($O_1 = 500$ and $O_2 = 100$) and the ratio in Eq. 2 should be constant if EUT is a valid model of choice in this task. Analysis: We used an adaptive staircase procedure to estimate the probability $p_1$ that corresponded to the point of indifference for choosing between the target zones. Results: Five subjects completed the experiment. Subjects’ mean probability ratios $p_1/p_2$ ranged from 0.25 to 0.55 for the range of probabilities tested, but the ratios were typically not constant. They were a convex function of $p$. For these subjects, EUT cannot account for performance in this visual decision task for any choice of utility function $U(O)$. 

This work was supported by DFG grant TR 528 1-3 (JT), Chaire d'excellence (PM), and NIH EY 08266 (LTM).

References
Unimodal or Bimodal Distribution of Synaptic Weights?
– Both can be Stable at the Same Time (with activity depending switching)!

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Most Hebbian learning rules or BCM rules used to describe receptive field development exhibit a spontaneous separation of synaptic weights into two groups, i.e., strong and weak synapses, so that the distribution of synaptic weights is bimodal. This implies that even rather ‘weak’, non-significant correlations lead to changes in synaptic weights, so that the neuron may specialise to ‘noise’ rather than to features of the outside world. Moreover, such a bimodal distribution seems to be difficult to reconcile with experiments in young rats where a unimodal distribution was found \cite{1}.

Other plasticity models, however, that exhibit always \cite{2} or for certain inputs \cite{3} a unimodal distribution of synaptic weights have the problem that they do not lead to long-term stability of the weights. In particular, if, after learning, the input pattern changes back to ‘weak’ correlations, the neuron ‘forgets’ its synapse pattern as rapidly as it was learned. Thus, those plasticity models are not useful for long-term memory.

We have developed a model of synaptic plasticity that shares features with spike-timing dependent plasticity; is sensitive to correlations in the input; and is useful for synaptic memory. Interestingly, input selectivity (sharply tuned receptive fields) based on a bimodal synapse distribution develops only if stimuli with strong features are presented. For input with ‘weak’ correlations, sharply tuned neurons with a bimodal synapse distribution can co-exist with unselective ones with a unimodal distribution.

We hypothesize that, during development, neurons initially start off with a unimodal distribution that remains stable as long as correlations in the input are weak, consistent with the unimodal distribution found in young rats \cite{1}. For strongly correlated input, the neuron becomes selective and a bimodal distribution develops. This bimodal distribution remains stable (and the neuron remains selective) even if the correlations in the input are again reduced to the previous ‘weak’ level. Thus the model exhibits long-term memory. Only if new and even stronger correlations appeared in the input the neuron would readapt.

Hence our model reconciles theoretical demands of sensitivity to new inputs with long-term stability and achieves this without an ‘ad hoc’ change of the global learning rate. Our model is derived from only three basic principles: (A) Synapses adapt their weights so that neurons can effectively transmit information; (B) homeostatic processes stabilize the mean firing rate of the postsynaptic neuron; and (C) weak synapses adapt more slowly than strong ones, while maintenance of strong synapses is costly.

Acknowledgments
Supported by the European Community (FACETS) and JSPS Grant-in-Aid No. 1806772

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28
Memory Lifetime Depends on Synaptic Meta-Plasticity and the Size of Cell Assemblies

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Changes of synaptic states are thought to underly learning and memory. The storage of new memories and the associated synaptic changes necessarily impair previously acquired memory traces, and the smaller this impairment the longer is a network’s memory lifetime. Two strategies have been suggested to keep old memories from being overwritten too rapidly while preserving receptiveness to new contents: either introducing synaptic meta levels to store the history of synaptic state changes [1] or reducing the number of cells that fire together in an assembly to decrease the interference between memory traces[2]. To compute memory lifetimes, synapse models cannot be considered independently of the size of synchronously active cell assemblies (sparseness) because the postsynaptic depolarization depends on both the presynaptic activity and the synaptic states.

We derive memory lifetimes in a randomly-coupled recurrent network [3] with synaptic meta-plasticity. Via simultaneous optimization of assembly size and synaptic complexity, we find the maximum memory lifetime to coincide with a high level of sparseness and a simple two-state synaptic model. If the sparse-coding limit is unfeasible, synapses with a high number of meta states can be beneficial. We discuss two alternative synaptic cascade models with binary weights and find that a serial topology of synaptic state transitions gives rise to larger memory capacities as compared to a model with cross transitions between states. The optimal number of synaptic states for a serial model topology grows much faster as a function of the network size and connectivity than for the cross transition model. For both cascade models of synaptically stored memories, however, sparseness of representation outweighs the virtues of meta-plasticity by orders of magnitudes.

As an example, we derived memory lifetimes for parameters corresponding to the hippocampal CA3 region of rats, where assemblies have been estimated to contain thousands of neurons. In this system, a sparser code could be prohibited by requiring dynamical stability of the replay of sequential activity patterns [4]. The evaluation of both meta-plasticity models in a CA3-like parameter regime yields a maximal lifetime of about 7,000 subsequent memories at an optimal cascade order $n = 2$ for the model with cross transition, and a lifetime of 13,000 memories at $n = 3$ for the serial topology. We thus conclude that low cascade orders are likely to be helpful to increase memory longevity in the hippocampus.

Acknowledgments
We thank S. Fusi, T. Gollisch, R. Schaette, and W. Senn for valuable suggestions. This work was supported by DFG grants (Emmy Noether program: Ke 788/1-3, SFB 618) and the BMBF grant 01GQ0410.

References
Reverse Replay in the Hippocampus as Optimal Smoothing

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The hippocampus is thought to play an important role in memory and learning. In particular, it has been implicated in the storage and recall of sequential memories such as those represented by place cells during navigation. It has been known for some time that such memories can be reactivated during sleep. A recent study reported that sequential reactivation of stored memories can also occur during awake periods immediately following spatial experience, but the reactivation occurs in a temporally reversed order [1]. It was suggested that such reverse replay of experience may allow reward-based learning of behaviors in a manner consistent with reinforcement learning theories.

We propose an alternative hypothesis for reverse replay in the hippocampus based on the idea of optimal smoothing. Optimal smoothing is an important concept in the fields of probabilistic inference and machine learning. It is an essential ingredient of most statistical algorithms for learning the parameters of a dynamic system. In optimal smoothing, on-line estimates of a random variable that were computed based on input data from time steps 1 to \( t \) are later corrected using information from time steps \( t+1 \) to \( T \), where \( T \) represents the end of the trial. The use of this additional information typically results in a much more accurate estimate for each time step \( t \) than the original on-line estimate. The procedure of optimal smoothing involves a forward pass through the data (on-line estimation or “filtering”) followed by a backward pass which computes the “smoothed” estimates in temporally reversed order (time steps \( T, T-1, \ldots, 1 \)). We propose that the reverse replay observed in the CA1 region of the hippocampus are neural correlates of this smoothing process. We suggest that the computation of such smoothed estimates allows accurate unsupervised learning of temporally sequenced information in the hippocampus and the neocortex. We explore the implications of this smoothing hypothesis via simulation studies, and investigate how optimal smoothing could be implemented by hippocampal circuitry.

The hypothesis we have suggested differs from the reinforcement learning interpretation of reverse replay in several ways: (a) it does not require the simultaneous activation and subsequent decay of a reinforcement signal such as dopamine, which is a suggested mechanism for reinforcement learning through reverse replay, (b) it can explain the occurrence of reverse replay in cases where the animal receives no reward, (c) it provides an explanation for why multiple reverse replays typically occur within a given rest period in terms of successive iterations of a statistical learning algorithm (the EM algorithm), and (d) it provides a new framework for understanding unsupervised learning of temporal input sequences in hippocampal and cortical circuitry.

Acknowledgments
This work was supported by NSF and the Packard Foundation.

References
A Computational Model of Rapid Task-Related Plasticity of Auditory Cortical Neurons

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It has been recently shown that receptive field properties of neurons in A1 can be rapidly and adaptively reshaped during task performance in accord with specific task demands and salient sensory cues [1]. This change may be characterized as modulation of auditory cortical receptive fields that is behaviorally driven by attentive focus on salient acoustic features necessary for task performance. Such modulatory changes selectively enhance overall cortical responsiveness to the target sound and thus increase the likelihood of detecting the attended foreground target against the acoustic background. Distinctive changes in cortical tuning characterize different auditory tasks, reflected in the spectrotemporal receptive field (STRF) of neurons [1,2]. The auditory tasks include detection of a tone in a noise background [1], discrimination of two tones with different frequencies [2] and discrimination of a temporal change in the repetition rate of a click train [3,4]. Our data suggests that there is an attention-triggered neural plasticity algorithm in A1 that can swiftly change STRF shape by transforming receptive fields to enhance stimulus discrimination in a task-dependent fashion [4].

In this study, we used a mathematical model to calculate the changes in the STRFs needed for the optimal discrimination between any two classes of sounds. The neurons are modeled as filters that change their spectro-temporal tuning properties in order to extract the discriminatory features of two sound groups. The changes are optimal in the sense they maximize the quadratic distance between the responses of the neurons to two classes of sounds over the time course of the stimuli. In addition, we describe how this optimization can be achieved under any set of arbitrary constraints on the spectro-temporal properties of neurons reflecting the biological limitations and finite resources that set boundary constraints on the extent of neural plasticity, (e.g. limited synaptic input to a neuron or finite temporal integration). We tested the predictive power of the model in several spectral and temporal tasks. In the conditions tested, the predictions of the model matched the existing experimental data from behavioral physiology, consistent with the suggestion that A1 neurons change their tuning in an optimal way. In addition, we use the model to predict optimal receptive field changes for other more complex classes of sound that can further motivate experimental research to test and extend the model.

Acknowledgments: This work was supported by NIDCD.

References
Learning Reward Timing using Reinforced Consolidation of Synaptic Plasticity.

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Learning interval timing is a crucial component in many behaviors. However, the physiological mechanisms underlying the representation and learning of interval timing have not yet been identified. Recent experimental results indicate that cells within the primary visual cortex can learn to predict the time of rewards associated with visual cues [1]. In this work, different visual cues were paired with rewards at specific temporal offsets. Before training neurons in visual cortex were active only during the duration of the visual cue. However, after sufficient training neurons developed persistent activity beyond the time of the visual cue. The duration of this persistent activity was correlated with the reward time and could be used to predict it.

How can a neural network learn to adapt its temporal dynamics in order to predict an expected reward time? Recurrent connections in a neural network can be tuned in order set different temporal dynamics for neurons within the network [2]. However, it is not clear how a network is able to learn the appropriate recurrent weights. A plasticity model that is able to accomplish this must be sensitive to reward timing, an event that at least initially occurs seconds after the network activity returns to its basal level. Therefore, in order to learn the appropriate dynamics, this network needs to solve a temporal credit assignment problem. In our model plasticity is an ongoing process changing the recurrent synaptic weights as a function of coincident pre- and post-synaptic activity. However, in the absence of reward this plasticity rapidly decays. An external reward allows consolidation of plasticity events that precede a reward, thus reinforcing those specific plasticity events which predict the reward [3]. Additionally we assume that the reward signal is inhibited by the network activity [4]. As a result the network dynamics are altered, acquiring dynamics that are correlated with reward timing. Both abstract and integrate and fire implementations of this network produce dynamics that are similar to experimental results [1].

Acknowledgments
We thank Marshal Shuler and Mark Bear. This work was supported by an NSF grant: CRCNS - 0515285.

References
Learning-related changes in coordinated fast oscillations (35-45 Hz) in the basolateral amygdala (BLA) and rhinal cortices during the acquisition of a trace-conditioning task

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The BLA is thought to facilitate memory formation by the medial temporal lobe in emotionally-arousing conditions. To study how the BLA mediates this effect, we simultaneously recorded neuronal activity in the BLA, perirhinal and entorhinal cortices. Given earlier findings suggesting that neuronal oscillations coordinate the activity of cerebral networks, we first tested whether there are correlated fluctuations in the power of BLA and rhinal field activity at any frequency. Field potentials were simultaneously recorded during the waking state and segmented in one second windows. FFTs were computed for each window, then pairs of these spectrograms were correlated to reveal how well each pair of channels was correlated over time at each frequency. With the exception of low frequencies (<4 Hz), correlated power fluctuations occurred only in the 35-45 Hz band. These fast oscillations were not volume conducted since, in each structure, firing probability fluctuated rhythmically with the fast oscillations recorded at the same site. Moreover, in all cats (n=3), the power of these fast oscillations was highest in the BLA.

To test whether fast oscillations coordinate BLA and rhinal activity during learning, cats were trained on a trace-conditioning task where a visual CS predicted a food reward 3s later. The predictive value of the CS was learned gradually over 10 days. We computed the power at 35-45 Hz in all recorded channels normalized by the total power. As learning progressed, there was an increase in power at 35-45 Hz within the BLA and rhinal cortices. This increase was specific to the delay period between the CS presentation and reward delivery. To determine whether learning produced changes in the correlation of 40Hz oscillations between the BLA and rhinal cortices, we computed the power spectra for all channels and correlated pairs of these spectrograms, as before. This analysis revealed an increase in correlated 35-45Hz power fluctuations during the delay period on late training days. These results were corroborated by computing perievent histograms of BLA and rhinal unit discharges using the positive peaks of fast field oscillations recorded in the BLA as references. BLA and rhinal neurons became rhythmically entrained with BLA oscillations during the delay phase. Thus, our data suggests that neuronal interactions are coordinated by fast oscillations in the BLA-rhinal network. By telescoping the periods of effective neuronal interactions in short recurring time windows, these fast oscillations may facilitate synaptic plasticity.

Acknowledgments
This work was supported by NIH grants RO1MH073610 and F32 MH076640-01A1.
Internally generated assembly sequences in the hippocampus and episodic memory

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Conclusions about the function of a brain structure often depend on the observational methods used. Single unit studies in rodents indicate that the hippocampus and associated structures are involved in spatial navigation (O’Keefe and Dostrovsky, 1971; Hafting et al., 2005, McNaughton et al., 1996), whereas studies in humans have provided firm evidence that hippocampal networks are critical in coding and retrieval of episodic memories (Scoville and Milner, 1957). It has been hypothesized that networks that serve spatial navigation may be ideal to represent episodes (Buzsaki, 2005).

A necessary condition for supporting this idea would be the demonstration that hippocampal networks can advance their intrinsic activity in the absence of external control cues, mimicking internally controlled free recall in humans. I provide evidence that cell assembly sequences in the hippocampus evolve perpetually even where rats are ‘frozen’ in space (i.e., running in a wheel) and suggest the hypothesis that hippocampal cell assemblies can be generated by the internal dynamics of the network. Specifically, I show that (a) the different environmental contexts give rise to unique evolving population sequences while the rat runs in the same wheel, (b) we can identify the conditions that initiate those sequences and (c) we can predict the future choice of the rat in the delayed spatial alternation task from the perpetually shifting sequence episodes during wheel running (i.e. the delay time). These physiological findings provide a link to understanding the mechanisms of episodic free recall and suggest an alternative coding mechanism of working memory, distinct from persistent activity of a circumscribed cell assembly.

Acknowledgments
This work was supported by Patterson Trust Fellowship.

References
Reverse Replay of Hippocampal Place Cells Reflects Most Recent Sequential Experience

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Sharp Wave/Ripples (SWR) in the hippocampus are accompanied by activity bursts of large percentages of CA1 neurons. These events are a salient feature of hippocampal activity, yet their function and supporting mechanism are largely unknown. Recently, Foster and Wilson[1] have shown that sequences of place-cells, corresponding to places traversed by rats during a run, are replayed in reverse during SWRs. Here, we record from CA1 and CA3 regions in rats running on a linear track. We confirm that reverse replay (RR) is indeed a robust phenomenon, as predicted[2], and demonstrate that the replayed sequence binds neurons that co-fired during preceding theta cycles to neurons that did not co-fire during any theta cycles (i.e. non-overlapping fields). This represents a type of pattern completion. We compare replay events on opposite ends the track, where a different sequence of place-cells are encountered on outgoing versus incoming trials. We find that, consistent with an experiential role for RR, only the sequence experienced in the immediately preceding trial is reverse replayed, rather than simply the replay of a fixed or potentiated pattern. Csicsvari et. al.[3] have more recently argued that residual place-related firing during SWRs is a potential mechanism, and furthermore, necessary for RR. Nevertheless, we demonstrate that cells participate in RR well beyond their 95% peak-rate place boundaries. Thus, RR may reflect transient (short-term) potentiation of selective synapses or related mechanisms that enhance excitability during SWRs.

References
A Feedforward Model of a Neural Integrator

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In neural integrator networks, transient inputs are accumulated into output signals that reflect the mathematical integral, over time, of their inputs. This computation has been identified as an important component in a wide variety of brain functions ranging from accumulation of sensory evidence for decision making\textsuperscript{1} to the motor control of eye movements\textsuperscript{2}. All current network models of neural integration assume that the conversion of transient inputs to sustained responses is accomplished by feedback among recurrently connected neuronal elements. Here we show that neural integration can occur even in feedforward networks and describe the properties of this novel class of integrators.

We consider a feedforward network consisting of multiple stages that each have a time constant $\tau$ with which they linearly filter their inputs. We show that the effective dynamics of this network can be reduced to that of a simple network consisting of a linear chain of neurons with input entering one end and getting successively filtered by each successive stage of the network. As a result of this filtering, later stages of the network have prolonged responses that peak at successively later times. Thus, the network effectively forms a delay-line set of basis functions that are localized in time and that can be flexibly summed to generate a variety of temporal responses. We show analytically that with appropriate choices of synaptic weights, the network can perform a nearly perfect integral of its inputs over a duration of time of order $N\tau$, where $N$ is the number of stages in the network. We further show that although the performance of the network is best understood in terms of basis functions corresponding to a delay-line, the responses of the actual neurons in the network will generally be linear combinations of these basis functions that may not be easily recognized as originating from dynamics governed by a delay line.

We compare the dynamics and robustness of the feedforward integrator network to that of recurrent integrating networks based on a single tuned integrating mode (line attractors). The robustness of the network to uniform decreases in all synaptic weights can be shown analytically to be nearly identical to that of linear recurrent networks. However, for increases in weights that cause uncontrolled exponential growth in the recurrent networks, the growth is contained in the feedforward network because the network activity must dissipate when the signals have finished propagating through the network.

In conclusion, this work suggests a novel mechanism for neural integration. Although we focus on its role as an integrator, the network bears strong similarities to previous networks proposed for temporal sequence recognition and production. This suggests that common underlying principles may be relevant to a host of temporal processing computations.

Acknowledgments
We thank C. Willis and V. Popic for computer simulations in the early stages of this project. This work was supported by NIH grant MH069726-01A2.

References
Correlations between Pairs of Neurons and Behavior in the Frontal Cortex During Smooth Pursuit Eye Movements

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In response to repeated presentations of an identically moving target, both neural activity and the eyes' smooth movement display considerable variation. We have previously demonstrated that the firing rate of individual cortical neurons describes a sizeable fraction of this variation, suggesting a direct role for the neurons in driving the trial-to-trial fluctuations of the eye movements. Intuitively, any pair of neurons that explains a large portion of the behavioral variance ought to have correlated activity. We have formalized this notion in an analytical model, and tested the model predictions against neural data. Our data set consisted of 104 pairs of neurons in the frontal eye fields of two monkeys engaged in a traditional step-ramp smooth pursuit task. Our model is a simple linear framework describing the relationship between the behavioral variance explained by a set of neurons, the correlation between the neurons, and the number of neurons in the active population. Neural activity is treated as a set of dependent random variables, and the behavior as their sum. Quantitative analysis suggests, in contrast to the simple intuition, that there is no relationship between the behavioral variance explained by the pair of neurons and the co-variation of neural activity.

Acknowledgments
We thank A. Colleague for helpful discussions. This work was supported by NIH grant DC999999.

References
A mathematical constant in the design of the visual cortex

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More than hundreds of tera byte of information would be necessary to describe the synaptic organization of the mammalian cerebral cortex. It is thus hardly conceivable that the roughly 20 thousand genes of a typical mammalian genome might be sufficient to directly specify the cerebral cortical structure. It has therefore been hypothesized that dynamical self-organization might play an important role in shaping neuronal circuits in the cerebral cortex. The notion of self-organization is meant to stress that in such systems although the process of structure formation is externally driven by e.g. sensory input, the structures that emerge are determined through interactions within the system itself. Mostly, from the study of non-living systems, it is well understood that self-organization often exhibits universality, meaning that the structures formed are largely insensitive to the precise details of the underlying intrinsic interactions, and therefore common to many systems which potentially exhibit major differences in their detailed nature.

Here we demonstrate in three species separated in evolution by more than 50 million years that the layout of orientation columns in the visual cortex adheres to a set of universal quantitative laws. Most suggestive of a mathematical structure underlying this universality, the average number of pinwheel centers per orientation hyper-column in all species is virtually identical and statistically indistinguishable from the mathematical constant $\pi$. Here, a hyper-column is the natural area unit $\Lambda^2$, where $\Lambda$ is the periodicity of the map. Universal behavior is also found for quantities characterizing the map design from scale of individual hyper-columns to the layout of the entire primary visual cortex. These results are obtained with a novel analysis method devised to selectively eliminate the many spurious pinwheels typically induced by high frequency noise and to account for spatial inhomogeneities often present in the structure of orientation maps.

To interpret these findings, we present a model for self-organization of visual cortical architecture that accounts quantitatively for all universal layout properties by a process of dynamical pattern selection. The model is derived from symmetry arguments and includes only key features of the visual cortex including non-local interactions mediated e.g. by the influence of long-range horizontal connections. The analysis of the model indicates that the development of orientation maps with the observed universal properties depends critically on assuming sufficient strength and range of non-local interactions (larger than at least $1\Lambda$). In fact, in the limit of large interaction range, the ensemble averaged pinwheel density converges to $\pi$ as shown analytically by perturbation theory.

Corroborating the idea of robust development through self-organization, we observe that the orientation map adheres to the universal behavior even if its organization exhibits marked overall inhomogeneities and when animals are raised under severe visual deprivation. Thus, because of the phenomenon of universality, self-organization appears suited to enable nervous systems to form similar neural architectures irrespective of differences in genetic background and sensory experience.
Prefrontal Control of Low Frequency Oscillations in Motor Cortex

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It has been proposed that low-frequency oscillations in motor cortex are signatures of preparation in anticipation of responding [1]. According to this idea, low-frequency oscillations in motor cortex should be controlled by regions such as prefrontal cortex that exert top-down control over response initiation. We tested this idea by recording local field potentials from both rodent prefrontal and motor cortex while animals performed a lever-release version of a delayed response task [2]. We found strong low-frequency power (1-20 Hz, peak 8-11 Hz) in the prefrontal and motor cortices. This band was selectively modulated while rats pressed, held, and released the lever. There was also low-frequency coherence between the prefrontal and motor cortices, which was maximal at 8-11 Hz during the delay period and during the collection of rewards. To establish that such low-frequency oscillations are controlled by prefrontal cortex, we studied field potentials from motor cortex in three animals in which prefrontal cortex was reversibly inactivated. Power in the 8-11 Hz range was specifically increased during the delay period when prefrontal cortex was inactivated.

These results provide evidence that low-frequency oscillations in motor cortex are controlled by prefrontal cortex, and support the idea that theta oscillations in motor cortex are related to preparatory activity. Based on previous studies from our lab [2], we suggest that this functional interaction between the prefrontal and motor cortices exerts top-down control over action that inhibits responding until the right time or the right stimulus has occurred.

Acknowledgments
We thank the Kavli Institute for Neuroscience at Yale and the John B. Pierce Laboratory for funding to ML and the Army Research Office for funding to NSN

References
Sparse Encoding Promotes Synchronous Firings
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Synfire chain is a simple neural network model which can generate stable synchronous firings called a pulse packet. The existence of synfire chain has been implied by some experiments\textsuperscript{[1,2]} and synchronous firing is thought to play key role in information processing in the brain\textsuperscript{[3]}. Therefore synfire chain is widely studied by many researchers. However how synfire chains coexist in one network remains to be elucidated. We have previously reported the activity of a layered network in which we embed memory patterns by the Hebbian Learning\textsuperscript{[4]}. In our previous report, a half of neurons belongs to each memory pattern, i.e., the firing rate of memory pattern $F = 0.5$, and then a memory pattern is activated synchronously. Therefore at first sight memory patterns seemed to be synfire chains. However under some input condition, synchrony of a memory pattern broken to groups (sublattices), and then the sublattices fire independently and synchronously with a time lag. This result suggests that in the $F = 0.5$ network synfire chain is each sublattice rather than memory pattern.

In this study, we show that when firing rate of memory pattern $F$ is smaller than 0.5, the stability of memory pattern as synfire chain seems to be promoted compared to the $F = 0.5$ network. Here we pay attention to two memory patterns embedded in the network and two groups of neurons. One group belongs to both of the two memory patterns. The other group belongs to only one of the two memory patterns and become silent when the other memory pattern is activated. We call the former group as $(++)$ sublattice, and the latter as $(+-)$ sublattice. Now we activate $(++)$ sublattice, and after 1 millisecond we activate $(+-)$ sublattice at the first layer. When $F = 0.5$, the firing of the two groups independently propagates (Fig. 1(a)). When $F = 0.4$, on the other hand, the time lag between the two group firings approaches to zero through layers and at last the firing of the two groups becomes synchronous (Fig. 1(b)). This result means that in the $F = 0.4$ network synchronous firings between different sublattices become more stable than in the $F = 0.5$ network. This result also implies that the sparse encoding makes memory patterns more robust synfire chains. At the Cosyne meeting I will show the details of this robustness with other data and the mechanism behind it.

**Acknowledgments**
This work was supported in part by grants from the JSPS (Nos. 14084212 and 16500093).

**References**
Timing sound: A study to identify brain areas underlying timing in the range of hundreds of milliseconds

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The neural mechanisms underlying the ability to time stimulus durations in the range of hundreds of milliseconds to seconds are not known. Even the identity of the brain areas responsible has not been conclusively determined. Adapting the methods of Mainen and colleagues and Zador and colleagues, we have trained separate groups of rats in two different two-alternative forced-choice tasks. In the first task, rats must discriminate between pure tone sounds based on the duration of the sound; on each trial rats must classify a pure tone as either “long” or “short”, as compared to a fixed standard. In the second task, rats must discriminate between pure tone sounds based on the frequency of the sound. Both these tasks present similar stimuli and require the same behavior to indicate discrimination of stimuli. Thus we have two audition-based decision-making tasks, only one of which requires the ability to time sound.

We are using excitotoxic chemicals (ibotenic acid) to lesion different auditory structures. If found, a lesion that affects duration discrimination, but not frequency discrimination, would identify the lesioned brain region as one required for timing-based behavior, but not required for aspects of the timing task shared with the frequency discrimination task (e.g., motivation, decision-making, motor control, etc.). Such a region would be considered critical for perceptual timing, at least in the auditory modality. If such a region is indeed found, we plan to record and analyze neural activity from it during performance of the duration discrimination task. We are targeting the auditory cortex (areas A1, AuV, AuD), the different divisions of the medial geniculate body, and the auditory striatum.

Acknowledgments
We thank the Mainen and Zador labs at Cold Spring Harbor Laboratory for their constant support. The ibotenic acid protocol was developed with guidance from Len Jarrard (Washington and Lee U), Kara Agster and Rebecca Burwell (Brown U), Rodrigue Galani and JC Cassell (U Strasbourg) and Jason Emsley (Harvard U). Shraddha Pai is a Beckman fellow of the Watson School of Biological Sciences at Cold Spring Harbor Laboratory.
An Efficient Computation of Continuous-time Correlogram of Spike Trains

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Precise time delay in transmission of a spike in the neural system is considered to be one of the key features to allow efficient computation [1]. Cross correlogram is a powerful tool that is often used to quantify the delay of spike propagation and connection strength given a pair of spike trains. This includes the auto correlogram as a special case for analysis of periodicity in a spike train. An efficient algorithm for estimating these correlograms [2] involves histogram construction with time interval bins. This quantization of time introduces binning error and leads to coarse time resolution. Furthermore, the cross correlogram does not take advantage of the higher temporal resolution of the spike times provided by current recording methods. However, continuous-time analysis methods would naturally benefit from such improvements. We propose a novel method that provides continuous time resolution on correlogram, yet achieving efficient computation.

The continuous time resolution is achieved by computing at finite points where the continuous cross correlogram has local maxima. The algorithm takes advantage of the fact that the cross-correlation at time lag $\Delta t$ of two smoothed spike trains (denoted as $i$ and $j$) can be estimated from samples expressed with simple double summation as

$$\frac{1}{N_i N_j} \int_0^T \sum_{m=1}^{N_i} h(t - t^i_m - \Delta t) \sum_{n=1}^{N_j} h(t - t^j_n) dt = \frac{1}{N_i N_j} \sum_{n=1}^{N_j} \sum_{m=1}^{N_i} \kappa(t^i_m - t^j_n + \Delta t).$$

The number of time lags to compute the summation is $N_i N_j$ which results in the straight forward computation time complexity to be $O((N_i N_j)^2)$. However, by using computational tricks for a widely used kernel, $\kappa(t - s) = \exp\left(-\frac{|t - s|}{\tau}\right)$, we can achieve $O(N_i N_j \log(N_i N_j))$. This kernel is a result of using a first order infinite impulse response low pass filter on the spike train, i.e. $h$ is a causal exponential decay function. Furthermore we can reduce the cost by focusing on the time lags of interest which is less than 500 ms in most physiological contexts.

We demonstrate the result to estimate the effective delays in a neuronal network from synthetic data and recordings of dissociated cortical tissue.

Acknowledgments
This work was partially supported by NSF grant 0422718. The work of A. Paiva was supported by FCT under grant SFRH/BD/18217/2004.

References


Computation on the Transient

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Line attractor networks have become standard workhorses of computational accounts of neural population processing for optimal perceptual inference, working memory, decision making and more. Such networks are defined by possessing a one- (line) or multi-dimensional (surface) manifold in the high dimensional space of the activities of all the neurons in the net, to a point on which the state of the network is projected in a non-linear manner by the network's dynamics. The standard view that the network represents information by the location of the point on this manifold at which it sits [1] is only appropriate if the computation to be performed by the network is aligned with the underlying symmetry implied by the manifold. In interesting cases, the computation that must be performed is orthogonal to this symmetry structure, and so an alternative computational view is required. Here, we illustrate the problem using a well-studied visual hyperacuity task, and suggest solutions involving different classes of computations during the network’s transient evolution.

We consider the bisection task, which involves deciding to which end bar, the middle of three parallel visual bars is closer [2]. As with other hyperacuity tasks, performance is impressively invariant to factors such as positional deviations arising from various forms of eye movement, which can at most only have been partially trained. The natural noise-removing line attractor for the population coded representation of this task has exactly the problem that the required computation (determining the sign of the miniscule displacement of the central bar) is orthogonal to the positional symmetry implied by the line. Li & Dayan [3] suggested that learning might create in V1 a different sort of attractor network, in which there are two different attractive lines, one for each possible decision. Unfortunately, this network only performs well over a limited range of retinal positions [3,4]. Here we suggest a completely different computational approach, in which the decision is based on the way that a readily computed statistic of the activity (the population centre of mass) changes over the transient evolution of the activity. This significantly improves performance, nearly up to the level of an ideal observer for the model input, even in the case that the network contains only one single attractive line.

Acknowledgments
This work was supported by Gatsby Charitable Foundation.

References
Estimating Population Receptive Fields in Space and Time

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Right from the first synapse in the retina, visual information gets distributed across several parallel channels with different temporal filtering properties. Yet, commonly used system identification tools for characterizing neural responses, such as the spike-triggered average, only allow one to investigate the individual neural responses independently of each other. Conversely, many population coding models of neurons and correlations between neurons concentrate on the encoding of a single-variate stimulus. We seek to identify the features of the visual stimulus that are encoded in the temporal response of an ensemble of neurons, and the corresponding spike-patterns that indicate the presence of these features.

We present a novel data analysis tool for the identification of such temporal population codes based on canonical correlation analysis (Hotelling, 1936). The “population receptive fields” (PRFs) are defined to be those dimensions of the stimulus-space that are maximally correlated with the temporal response of the entire neural population, irrespective of whether the stimulus features are encoded by the responses of single neurons or by patterns of spikes across neurons or time. These dimensions are identified by canonical correlation analysis, a convex optimization technique which essentially solves an eigenvalue problem and is not prone to local minima.

Each receptive field can be represented by the weighted sum of a small number of functions that are separable in space-time. Therefore, non-separable receptive fields can be estimated more efficiently than with spike-triggered techniques, which makes our method advantageous even for the estimation of single-cell receptive fields.

The method is demonstrated by applying it to data from multi-electrode recordings from rabbit retinal ganglion cells in a whole mount preparation (Zeck et al, 2005). The figure displays the first 6 PRFs of a population of 27 cells from one such experiment. The recovered stimulus-features look qualitatively different to the receptive fields of single retinal ganglion cells. In addition, we show how the model can be extended to capture nonlinear stimulus-response relationships and to test different coding-mechanisms by the use of kernel-canonical correlation analysis. In conclusion, we suggest to characterize responses of ensembles of neurons in terms of PRFs, rather than discussing stimulus-neuron and neuron-neuron dependencies separately.

References
Paired Recording Reveals Temporal Decorrelation of Retinal Inputs in the Thalamus

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It has been proposed that the lateral geniculate nucleus (LGN) of thalamus temporally decorrelates the retinal inputs during natural viewing to achieve efficient coding (Dong and Atick, 1995, Truccolo and Dong 2001). To directly assess this potential role of thalamus, we made paired recordings of LGN neurons and their apparent corresponding retinal inputs (S-potentials), in awake cats free-viewing natural time-varying images. We derived the retina-LGN transfer function from the measured LGN input and LGN output. We found that the function is indeed a temporal difference filter, the LGN output is more decorrelated than the LGN input, and LGN contains much less information about saccade timing than the retina.

The results are consistent with the prediction of the theory of efficient coding.

Acknowledgements
This work is supported in part by LSUHSC Research Board, FAU RIA-25 and NIMH1151-019-42

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Pre-selection and Multiple Testing Contaminates Neural Response Analysis

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Recent advances in single unit neurophysiology allow experimenters to record from a large number of neurons with the intent of analyzing that data offline. In order to understand the responses of large populations of neurons, one needs screening tools to select those neurons which are interesting in terms of a particular experiment. One strategy is to pre-select cells which respond to any of the experimental manipulations and then further test those cells for particular experimental effects. For example, choosing neurons which have a response to one or more images, and then testing for differential responses between images, thus, detecting an effect of the images on the response.

This sequential application of two tests to the same data carries the risk that random variations of the data causing pre-selection may cause the second test to show an exaggerated effect. The interaction between these two tests can be subtle and difficult to ascertain. To determine the extent to which this interaction may be important for typical neurophysiological recordings, we simulated the responses of 32 neurons to a varying number of stimuli, each presented for 10 repetitions. The responses were randomly chosen from a Poisson distribution with varying rate, the same for all neurons and stimuli. The neurons were first pre-selected for a response to any of the stimuli (Wilcox rank-sum, p-values 0.1, 0.05, 0.01, 0.001). All neurons having one or more responses to any stimuli were then subjected to an ANOVA for an effect of stimulus on the response (p-values 0.05, 0.01).

For these simulated conditions, the fraction of neurons with a significant effect of stimulus was compared to the fraction expected by chance (p-value ratio, PVR). This ratio ranged as high as 4.5, and depended on p-value of the pre-selection (lower p-value increases PVR) as well as the number of stimuli (fewer stimuli increases PVR). Across these parameter variations, the fraction of cells excluded by the pre-selection (exclusion fraction, EF) correlated with the PVR. In general, EFs > 10\% materially increase the PVR and give rise to artifactually large number of neurons with an apparent significant effect of stimulus on the response.

These increases in PVR arise because the random variations in the data used to perform the pre-selection are the same as the random variations assessed by the second test for an effect of the stimuli. The increase can be avoided by performing the pre-selection on a set of data which is independent of the second test, either part of a separate selection experiment or a separate subset of the trials within an experiment. The interactions between two tests on the same data can be difficult to ascertain: a preliminary search of neurophysiological research papers in recent years suggests that 25\% of papers apply a pre-selection to reduce the amount of data and may be subject to this increase in p-value ratio.

Acknowledgments

We thank Stephen Helms-Tillery for informative discussions. Supported by the Whitaker Foundation and Arizona State University.
Bayesian Receptive Fields and Neural Couplings with Sparsity Prior and Error Bars

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Here we apply Bayesian system identification methods to infer stimulus-neuron and neuron-neuron dependencies. Rather than reporting only the most likely parameters, the posterior distribution obtained in the Bayesian approach informs us about the range of parameter values that are consistent with the observed data and the assumptions made. In other words, Bayesian receptive fields always come with error bars. In fact, we obtain the full posterior covariance, indicating conditional (in-)dependence between the weights of both, receptive fields and neural couplings. Since the amount of data from neural recordings is limited, such uncertainty information is as important as the usual point estimate of the receptive field itself.

We employ expectation propagation, a recently developed approximation of Bayesian inference, to a multicell response model consisting of a set of coupled units, each of which is a Linear-Nonlinear-Poisson (LNP) cascade neuron model. The instantaneous firing rate of each unit depends on both the spike train history of the units and the stimulus. Parameter fitting in this model has been shown to be a convex optimization problem [1], which can be solved efficiently. By doing inference in this model we can determine excitatory and inhibitory interactions between the neurons and the dependence of the stimulus on the firing rate. In addition to the uncertainty information (error bars) obtained within the Bayesian framework one can impose a sparsity-inducing prior on the parameter values. This forces weights actively to zero, if they are not relevant for explaining the data, leading to a more robust estimate of receptive fields and neural couplings, where only significant parameters are nonzero.

The approximative Bayesian inference technique is applied to both artificially generated data and to recordings from retinal ganglion cells (RGC) responding to white noise (m-sequence) stimulation. We compare the different results obtained with a Laplacian (sparsity) prior and a Gaussian (no sparsity) prior via Bayes factors and test set validation. For completeness, the receptive fields based on classical linear correlation analysis and maximum likelihood estimation are included into the comparison.

Illustration of Bayesian receptive field.

The figure shows the inferred receptive fields of one neuron (lower) as well as the confidence range of the sorted pixel values (upper) when using a different fraction of the data (0, 10, 50, and 100% , n=8452 spikes).

References
Distinct contributions of the amygdala and prefrontal cortex in the regulation of fear.

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The lateral nucleus of the amygdala (LA) and the medial prefrontal cortex (mPFC) seem to play opposing roles in the regulation of fear: activity in the LA covaries positively with fear expression and activity in the mPFC covaries negatively with fear expression [1]. Based on the putative roles of these structures, we hypothesized that the LA would signal the onset of fear and the mPFC would signal the offset of fear. Rats lick at 6-8 Hz, thus conditioned lick suppression allows for the measure of the onset and offset of fear at a temporal resolution of ~100 ms, an order of magnitude faster than freezing, which is the most common measure of fear expression. By combining this measure of fear expression with single unit recording from awake rats, we could analyze neural and behavior activity at millisecond timescales.

We found that neural activity in the LA and mPFC was not simply negatively correlated. Rather, neurons in the LA seemed to use an adaptive code to trigger the onset and offset of fear: activity ramped up before the onset of fear and ramped down before the offset of fear, with essentially no activity during sustained behavior. In the mPFC we found ‘up’ neurons that covaried positively with fear and also ‘down’ neurons that covaried negatively with fear. The timing of changes in neural activity in relation to the onset and offset of lick suppression was consistent with the notion that the LA drives fear and the mPFC inhibits fear.

The existence of ‘up’ and ‘down’ neurons in mPFC is reminiscent of other reports of prefrontal activity. An elegant explanation for this type of redundant encoding is that these two populations can instantiate an attractor network via mutual inhibition, which subserves working memory and decision-making [2]. We are currently investigating whether the ‘up’ and ‘down’ neurons might encode a working memory of fear in the mPFC.

Acknowledgments
Jeffrey C. Erlich was supported by a HHMI predoctoral fellowship from 2000-2005.

References
Population Codes: Decoding Quadratic Forms

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We have argued for some time [1, 2] that the computation of quadratic forms by neuronal circuits is essential for contextual inference, dynamic routing of information, and dynamic control of motor outputs. In [2] it is shown that when a vector space X is represented by a large population of neurons with a broad range of monotonic tuning curves a(X), then the principal components of the tuning curves form a set of relatively smooth functions of the form

\[ F(X) = R a(X) = A_0 + A_1 \cdot X + X^* A_2 X + \ldots, \]  

(1)

where the rotation matrix \( R \) diagonalizes the correlation matrix \( C = \langle a^*(X) a(X) \rangle_X \). This provides a mechanism by which neuronal circuits can compute quadratic forms. Several important facts about this observation not previously noticed are: 1) These functional forms constitute the primary information that can be extracted from the neuronal population by linear projections into the soma currents of other neurons; 2) the noise level of these functions is the same as the individual neuronal noise level, but is Gaussian regardless of the statistics of the neuronal noise because of the law of large numbers. (This makes the issue of Poisson statistics moot in redundant population code modeling); 3) recent fits to spatio-temporal receptive field properties utilize this form [3], providing neurobiological experimental support for the high level analysis leading to equation (1). In essence, these observations enable high level modeling to be combined with low level neuronal analysis (see [4]). For example, making the low dimensional system variables explicit should make it easier to extend the MT model by [5] to other systems. Also, point (1) implies it should be more efficient for those who want to model large neuronal circuits without modeling all the details of the individual neurons to use quadratic forms for their basic units rather then pseudo-neuron like units[6].

This work details how properties of the principle components \( F(X) \), such as the SNR, scale with neuronal number, the dimensionality of the space, and the distribution of the tuning curves. The efficiency of the representation drops as the dimensionality increases, which implies neurons should only respond to multiple parameters that interact with one another in the computation the circuit is performing. Also, for large dimensional spaces the neuronal background firing rates should be low, or zero, like many cortical neurons.

Acknowledgments

This work was supported by the Mathers Foundation and the McDonnell Center for Higher Brain Function.

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[6] Private conversations with Seth Herd, UC Boulder, CO.
Linear Fisher Information in a network of LNP spiking neurons

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Deriving an analytical expression for the rate of Fisher information transfer across multiple layers of recurrently connected spiking neurons is a critical step toward understanding the neural basis of a wide variety of problems such as perceptual learning, decision making, attention and optimal Bayesian inference. Here, we address this issue by deriving an expression for linear Fisher information loss in a network of Linear-Nonlinear-Poisson (LNP) spiking neurons receiving spatially correlated spiking inputs. By linear Fisher information, we mean the Fisher information available to an observer with knowledge of the first and second order statistics of the output layer of the network. Linear Fisher information is particularly important in computational neuroscience as linear Fisher information is recoverable by delta rule learning and linear Fisher information has been shown to represent the quantity of information available to decoder implemented by an attractor neural network. Our analysis is based on linearization of the networks dynamics, and yield a surprisingly simple expression for the rate of information loss which takes into account both the spatial and temporal covariance structure of the spike trains. This equation allows us to determine precisely where information loss occurs. We show that critical factors are:

1- The feedforward weights: information loss is roughly inversely proportional to feedforward connection strength provided noninvertible feedforward connection matrices (such as the ones between the LGN and orientation selective V1 cells) are tuned so as to avoid filtering out informative collections of neurons.

2- The nonlinear activation function: any activation threshold will lose information but, more importantly, the shape of the activation function is critical. The most informative neurons should respond where the derivative of the square root of the activation function is the highest in order to minimize information loss. This indicates the utility of a gain control mechanism.

3- Large recurrent weights: the information loss increases with the norm of the recurrent weights. This can be balanced by a comparable increase in feedforward connection strength or optimizing output rate

4- Amplitude of the output activity: surprisingly, information loss may grow with firing rate, i.e., large firing rates are not necessarily advantageous.

5- The Poisson step: this is the only stochastic step in LNP neurons and, not surprisingly, it leads to information loss. However, this factor can be minimized if the number of neurons is very large and the information is finite. In other words, this source of information loss is minimized when the neurons are highly correlated. This implies that, once a redundant code has been established, a large number of neurons is subsequent may be fixed with only small consequences to information loss.

This work also suggests an interesting perspective on the origin of noise in the brain. Information loss is equivalent to adding noise. When we say that the nervous system is ‘noisy’, we are effectively saying that it looses information. Interestingly, the main source of noise in the brain is thought to be the Poisson step (or its underlying cause, such as chaotic dynamics). Yet, according to our analysis, this source of information loss (or ‘noise’) is in fact easy to minimize across multiple layers of cortex. Thus, it seems likely that most of the ‘noise’ in the cortex has little to do with the Poisson step but is, in fact, related to accurate perceptual filtering and task relevant stimulus identification. There is a natural Bayesian interpretation of this effect. The brain cannot know with certainty the statistics of its inputs. As a result, it learns approximate distributions which are embedded in the connectivity. The mismatch between the presumed and true statistics could potentially be the main source of noise.

Acknowledgments: This work was supported by NSF, NIDA and the James S. McDonnell Foundation.
The neural representation of an auditory spatial cue adapts to stimulus statistics

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Recently it has been shown that neurons in the auditory midbrain nucleus of the inferior colliculus (IC) can quickly adapt to local stimulus statistics so as to improve the neural representation of the most commonly-presented sound intensities \cite{1}. The neural mechanisms behind this effect could arise at multiple levels of the auditory pathway, from the periphery to the IC. Here, we demonstrate that a similar adaptive phenomenon also occurs in the coding of the interaural (between ears) time difference (ITD) in the IC, suggesting that it may be a more general phenomenon. ITD is a major cue for sound localization, and is first represented by the neurons of the medial superior olive (MSO), where the information from the two ears is brought together. MSO neurons directly excite ipsilateral IC neurons and are three synapses downstream of the sensory hair cells of the cochlea. Thus for ITD coding, this adaptive phenomenon must originate entirely in non-peripheral neurons.

To examine the effect of stimulus statistics on IC neuron responses, we presented a ~7 min continuous binaural broadband noise to anaesthetized guinea pigs whilst recording extracellularly from single IC neurons. The ITD of the noise was randomly selected every 50 ms from a probability distribution that spanned the range of ITDs that can naturally occur for the guinea pig head size (+/-325 µs) and had a 130 µs wide high-probability region from which ITDs were chosen 80% of the time. The ITDs of each noise stimulus were divided into 100 equal bins, and rate-ITD functions were constructed from the mean spike rate over all the 50ms instances in each ITD bin. Figure 1a shows the rate-ITD functions (smoothed with a 3-point average) of a typical IC neuron, for noise stimuli with different high probability regions denoted by the colored bars on the abscissa. Figure 1b shows the corresponding Fisher information, a measure of accuracy of representation, for each rate-ITD function. Observe that the peak Fisher information (over the rate-ITD function slope) moves with the high probability region when that region lies in the range of ITDs that lead at the ipsilateral ear (negative ITDs). Figure 2 shows the population Fisher information curve for each position of the high probability region. This was constructed as the sum of the Fisher information of all neurons (n=10), with the added assumption, from brainstem symmetry, that each neuron has a partner whose attributes were identical but reflected about 0 ITD. We can see that the neural population appears to adapt to stimulus statistics so as to crudely move its region of highest coding accuracy (its peak population Fisher information) towards the most probable ITDs.

References

Task and behavior related formation of cell assemblies

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Identifying the principles of neuronal information processing is one of the most important and most controversially discussed issue in experimental and theoretical neuroscience. Part of the reason for ongoing disputes is the still debated role and existence of fine temporal coordination of spiking activity, as it was hypothesized for assemblies and synfire chains. To help resolving this issue, we present, first, a method called NeuroXidence that allows to draw a line of demarcation between the rate and the temporal codes, and second, experimental results that provide strong evidence for task, behavior and stimulus related formation of neuronal cell assemblies on a timescale of 3-5 ms. NeuroXidence is a non-parametric and computationally-efficient method that detects coordinated firing of two or more neurons and tests whether the observed level of coordinated firing is significantly different from that expected by chance. The method considers the full auto-structure of the data, including the changes in the rate responses and the history dependencies in the spiking activity. Also, the method accounts for trial-by-trial variability in the dataset, such as the variability of the rate responses and their latencies. NeuroXidence can be applied to short data windows lasting only tens of milliseconds, which enables the tracking of transient neuronal states correlated to information processing. It can identify changes of coordinated firing that co-occur with changes in firing rate. We demonstrate, on both toy-data and single-unit activity recorded in cat cortex, that NeuroXidence discriminates reliably between significant and spurious events that occur by chance. Using NeuroXidence for the analysis of three data sets (1. primary motor cortex in an awake monkey performing a delayed pointing task, 2. prefrontal cortex in an awake monkey performing a delayed matching to sample task, 3. responses to moving gratings from anesthetized cat area 17), with up to 42 simultaneously recorded single units revealed coordinated spiking activity that involved 2 to 8 neurons in individual patterns on a timescale of 3-5 ms. To identify behavior, task, and stimulus induced changes of the neuronal synchronization we performed bi- and multi-variate tests.

Our Results demonstrate, first, that cell assemblies exist and involve large groups of cells, and second, that the formation and synchronization of cell assemblies is task, behavior and stimulus dependent.

Acknowledgments This work was in part funded by the Hertie Foundation (GP, DN, WS).

References


Multipliciative Auditory Responses in the Midbrain of the Barn Owl

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Space-specific neurons in the barn owl’s auditory space map gain spatial selectivity through tuning to combinations of the interaural time difference (ITD) and interaural level difference (ILD). The combination of ITD and ILD in the subthreshold responses of space-specific neurons in the external nucleus of the inferior colliculus (ICx) is well-described by a multiplication of ITD and ILD [1]. It is unknown, however, how ITD and ILD are combined at the site of ITD and ILD convergence in the lateral shell of the central nucleus of the inferior colliculus (ICcl) and therefore if ICx is the first site in the auditory pathway where multiplicative tuning to ITD and ILD occurs. We used extracellular recording of single neurons to determine how ITD and ILD are combined in ICcl.

By comparing additive and multiplicative models of neural responses we show that ITD and ILD are combined nonlinearly in ICcl, but the interaction of ITD and ILD is not uniformly multiplicative over the sample. A subset of the neural responses are well-described by a multiplicative interaction of ITD and ILD indicating that ICcl is the first site where multiplicative tuning to ITD and ILD occurs. ICx, however, is the first site where multiplicative tuning is observed consistently. While the fit to the data is better for the multiplicative model than the additive model for 94\% of the cells, there are properties of the neural responses to ITD and ILD that are not consistent with multiplication. ITD tuning curves of some ICcl neurons shifted with changes in ILD and vice versa. In several neurons, ITD tuning disappeared at large positive or negative ILD values while neurons continued to respond to the sound. Also, most neurons showed changes in the shape of the ILD tuning curve for different ITDs.

We constructed a network model to determine if a linear combination of the responses to ITD and ILD observed in ICcl is sufficient to produce the multiplicative subthreshold responses to ITD and ILD seen in ICx [1]. In this model we treat ICcl as a set of hidden units that combine ITD and ILD in a diverse set of responses. For each ICx subthreshold response examined, it was possible to find connection weights between the ICcl units and the ICx unit so that the correlation coefficient between the ICx data and the model approximation was greater than 0.99. These results support a model where multiplicative tuning to ITD and ILD develops in stages in the barn owl’s inferior colliculus.

Acknowledgments
This work was supported by NIH grant DC00134.

References
Processing of Complex Activity Patterns at the Calyx of Held Synapse: A Computational Analysis

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Cells in the auditory brainstem show high levels of spontaneous activity with rates of up to 100 Hz. In-vitro studies examining synaptic properties done in acute brain slices typically neglect this fact. The source of the spontaneous activity, namely the auditory hair cells, is removed in brain slices, resulting in an artificially low level of synaptic activity. As a model, we investigated synaptic transmission by the Calyx of Held synapse in the Medial Nucleus of the Trapezoid Body (MNTB) to determine the effect of sustained in-vivo like firing on the dynamics of transmission. In previous work (publication in progress) we showed that synaptic properties such as vesicle release probability changed, when the synapse was conditioned by stimulation with activity patterns similar to the normally present spontaneous firing.

In this study we present a vesicle release model, which can predict the short-term dynamics in conditioned synapses. Experimental data were obtained by recording evoked excitatory postsynaptic potentials (EPSC) in MNTB cells. We stimulated the afferent fibers with patterns mimicking the complex and highly varying natural input. These trains of activity had a Poisson like distribution with alternating mean frequencies ranging from a 5 Hz up to 300 Hz. The main features of the model that we used to predict our experimental traces were a constant release probability and a single exponential recovery.

In contrast to other studies [1] we find that a very basic prediction model with only three free parameters already gives a very good estimation of the recorded EPSC amplitudes. The correlation coefficient of the prediction and its underlying recording is almost 0.9 and therefore very close to the ceiling of predictability. The discrepancy between our study and other studies suggests that effects, which can be observed in artificially silenced brain slices may not necessarily affect the dynamics of synaptic transmission at in-vivo like activity levels.

Furthermore, the model predicts an apparent vesicle pool size, which is decreased to almost half of its value in rested synapses. Recovery experiments showed that this could only partly be attributed to the slow recovery time constant known from other studies [2, 3].

**Acknowledgments**
This work was supported by DFG Sachbeihilfe KL 1842.

**References**
Comparing Glomerular Maps in the Olfactory Bulbs of Mice and Rats

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Mice and rats use 1000-1500 odorant receptor types to probe chemical space. The receptor neurons in the nose project their axons to the olfactory bulb and form anatomical units called glomeruli. Each glomerulus receives input from a single type of receptor. Thus each point on the surface of the bulb has a specific chemical response spectrum, derived from the associated odor receptor. This map of odors to glomeruli has been a subject of great interest, because it forms the physical layout on which neural computation takes place in the olfactory bulb. On this background, we would like to understand: How precise is the glomerular layout? What is the variability across the two hemispheres and across animals? Is the layout different for the two species? Are there functionally identical glomeruli in mice and rats?

To examine these issues, we recorded the odor response spectra of many glomeruli to a diverse battery of 100 odors at low concentration. We imaged neural activity in the dorsal olfactory bulb by two methods: (1) Intrinsic optical signals under deep red illumination can be used in both mice and rats, but their physiological origin is somewhat uncertain. (2) SynaptopHluorin is a fluorescent reporter of synaptic activity in olfactory receptor neurons of genetically engineered mice. Its output is tied specifically to synaptic release, but it is not available in the rat. To test the correspondence between the two probes, we recorded the same odor response in a mouse using both methods, by rapidly interleaving blue and red excitation light. We found an excellent match between the two imaging methods in both the pattern of glomeruli activated and their relative response amplitudes. Therefore, the intrinsic optical signal correlates well with synaptic activity in olfactory receptor terminals and can be used in rats to investigate receptor neuron responses.

In both mice and rats, our odor set allowed stimulation of ~80 glomeruli on the dorsal surface of the olfactory bulb. Many glomeruli can be identified uniquely by their odor response spectra. Thus one can recognize the corresponding glomerulus across hemispheres of the bulb and across animals. We found that the placement of glomeruli is precisely controlled. The location of a given glomerulus in the map varies by only ~1 glomerular diameter across hemispheres and ~2 diameters across animals. In rats, placement was more precise along the medial-lateral axis of the bulb than in the anterior-posterior direction (~0.9 diameters vs ~1.8 diameters). No such anisotropy was seen in the mouse.

Several glomeruli in the mouse have a partner in the rat with the identical odor response spectrum. Since there are no matching receptor genes in the two species, it appears that different receptor proteins can produce almost indistinguishable function. Presumably these two species, with similar ecological environments, have a need for some of the same chemical sensors. However, the spatial distribution of these glomeruli on the olfactory bulb was entirely different in mouse and rat. This suggests that the layout of glomeruli, though it is precisely controlled among individuals of the same species, is not an essential determinant of subsequent computations.
A Model of Binocular Gaze Estimation

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Binocular image-pairs contain information about the three-dimensional structure of the visible scene, which can be recovered by the identification of corresponding points. However, the resulting disparity field also depends on the orientation of the eyes. If it is assumed that the exact eye-positions cannot be obtained from oculomotor feedback, then the gaze parameters must also be recovered from the images, in order to properly interpret the retinal disparity field.

Existing models of biological stereopsis have addressed this issue independently of the binocular-correspondence problem. It has been correctly assumed that if the correspondence problem can be solved, then the disparity field can be decomposed into gaze and structure components, as described above. In this work we take a different approach; we emphasize that although the complete point-wise disparity field is sufficient for gaze estimation, it is not in fact necessary. We show that the gaze parameters can be recovered directly from the images, independently of the point-wise correspondences.

The relationship between binocular vergence and the resulting epipolar geometry is derived. Our algorithm is then based on the simultaneous representation of all epipolar geometries that are feasible with respect to a fixating oculomotor system. This is done in an essentially two-dimensional space, parameterized by azimuth and viewing-distance. We define a cost function that measures the compatibility of each geometry with respect to the observed images. The true gaze parameters are estimated by a simple voting-scheme, which runs in parallel over the parameter space. We describe an implementation of the algorithm, and show results obtained from real images.

Our algorithm requires binocular units with large receptive-fields, such as those found in area MT [1]. The model is also consistent with the finding that depth-judgments can be biased by microstimulation in MT [2]; if the artificial signal generates an ‘incorrect’ set of gaze parameters, then we would expect the subsequent interpretation of the disparity field to be biased. Our model could be tested using binocular stimuli based on the patterns of disparity that we describe. We note that these patterns are geometrically analogous to parametric motion fields. It has already been shown that such flow-fields are effective stimuli for motion-sensitive cells in area MST [3]; we predict an analogous binocular ‘gaze-tuning’ in the extrastriate cortex.

Acknowledgments
This work is part of the Perception on Purpose project, supported by EU grant 027268.

References
The effect of contrast on velocity encoding in Macaque area MT

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When two patterns moving at the same speed are presented simultaneously, the lower contrast one appears to move slower [1]. This effect of contrast on perceived speed has proven to be a challenge for physiological and theoretical models of motion perception. MT is often implicated in mediating motion perception, yet the effect of contrast on the speed tuning of neurons in MT is inconsistent across studies, perhaps because of differences in experimental preparations and stimuli. Studies using single sinusoidal gratings show no effect of contrast on the temporal frequency tuning of MT neurons over a limited range of test contrasts [2]. On the other hand, studies using moving dots show a robust effect of contrast on velocity tuning; the preferred speed of MT neurons shifts to lower speeds at lower contrast [3,4].

With the goal of arriving at a population model that would link the physiology with the psychophysics, we measured the effect of contrast on velocity tuning in anaesthetized macaque area MT. We chose broadband gratings, consisting of three sinusoidal gratings of fixed spatial frequency (0.5 c/deg, 1 c/deg, 2 c/deg) summed with randomized phases, moving at 8 different speeds (over the range [3,60 deg/sec]), at three contrasts (5%, 20% and 80%) on a gray background. We presented the same set of stimuli to every cell, without optimizing for the spatial frequency or speed preferences.

Across the population of recorded neurons (n= 41), we find that reducing the contrast from 80% to 20% reduces the preferred velocity of the neuron by a factor of ~2.7. Although the measurements were noisier, reducing the contrast to 5% produced an even larger shift. This effect was more pronounced in cells that preferred high speeds at high contrast. By recording the same data set on every neuron without optimizing for the neuron’s preference, and using the same stimuli used in a recent psychophysical study [5], our data set supports the formulation of a quantitative model linking the physiology with behavior.

Acknowledgments
This work was supported by NIH EY04440 and HHMI.

References
High Resolution Retinotopy Obtained by Voltage Sensitive Dye Imaging in the Behaving Monkey

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Retinotopy is one of the most fundamental organizing principles of the visual cortex. Over the years, a variety of approaches including electrophysiological recording, tracer injection and intrinsic optical imaging have been applied to examine it. Voltage sensitive dye imaging (VSDI) provides a way to monitor neuronal population activities at a high spatial and temporal resolution. Here we present a protocol for retinotopic mapping at unprecedented resolution in the behaving monkey using VSDI. Two sets of periodic stimuli for polar and eccentricity mapping were presented to macaque monkeys performing a fixation task. VSDI signals were collected with a fast CCD camera from a region of ~1 cm² over the dorsal portion of areas V1 and V2 near the V1/V2 border. Within the appropriate range of temporal frequencies, the stimuli generated periodic VSDI responses with power concentrated at the periodic stimulus frequency. Due to the systematic delay of the time at which the stimulus traveled to subsequent spatial locations, VSDI signals created waves that propagated across the cortical surface. The phase of VSDI signals obtained by FFT linked stimulus location in the visual field and its neuronal representation on the cortical surface. A total of 2-3 minutes of imaging over a 30 minute session of data collection were enough for creating a high resolution retinotopic map. We used this approach to obtain retinotopy from two rhesus macaque monkeys. Retinotopy obtained in this way had a high spatial precision of 0.17-0.24 mm with 32 trials, was consistent across experiments and could be used to reliably predict the locations of the peak response to small localized stimuli. An initial analysis showed no obvious local distortion in the retinotopic maps. However, the measurements revealed a larger cortical magnification factor (CMF) in V1 near the fovea than previous estimates obtained by several different methods. For one monkey, average CMF in V1 within 2.5-2.7 degrees of eccentricity was 8.58 mm/deg angularly (along an iso-eccentricity ring), and 12.28 mm/deg radially (along an iso-angular ray). For another monkey, within 1.8-2.1 degrees of eccentricity, average CMF was 9.08 mm/deg angularly and 7.43 mm/deg radially. Finally, by running a bootstrap procedure to infer the structure of retinotopy at the limit of an infinite number of trials, we found that most locations within the ROI had infinite resolution. This final result indicates that the circuitry from retina to LGN to V1 that establishes retinotopy does little to limit the very high spatial resolution of cortical retinotopic maps.

Acknowledgments

This work was supported by NIH-NEI grants RO1EY016454 to ES and RO1EY016752 to DJH and ES.
On the limits of feed-forward processing in visual object recognition

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The primate visual system shows a high degree of selectivity while at the same time being robust to large transformations of the images\textsuperscript{1}. This remarkable degree of invariance and specificity can be achieved quite rapidly as evidenced by the short latency of selective spike responses in higher levels of visual cortex and also by psychophysics performance in rapid visual presentation tasks and backward masking tasks\textsuperscript{2-4}. The speed of processing in the visual system has led to the notion that feed-forward processing can account for several aspects of visual object recognition. Indeed, a purely feedforward computational model is very successful in explaining physiological responses in several areas of visual cortex from primary visual cortex through inferior temporal cortex and also several psychophysical observations where humans need to rapidly identify or categorize objects\textsuperscript{5-7}.

Here we quantitatively explore the limits of feedforward processing by examining how well a purely feedforward model can perform identification and categorization tasks in images containing multiple objects or other scenarios where we parametrically vary the amount of clutter in the image. We first show that the performance of the model in response to isolated objects matches the electrophysiological properties of IT neurons in terms of their accuracy as well the robustness to changes in object scale and position. We then show that performance degrades with increasing number of objects or with increasing degrees of clutter in natural scenes. These results point to the limits of feedforward processing in visual object recognition and emphasize the role of attention in processing and interpreting complex natural scenes.

Acknowledgments
We thank Minjoon Kouh for helpful discussions. This work was supported by a McGovern Institute Fellowship and the Children’s Hospital Boston.

References
Receptive Fields of Awake Animals Free-Viewing Natural Time-Varying Images

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One of the major aims of neuroscience is to understand how neurons code sensory input of an animal’s natural environment. The basic approach has been the usage of a neuron’s receptive field, which is extended over space, time and other sensory input dimensions to predict responses of a neuron to sensory input by a weighted summation or filtering of the input.

Most of the existing understanding of sensory systems are derived from measurements made using unnatural stimuli, and animals that were paralyzed and/or anesthetized. It is questionable whether the receptive field measured this way can describe the neuronal responses to natural stimuli experienced by awake behaving animals. In fact, receptive fields are dynamic (non-stationary), adapt to sensory input statistics, and change with behavioral state. Prior investigations did not employ natural stimuli because their importance was not understood, nor were approaches to analyses of their statistical properties readily apparent. Furthermore, it is technically demanding to use awake behaving animals where eye movements have to be tracked to analyze receptive fields.

We demonstrate that it is not only possible to derive the receptive fields this way but also essential when studying neurons whose receptive field structure is unknown. In particular, we recorded in the lateral geniculate nucleus (LGN), visual cortex (V1/V2), middle temporal (MT), and pulvinar (Pul) areas. We verify that our method and random-dots sequence both derive LGN receptive fields. However, it is not straightforward to design other simple stimuli to derive receptive fields in V1/V2, MT, and Pul areas — unless one has more knowledge about their receptive field properties. Yet our method worked for the other areas just as LGN, mainly because neurons are activated during free-viewing natural time-varying images. The neurons without activity are probably not visual or are not important in natural vision.

Acknowledgments
This work is supported by the NEI grant EY015272-01A1
Fire Together – Wire Together – Come Together

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The mechanical tension within axonal and dendritic connections has been proposed to explain structural features of the brain such as cortical folding [1]. Another feature, the structure of orientation maps, has been shown to minimize the length of horizontal connections in V1, given certain connection patterns as a function of orientation difference [2]. Other connection patterns would be length-minimized by orientation maps which have a structure that is different from that observed in biology. We take learned horizontal connections of a V1 model, and test whether their length minimization leads to a realistic orientation map.

Learning of Horizontal Connections  The horizontal weights of the model V1 constitute an associator network. They have been trained to memorize the edge detector neurons’ activations $\bar{s}$ that follow presentation of natural images: initialized with $\bar{a}(t^0) = \bar{s}$ the activations $\bar{a}$ should remain stored within the recurrent activation update until $t^\text{end}$. Activation update, and learning rule are [3]:

Activity update: $a_i(t + 1) = f(\bar{w}_i \bar{a}(t))$. 
Learning: $\Delta w_{ij} \approx (s_i - a_i(t^\text{end})) \cdot a_j(t^\text{end}-1)$.

Hence, learning stops if the network activations $\bar{a}$ equal the upcoming activations $\bar{s}$. Such an associator network will remove noise, compute invariances, predict activations, or segment and bind via synchronization.

Length Minimization by Cell Shifting  We modified the position of neurons on the model cortical sheet by lateral connection-dependent physical attraction. An additional distance-dependent repulsion prevents the map from collapsing into one point. This procedure performs a gradient descent on a weight length dependent energy function. After convergence, horizontally directed tension forces are in balance, i.e. forces on each neuron sum to zero. The results with 1024 neurons and a retinal input of $16 \times 16$ pixels show that the neurons arrange topographically and form an orientation map similar to a hypercolumn in V1.

The Figure shows the resulting map where each dot corresponds to one of the 1024 neurons. They have shifted into positions exhibiting local topography and smoothly varying orientation preferences. Here neuronal tension within the given weights is in balance.

Acknowledgments

References
Quantitative analysis of visual plasticity in the adult LGN

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The developing visual system has been at the forefront of studies examining the rules that govern synaptic plasticity and the consequences that different forms of plasticity have on sensory processing. Past studies suggest that ON- and OFF-center retinal ganglion cells occasionally provide mismatched input to LGN neurons of the opposite response signature (e.g. OFF-center retinal input to an ON-center LGN neuron) [1]. This finding raises the possibility that manipulations to the primary source of retinal drive to the LGN could unmask or augment geniculate responses to the otherwise weak, mismatched inputs.

By blocking the ON-center pathway in the retina with intra-ocular injections of DL-2-amino-4-phosphonobutyrate (APB), we found that rapid visual plasticity could be induced in cat LGN cells [2]. As expected, APB blocked ON responses, but not OFF responses, in the retina. ON-center neurons in the LGN initially showed a similar effect. Surprisingly, however, many ON-center neurons rapidly began to display OFF-center responses. We interpret this switch in response signature as evidence of rapid synaptic plasticity, possibly involving weak mismatched inputs that are normally masked. Here, we performed a quantitative examination of LGN receptive field properties before and after application of APB in the retina. Response latency, center and surround subfield strength, and a transience index derived from impulse responses were quantified for individual neurons before and after application of APB. Spatial properties of the receptive fields, including size and location, were also assessed before and after APB application. Ongoing analysis is directed at determining the extent to which the rapid time-course of this plasticity depends on visual stimulation.

Acknowledgments
We thank H. Alitto, D. Rathbun, D. Sperka, and K. Henning for helpful discussions and technical support. This work was supported by the McKnight Foundation and NIH grants EY13588 and EY12576.

References

Cerebellar motor learning; from behavioral studies to system biology model of LTD

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The cerebellar internal model theory postulates that the cerebellar cortex acquires many internal models of controlled objects, dynamical processes in the external world, and even other one’s brain dependent on long-term depression (LTD) of Purkinje cells. A specific version of this theory, the feedback-error-learning model postulates that the climbing fiber inputs to Purkinje cells carry the feedback motor command, which could be regarded as an approximation to the error signal for motor commands and can supervise learning of inverse dynamics models. Many experimental supports were obtained from the ventral paraflocculus of the cerebellum during monkey control of ocular following responses. For arm movements under multiple force fields, firings of many Purkinje cells correlate with dynamics [1]. fMRI studies mapped forward and inverse models of manipulated objects and tools in the cerebellar cortex.

One specific prediction of the feedback-error-learning model is that the climbing fiber inputs should be of low firing rates but should convey high-frequency information. Accordingly, Takahashi, Funabiki, and Hirano recently found that mGluR delta 2 knockout mice with high climbing-fiber firing rates exhibit delayed optokinetic eye movements. A network model of inferior olive nucleus reproduces rhythmic and synchronized firings for strong electrical coupling, but demonstrates chaotic and desynchronized firings for intermediate coupling, which is advantageous for information transmission with low firing rates of climbing fibers [2]. This prediction was also recently supported from unit recording data.

Kinetic models of LTD [3, 4] suggest a cascade of excitable and bistable dynamical processes, which may resolve plasticity-stability dilemma at single spine level. That is, even a single pulse of climbing fiber input combined with an early train of several parallel fiber pulses can induce Ca^{2+} induced Ca^{2+} release via IP3 receptors on ER. The MAPK positive feedback loop leaky integrates resulting large Ca^{2+} elevation and if it crosses the threshold then the state moves to the depressed equilibrium. These models explain diverse LTD experiments and clearly demonstrate that LTD is a supervised learning rule, and not anti-Hebbian as erroneously characterized. The MAPK positive feedback loop model [3] was recently supported by a Ca^{2+} photo-uncaging and imaging experiment [5] that suggests LTD all-or-none character.

References
Motor learning with unstable neural representations

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It is often assumed that learning takes place by changing an otherwise stable neural representation. To test this assumption, we analyzed data of a recent experiment, which measured changes in the directional tuning of primate motor cortical neurons during reaching movements, performed in both familiar and novel environments (Padoa-Schioppa et al., J Neurophysiol. 2004). During the familiar task, tuning curves exhibited slow random drift. During learning of the novel task, random drift was accompanied by systematic learning-related changes. Our analysis suggests that motor learning is based on a neural representation which is surprisingly unstable.

To explain the observed instability of the neural representations we propose a theory which is based on two assumptions: (1) motor cortex is redundant, i.e. it uses more neurons than required to produce the desired sensorimotor transformation, (2) when practicing a task, synapses are changed by a stochastic gradient descent learning rule. We demonstrate that these two assumptions are sufficient to explain the observed instability by simulating a model of a redundant motor cortical network. Because our network has more neurons than necessary, a desired sensorimotor transformation can be realized by a continuum of configurations of synaptic strengths, which we term the optimal manifold. Changing synapses along the optimal manifold changes the neural representation, but not the sensorimotor transformation. Our second assumption, of stochastic gradient learning, produces such behaviorally irrelevant changes. These learning dynamics can be described as stochastically moving down an error landscape which has a valley of minima at the optimal manifold (see schematic figure below). At the late stages of learning, noise driven changes are channeled along this valley by the gradient term, and thus the neural representation drifts although performance is nearly fixed.

We show that our model accounts reasonably well for the observed changes in the neural representations, in both familiar and novel environments. Furthermore, we infer several properties of synaptic plasticity underlying motor learning: (1) signal-to-noise ratio is around 1, (2) the source of variability is local, i.e. at individual synapses or neurons, rather than global noise from the environment, (3) plasticity noise is additive, and (4) it takes plasticity noise at least thousands of trials to change synapses completely. Additionally, we show that contrary to common views, a cell’s tuning properties may be only weakly related to its anatomical connections to the motor output. Finally, we discuss what other evidence there are for our theory and how it could be further tested with brain computer interface experiments.
Sleep and Learning

Daniel Margoliash

University of Chicago

I will begin by briefly reviewing work in humans and songbirds demonstrating the contribution of sleep to learning in a number of behaviors. This will set the stage for an analysis of the potential neural mechanisms of sensorimotor vocal learning in songbirds.
Spike latencies in retinal ganglion cells encode spatial image details

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Vision is a highly dynamic process, structured by frequent eye movements that bring a new image onto the retina and initiate a short episode of visual processing. Analysis of the spatial scene can be extremely rapid and precise: For example, human subjects can detect and classify objects in brief image presentations of ~100 ms [1]. What neural codes underlie such rapid image processing has been a longstanding question.

We investigated the structure of visual information emerging from the eye, by recording spike trains from many ganglion cells in the isolated salamander retina. A square-wave grating stimulus was flashed briefly onto the retina, and the considered image analysis task consisted in identifying the grating’s spatial phase. Most ganglion cells responded with a burst of spikes to all presentations, regardless of phase and sign of the grating. We recorded the time of the first spike in the burst (latency) and the total number of spikes (spike count). The response latency varied systematically with grating phase, with a range up to 40 ms. The precision of this latency for identical stimuli was 3-5 ms. These stimulus-dependent latency variations generally contained much more information about the stimulus than did the spike count.

Since the brain circuits that receive retinal spike trains may not know the time of stimulus onset other than through retinal activity itself, we further investigated what information is carried by the relative latency of two neurons. For some cell pairs, the relative latency was more informative than any single-neuron latency. Furthermore, these latency differences were largely invariant with stimulus contrast, since each cell’s response latency tended to decrease with increasing contrast. In addition, we found stimulus-independent fluctuations in latency, with strong covariation across neurons; this resulted in low fluctuations of the latency difference. Altogether, this suggests that a population latency code would be a powerful mechanism for transmitting spatial detail of a briefly exposed scene. It is robust to retinal noise; it encodes stimulus shape independent of the overall contrast level; and it provides the information in the shortest possible time, namely with the first spike.

Finally, we explored how these response patterns might be produced within the retinal network, and analyzed several models consistent with known anatomy. Two features of spatio-temporal integration were found to contribute: the combination of inputs from both ON and OFF pathways, and the strong rectification of those signals before spatial integration at the ganglion cell.

Neural coding of natural signals: theory, computation, and data

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Neural codes must serve a wide range of sensory tasks. With a myriad of possible codes, why do biological sensory system use the codes they do? Can we develop theories that explain sensory coding in terms of fundamental principles? One such principle is efficient coding theory. This postulates that the goal of sensory coding to encode signals accurately and efficiently. In this talk, I will review recent progress in this area and focus on how this theoretical approach can be extended to learn efficient auditory codes using a spiking population code. In this model, an idealized spikes encode the precise temporal positions and magnitudes of underlying acoustic features. When the set of acoustic features is adapted to optimally encode natural sounds, the spike code achieves far greater coding efficiency than conventional representations. Furthermore, the inferred features show both striking similarities to measured cochlear filters and a similar bandwidth versus frequency dependence across the population. These results provide evidence that the neural coding of auditory signals approaches an information theoretic optimum. Finally, I will present evidence that suggests speech itself is adapted to the coding capacity of the mammalian auditory system.
Bayesian inference underlies contraction bias
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In magnitude estimation tasks, participants tend to overestimate the physical magnitude of small variables and underestimate the magnitude of large ones, an illusion known as ‘contraction bias.’ Although contraction bias was discovered a century ago, the computational principles underlying this bias in estimation have remained unclear. We investigate this question in the framework of Bayesian inference.

In order to study the bias, participants performed a two-alternative forced-choice task in which they judged whether the length of a memorized bar ($L_1$) was longer than that of a second bar ($L_2$). Contraction bias was demonstrated by analyzing choice behavior in trials in which the lengths of the first and second bars were equal. In these impossible trials, subjects frequently reported short $L_1$ bars to be longer, and long $L_1$ bars to be shorter than their veridical lengths (Fig. 1, circles). We show that this bias is consistent with the performance of an ideal observer who uses Bayesian inference to incorporates a noisy representation of the memorized $L_1$ bar with the prior distribution of the bar lengths.

The hypothesis that contraction bias results from Bayesian inference yields two predictions. First, the bias is independent of the physical range of the stimuli. Second, increasing uncertainty in the memory of $L_1$ is expected to increase the reliance of its estimate on the prior distribution and therefore enhance the contraction bias. The first prediction is confirmed by showing that contraction bias is not significantly different between two groups of subjects who were tested using different uniform distributions (Fig. 2, blue circles and black squares). In order to test the second prediction, we modified the task such that on selected trials, a secondary task had to be performed between the presentation of the first bar and the second bar, thus increasing the uncertainty in the representation of the memorized $L_1$ bar. As predicted, contraction bias was enhanced in the trials associated with the secondary task (Fig. 3, red squares). Thus we conclude that contraction bias results from Bayesian inference in which a noisy measurement is combined with a-priori knowledge about the distribution of magnitudes in order to improve performance.

Figure 1: Contraction bias. Circles, fraction of times one subject reported $L_1$ as longer than $L_2$ in impossible trials, as a function of logarithmic bar length. Line, Bayesian prediction.

Figure 2: Shifting the prior results in a horizontal shift of the bias curve. Circles, range 50-200 pixels. Squares, range 150-600 pixels. Line, Bayesian prediction.

Figure 3: Adding noise to memory increases the slope of the bias curve. Circles, standard trials. Squares, trials with a secondary task. Line, Bayesian prediction.
Dendritic arithmetic: Some new twists and curves

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Discovering appropriate simplified models for individual neurons remains a central problem of neuroscience. Nearly three decades of experimental and modeling studies suggest that the large dendritic trees of CNS neurons are highly articulated, active processors, supporting a variety of internal computations as they convert their synaptic inputs into output spikes. But what are the specific “arithmetic” operations that govern how multiple excitatory and inhibitory synaptic inputs, activated at different places and times within the dendritic arbor, are combined to determine the cell’s output firing rate and/or pattern? Several new results will be presented relating to (i) biophysical mechanisms underlying nonlinear dendritic integration in pyramidal cells, (ii) some unexpected nonlinear spatial and temporal integration effects that depend on NMDA channels, (iii) the dastardly complicated interactions between excitation and inhibition, and (iv) implications of dendritic subunitization for the information processing functions of the surrounding cortical circuit.
Small fields change spike timing: A functional role of local-field potentials?

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Small electric fields will polarize neurons by only a small amount; for this reason small electric fields have previously been suggested to have no physiologically relevant effects. However, in recent years evidence has been mounting that small fields can entrain network activity [1], and have indeed a causal effect on brain function [2]. To date, there is no proven mechanistic theory on how this causal interaction may occur. We propose a simple mechanism whereby an extracellular field incrementally polarizes the neuron’s membrane and thus advances (or delays) the timing of a synthetically driven action potential. Assuming a steady firing threshold and knowing that a membrane polarizes in proportion to field strength [3], i.e. $\Delta V = cE$, one can make a number of quantitative predictions on the effects of extracellular fields on a neuron’s spike timing:

1. Spike timing changes linearly with increasing steady-state field strength: $\Delta t \propto E$. (2) This effect is proportional to the inverse of the driving synaptic membrane potential slope: $\Delta t = \Delta V / cE = \Delta V / \bar{V}$. (3) Oscillating fields will shift firing times with their mean falling within 1/4 of the oscillatory cycle (the rising edge). (4) This mean firing time advances with increasing field strength and decreasing ramp slope, i.e. it increases with $cE / \bar{V}$. (5) The strength of the coherence as measured by the Rayleigh coefficient (vector strength) also increases with $cE / \bar{V}$.

To test these predictions we measured the effect of applied uniform fields on the timing of action potentials of CA1 pyramidal cells in vitro. Spikes were evoked by injecting intracellular current ramps that simulated depolarizing synaptic drive in the theta range (4-8Hz) while applying steady-state fields as well as field oscillations in the gamma range (30Hz). These experiments confirmed all our predictions. Thus, we show that steady-state fields with field strength of $E = 1 \text{mV/mm}$ and synthetically driven theta ramps can advanced spiking by up to $\Delta t = 1 \text{ms}$, while gamma fields showed synchronized spiking coherent with the applied oscillation. We note that this field strength is well within the physiological range of normal gamma activity in the hippocampus [4]. For the hippocampus we argue that an additional synchronizing effect may result during recurrent network activity as synchronous firing causes coherent local field potentials which in turn coherently polarize many cells leading to small changes in time that can add up over multiple cycles [5].

In summary, our theory explains how small fields can advance or delay spike timing and how they may affect synchronization in ongoing network activity. It provides the first experimentally verified mechanism by which small electric fields, such as those generated during normal brain activity, could have a functional role, and gives a plausible explanation for the entrainment that has been observed in response to applied fields in humans [2].

References

Cerebellar glomeruli: Can limited extracellular calcium propagate information among distant synapses?

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A class of synaptic learning models – in which presynaptic terminals have access to a weighted sum of the postsynaptic activity – has traditionally been dismissed as biologically unfeasible. This rejection is not surprising under traditional notions of synaptic connectivity, since postsynaptic cell bodies may be far apart, and there are no backwards signals known to sum activity in a terminal-specific manner. However, many synapses in the CNS become specialized by glial cell ensheathment¹. We suggest that such ensheathment may force neighboring cellular elements to share a limited resource: extracellular calcium²-⁴. We propose the novel theory that certain glomeruli are configured so that the instantaneous external calcium concentration will encode the level of spike activity in postsynaptic cells. We concentrate on the specialized glomeruli that exist in the cerebellum at the interface of the mossy fiber and granule cell layers. Here, dendrites from scores of granule cells swirl around a mossy fiber terminal, and the whole structure is tightly ensheathed in an astrocyte⁵-⁶. Simulations demonstrate that the calcium concentration is indeed proportional to a sum of postsynaptic activity in the granule cells. We demonstrate that these extracellular calcium changes are interpretable from an information-processing point of view, generating a novel learning rule for control of plasticity at the mossy fiber/granule cell synapse. This learning rule suggests a sparsely distributed and statistically independent representation in the parallel fibers. Both of these coding properties reduce the complexity of the credit assignment problem between active parallel fibers and climbing fiber at a Purkinje cell. Although traditional models of neural function only emphasize neurotransmitters and point-to-point connections, our results highlight the need to quantitatively address the extracellular context in which axon terminals and dendrites are found.

Acknowledgments
This work was supported in part by the SENSOPAC European Contract IST-028056 (www.sensopac.org), and Sony CSL.

References
Testing hypotheses about computation and coding in the visual system

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The subject of neural coding has generated much debate. A key issue is whether the nervous system uses coarse or fine coding. Each has different strengths and weaknesses and, therefore, different implications for how the brain computes. For example, the strength of coarse coding is that it’s robust to fluctuations in spike arrival times. Downstream neurons don’t have to keep track of spike train structure. The weakness, though, is that individual cells can’t carry much information, so downstream neurons have to be able to pool signals across cells and/or time to obtain sufficient information. With fine coding, individual cells can carry a great deal of information, but downstream neurons have to be able to resolve spike train details to obtain it. Here we set up a strategy to determine what the neural code can and can’t be and used it at the level of the retina. We recorded from essentially all the retinal output cells an animal uses to solve a task, evaluated the cells spike trains for as long as the animal evaluates them, and used optimal, i.e., Bayesian, decoding. This makes it possible to obtain an upper bound on the performance of codes and thus eliminate those that aren’t viable. Our results show that standard coarse coding is insufficient; finer, more information-rich codes are necessary.
A model of temporal integration during electrical stimulation of the human retina

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Purpose: Retinitis Pigmentosa is a photoreceptor disease that frequently results in blindness (Friedman, 2004; Bunker, 1984). However, cells of the neural retina (bipolar, amacrine, and ganglion cells) remain functional, albeit in smaller numbers, and with disorganized connectivity (Marc, 2003). There have been recent attempts to restore vision in these patients using an epiretinal prosthesis, analogous to a cochlear implant, that can activate remaining neurons via direct electrical stimulation (Humayun, 1999; Rizzo, 2003). While it has been demonstrated that electrical stimulation can produce visual percepts in human subjects, the neural pathway from stimulation to percept is still unclear. Here, we present psychophysical threshold and suprathreshold data examining the temporal aspects of electrical stimulation. We fit this data using a biologically feasible model similar to those recently used to describe temporal contrast adaptation in retinal ganglion cells (Chichilnisky, 2001; Rieke, 2001; Meister, 2002).

Methods: Stimuli were pulse trains that varied in their temporal parameters (pulse width, frequency, and pulse number). We measured threshold for single pulse and pulse train stimulation. Current amplitude thresholds were measured using a yes-no paradigm where 50% of the trials were catch-trials containing no stimulus. Suprathreshold contrast was measured using a two-interval brightness-discrimination task so as to obtain equibrightness curves.

Results and Conclusions: Threshold and suprathreshold data were fit using a biologically plausible linear-nonlinear model. The model began with convolution of the stimulus with an impulse response filter that used a 1-stage gamma function, 
\[ r(t) = \int_{-\infty}^{\infty} f(\tau) \delta(t - \tau) d\tau = f(t) * \delta(t), \]
and was then rectified before being passed through a shifting and expanding nonlinearity, 
\[ r(t) = (r(t) - k \int_{-\infty}^{t} r(\tau) d\tau)^\beta. \]
The output of the nonlinearity was then convolved with a second slow integrating filter. In our model, we assumed that the response reached threshold or a perceived brightness level when the maximum response reached some threshold value. This model fit a wide range of data with parameter values that varied little across subject or electrode.

The ability to predict the effects of stimulation is a prerequisite for developing a successful retinal implant. These data are the first to show that electrical stimulation patterns produce predictable and reliable percepts, which can modeled quantitatively.
Multi-tasking of Attention and Working Memory Signals in Prefrontal Cortex

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We recorded the activity of 957 single neurons in the dorsolateral prefrontal cortex (PFdl) of two rhesus monkeys, as they performed an eye-movement task. On each trial of the task, a visual cue consisting of a white circle appeared initially either up, down, left or to the right from a central fixation point. The cue then revolved smoothly along a circular trajectory to another of these four positions and stopped. During the delay period that followed, the monkeys had to attend to the cue covertly in order to detect a subtle luminance change. Until that event, the monkeys had to maintain central fixation. Brightening of the cue instructed a saccade to its initial, remembered location; dimming instructed a saccade to the cue’s final, attended location. Thus the task required the monkeys to remember one location while attending to another. The present analysis focused on understanding how these two locations are represented in PFdl.

A two-way ANOVA showed that firing rates during the delay period exhibited significant main effects of the remembered location, the attended location or both for 555 neurons ($p \leq 0.05$). In agreement with our previous report [1], most of these neurons (70%, 390/555) exhibited a single main effect. Attention tuning occurred three times more frequently than memory tuning for this cell population, with greater depth of tuning as well. Attention-tuned cells were significantly more prevalent in lateral parts of PFdl, whereas memory tuned cells were concentrated more medially ($p < 0.0001$, $\chi^2$ test) [1]. Thus, the cognitive operations of memory and attention for these cells tend to be relegated to separate neurons and to spatially segregated parts of PFdl.

In contrast to this overall tendency, 30% of the tuned neurons (165/555) exhibited main effects of both attention and memory. For these neurons, we calculated one preferred direction (PD) for memory and another one for attention by vector averaging the firing rates over the four remembered and attended locations, respectively. Surprisingly, most of the neurons with both main effects were not tuned to a single direction, but instead had large differences in their PD for memory versus attention. The PDs for memory and attention differed by more than $30^\circ$ for 140 of the 165 neurons (85%) that showed both main effects. Close agreement, defined as less than a $30^\circ$ difference, occurred no more frequently than expected for a uniform distribution of angular differences between two PDs. Most common were neurons with a memory PD that was nearly diametrically opposite their attention PD (differences of $150^\circ$–$180^\circ$). This large difference was found in 57 of the 165 neurons exhibiting both main effects (35%), more than twice as many as expected for a uniform distribution. Thus, during the delay period, some PFdl neurons discharged when the cue had initially appeared near its memory PD or stopped near its attention PD — and these directions were often opposite one another.

These results indicate that, although most PFdl neurons process attentional or mnemonic signals almost exclusively, other neurons contribute to both of these cognitive operations. Such cognitive multitasking represents an efficient way of encoding and distinguishing between different executive processes within a neural network of fixed resources.

Decision-theoretic saliency: computational principles, biological plausibility and implications for neurophysiology and psychophysics

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A decision-theoretic formulation of visual saliency, first proposed for top-down processing (object recognition) in (Gao & Vasconcelos, 2005) is extended to the problem of bottom-up saliency. Under this formulation, optimality is defined in the minimum probability of error sense, under a constraint of computational parsimony. The saliency of the visual features at a given location of the visual field is defined as the power of those features to discriminate between the stimulus at the location and a null hypotheses. For bottom-up saliency, this is the set of visual features that surround the location under consideration. Discrimination is defined in an information-theoretic sense and the optimal saliency detector derived for a class of stimuli that complies with known statistical properties of natural images.

It is shown that the optimal detector consists of what is usually referred to as the standard architecture of V1 (Carandini, Demb, Mante, Tolhurst, Dan, Olshausen, et al., 2005): a cascade of linear filtering, divisive normalization, rectification and spatial pooling. The optimal detector is also shown to replicate the fundamental properties of the psychophysics of saliency (Treisman & Gelade, 1980): stimulus pop-out, saliency asymmetries for stimulus presence vs. absence, disregard of feature conjunctions, and Weber’s law. Finally, it is shown that the optimal saliency architecture can be applied to the solution of generic inference problems. In particular, for the class stimuli studied, it performs the three fundamental operations of statistical inference: assessment of probabilities, implementation of Bayes decision rule, and feature selection.

Acknowledgments
This research was supported by NSF Career award IIS-0448609, NSF award IIS-0534985, and a gift from Google Inc.

References


Spatial Attention in Early Vision for the Perception of Border Ownership

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Visual attention enhances our perception, even alters the perception of figures as we often see in ambiguous figures. We investigated computationally the role of early vision for the attentional modulation of the perception of direction-of-figure (DOF). Spatial attention alters local contrast gain in early vision, thus apparent local contrast will be modulated. If the local contrast is a basis for the determination of border-ownership (BO) that tells on which side of a contour owns the border [2], BO will be modulated based on the local contrast that is altered by the attention. If the effect of attention is significant, the activity of BO-selective neurons will be facilitated/suppressed so that the DOF will be switched.

The model consists of three modules, V1, V2 and Parietal (PP) modules, as illustrated in Fig.1. Top-down and bottom-up pathways link mutually these modules, except for PP to V2. In the V1 module, local contrast is extracted, and spatial attention modulates the contrast gain. The V2 module determines the BO based on the modulated contrast [2]. Because a wide variety of BO selectivity has reported in physiology [1], we implemented ten types of BO cells. The PP module encodes spatial location and facilitates the processing around the attended location. Note that spatial attention does not directly affect BO-selective cells in V2 module.

We carried out simulations of the model with a variety of stimuli, in order to test quantitatively the characteristics of the attentional modulation. Specifically, we investigated whether our model realizes the switch of DOF by altering the location of attention. For example, we tested the model with ambiguous block-figures as illustrated in Fig.2. When we applied attention to one side (e.g. right), the model determined the white blocks as figure. When the attention side was reversed (to the left), the DOF was flipped to the black blocks. The magnitude of modulation of DOF depended on each block-figure. We carried out psychophysical experiments to test whether such phenomena are observed with the same stimuli. The results of psychophysics show a good agreement with the model. These results suggest that covert spatial attention is a crucial factor for the modulation of DOF, and that gain control in early vision plays an important role for the attentional modulation.

References
Neural Circuits for Attending to Salient Proto-Objects

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Attention as a selective gating mechanism is often compared to a spotlight [1], enhancing visual processing in the attended (“illuminated”) region. In a modified version, the size of the attended region can be adjusted, making attention similar to a zoom lens [2]. Neither of these theories considers the shape and extent of the attended object. This may seem natural, since commonly attention is believed to act before objects are recognized. However, experimental evidence suggests that attention can be tied to objects, object parts, or groups of objects in a variety of experimental conditions [3]. How can we attend to objects before we recognize them? In his coherence theory of visual cognition Rensink described proto-objects as volatile units of visual information that can be bound into a coherent and stable object when accessed by focused attention [4]. I present a biologically plausible computer model of forming and attending to proto-objects in natural scenes as a possible solution to the problem of attending to objects before they are recognized [5].

The model operations consist of two main steps. First, in a feed-forward processing stream, feature maps for center-surround contrasts in simple features are combined into a saliency map, similar to the bottom-up attention model by Itti and Koch [6]. Winner-take-all competition in the saliency map results in spatial attention to be focused at one particular location. Second, in a feedback stream, visual information at this particular location is examined, the feature map contributing most to the saliency at this location is identified, and the shape of a proto-object is determined from a contiguous region of high activity in this feature map.

In my presentation I will put special emphasis on two key operations that are not obviously biologically realistic: an argmax operation for identifying the feature maps with the strongest contribution to the saliency of the attended location, and an operation for spreading activity over the contiguous region in the respective feature map. I present simulations of these key operations with neural networks, underlining the biological plausibility of the proposed model. Finally, I will show examples for applying the model to locating proto-objects in cluttered natural scenes. All code is publically available in a Matlab toolbox at: http://www.saliencytoolbox.net.

Acknowledgments

Parts of this work originated from my Ph.D. work with Christof Koch at Caltech. Funding was provided by a Beckman Postdoctoral Fellowship.

References

Selective attention integrates sparse and population codes

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How visual information is represented in the brain is the crucial question that drives most research in the field, and answering it will mean significant theoretical and practical advances in the understanding of the brain. Proponents of sparse representations suggest that highly selective, specialized neurons, introduced as cardinal cells by Barlow [1], explicitly code each percept. Energy minimization and information theoretic arguments have been used to justify relatively sparse representations. The main problem with this solution is the combinatorial explosion in the number of units needed to represent all the different possible stimuli. At the same time, one distinct advantage of sparse codes is their capacity to encode multiple stimuli in parallel. Others have suggested distributed/population codes [2]. While these representations have high encoding capacity, they suffer from the source separation problem, not allowing any significant degree of parallelism. Interestingly, there is significant experimental evidence for both representations in the primate brain, and the brain exhibits behavior consistent with both representations under different conditions.

One characteristic of vision is that not all stimuli in the visual field can and need to be represented at the same time to a high degree of accuracy [3]. This implies that some selection needs to be made, constrained by some requirements: important stimuli need to be detected as fast as possible, multiple important stimuli must be represented simultaneously, and non-important stimuli can wait, or can even be ignored. The fact that these requirements and their time course match those of visual attention strongly indicates that attention forms the glue between a sparse, fast, and parallel initial representation that supports object detection and a slow, serial, and detailed representations needed for full recognition. Taking cues from behavioral and physiological studies, we propose that the initial representation is sparse, corresponding to the categoric level, that can be represented sparsely due to the fact that the number of biologically relevant categories is very limited. The Selective Tuning (ST) model of (object based) visual attention [4] can be used to recover the spatial location and extent of the visual information that has contributed to a categoric decision. This allows for the selective detailed processing of this information at the expense of other stimuli present in the image. The feedback and selective processing create the detailed population code corresponding to the attended stimulus. We suggest and demonstrate a possible binding mechanism by which this is accomplished in the context of ST, and show how this solution can account for existing experimental results. We present a number of predictions of this model and suggest experiments to validate them.

References


Disruption of Balanced Cortical Inhibition by Acoustic Trauma

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Sensory deafferentation results in rapid shifts in the receptive fields of cortical neurons, but the synaptic mechanisms underlying this plasticity remain unknown. The rapidity of these changes has led to the suggestion that subthreshold inputs may be unmasked by a selective loss of inhibition. We used in vivo whole cell recordings to directly measure tone-evoked excitatory and inhibitory synaptic inputs in auditory cortical neurons before and after acoustic trauma. Here we report that acute acoustic trauma disrupted the balance of excitation and inhibition by selectively increasing and reducing the strength of inhibition at different positions within the receptive field. These changes led to an expansion of receptive fields and a disruption of temporal precision. These results suggest that the synaptic mechanisms underlying cortical receptive field shifts include changes within the auditory cortex as well as at subcortical levels. These effects, which occurred for sounds of comparable intensity to those delivered by an iPod at maximum volume, may help to explain how noise-induced hearing loss can result in the phantom ringing in the ears known as tinnitus.
Differences in subthreshold oscillations of stellate cells map to differences in periodicity of grid cells

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As a rat moves through an environment, neurons in layer II of medial entorhinal cortex (mEC) fire at regular repeating intervals arranged in a hexagonal grid pattern. The periodicity of the grid changes along the dorsal to ventral axis of mEC, with smaller periodic distances between grid fields in dorsal mEC and larger periodic distances between grid fields in ventral mEC. Computational models suggest that the difference in grid cell periodicity could depend on changes in intrinsic oscillations along the dorsal to ventral axis of EC\textsuperscript{1,2}. Using in vitro, whole cell patch clamp techniques, we recorded from 57 stellate cells in layer II mEC and found a difference in frequency of subthreshold oscillations along the dorsal to ventral axis. The mean frequency of subthreshold oscillations in dorsal cells (3.8 – 4.9 mm from the dorsal surface of the brain) was significantly larger than the mean frequency of subthreshold oscillation in ventral cells (5.0-7.1 mm from the dorsal surface of the brain) at an approximate membrane potential voltage of \(-50\) mV (Dorsal = 6.42 ± .401, n = 28; Ventral = 4.23 ± .32, n = 25; \(p < .001\)) and \(-45\) mV (Dorsal = 7.18 ± .50, n = 14; Ventral = 4.88 ± .59, n = 7; \(p < .01\)) as determined by an autocorrelation analysis. Plotting subthreshold oscillation frequency relative to the cells location from the dorsal surface of the brain clearly indicates that the frequency of subthreshold oscillations is larger in more dorsal portions of entorhinal cortex and smaller in more ventral portions of entorhinal cortex (-50 mV: \(r = .48, Slope = -1.26\); at -45 mV: \(r = .60, Slope = -2.48\)). The rate of change of frequency with anatomical position has slopes at -50 mV and -45 mV that have rates of change that straddle the rate of change for the distance between grid fields relative to anatomical position. These data support the explicit prediction by Burgess and O’Keefe\textsuperscript{1}, based on their computational model of grid cell formation, that the difference in spatial frequency of grid cell firing fields would result from differences in temporal frequency of intrinsic subthreshold oscillations of individual entorhinal neurons. Simulations of the Burgess and O’Keefe model demonstrate that a difference in the baseline temporal frequency of somatic oscillations result in a difference in spatial frequency of grid fields (Figure A).

A. High frequency (8 Hz) Low frequency (4 Hz)

Acknowledgments
Research supported by NIMH MH60013, Silvio O. Conte Center grant NIMH MH71702 and NIDA DA16454 (part of the CRCNS program).

References
Prediction and validation of a novel allosteric kinetics of NMDARs as a spike-timing detector

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Spike-timing-dependent synaptic plasticity (STDP), which depends on the relative timing of pre- and postsynaptic spiking, plays an important role in neural development and information storage. However, the mechanisms by which spike-timing information is encoded into STDP remains unclear. Here we show that a novel allosteric kinetics of N-methyl-D-aspartate receptors (NMDARs) codes spike-timing information into STDP (Figure). We developed a biophysical model of STDP, and found a requirement of slow and rapid suppression of NMDARs by Ca²⁺-calmodulin with pre- → post- and post- → pre-spiking, respectively, which led us to predict an allosteric kinetics of NMDARs during induction of synaptic plasticity. We experimentally validated the allosteric kinetics by examining peak-amplitudes and time of NMDAR-mediated EPSPs [1]. The allosteric kinetics of NMDARs was also experimentally valid for synaptic plasticity induced by more complex spike trains [2]. Simplification of the model revealed that intracellular Ca²⁺ concentration, at the time when glutamate binds to NMDAR, is the dominant spike-timing information carrier. These findings demonstrate that the simple allosteric kinetics of NMDARs governs the coding of complex spike-timing information into long-term changes in synaptic strength, which may restructure neural circuits and embed experiences into the brain.

Figure: Prediction and validation of the novel allosteric kinetics of NMDARs.

The conventional no-allosteric kinetics of NMDARs, with which the STDP model failed to induce LTD in STDP (left). We found a requirement of the distinct suppression of NMDARs in a spike-timing-dependent manner for STDP, which led us to predict the allosteric kinetics of NMDARs, with which the STDP was induced (right). We experimentally validated the allosteric kinetics of NMDARs by NMDAR-EPSP and spike-triplets STDP.

Acknowledgments
We thank Mitsuo Kawato (ATR, Japan) for helpful discussions.

References
Model-based smoothing of noisy, intermittent biophysical signals

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Noise is an omnipresent issue that is often handled suboptimally. For example, noise is an issue in voltage-sensitive imaging – even the best dyes achieve signal-to-noise ratios of no more than \(\sim 1 - 6\%\). Averaging noise out is not always possible and sometimes not even desirable. Missing data are often burdensome too: in voltage dye experiments, the laser has to be moved between sites of interest and thus the data is not acquired simultaneously, leading to gaps in the data. Despite advances, this problem becomes more prominent the more sites one attempts to record from. More generally, we might even be interested in a variable that has not been observed directly at all, such as the voltage in a Ca\textsuperscript{++} imaging experiment. Principled methods to filter out noise, to interpolate between data points and to infer unobserved variables could substantially complement advances in data acquisition methodology.

Here we show how, when time series recordings of a dynamical system (e.g. the voltage of a cell) are made, knowledge of the dynamical system can be used to both filter and interpolate between the measurements, providing a principled alternative to heuristics such as temporal smoothing or low-pass filtering. Neural dynamics are usually specified as Markov chains. If these dynamics are hidden (due to noisy or indirect measurements), the task of recovering the distribution over the true underlying state evolution of the neuron over time is equivalent to inference in nonlinear state space models. These models, together with their discrete analogues such as intermittent Kalman filters and Hidden Markov Models have been analysed extensively and are very well understood. If the hidden variables do indeed evolve in a Markovian manner (as is often the case), a number of algorithms from the machine learning literature allow efficient sampling, despite the huge size of the state space.

We find that the combination of a nonlinear Gaussian state space model with Gaussian observation noise and a forward-backward formulation of a particle filter allows us to recover the true voltage of a Fitzhugh-Nagumo or a Hodgkin-Huxley spiking model very well at low signal-to-noise levels that qualitatively match those encountered in voltage imaging experiments. It is possible to formulate dynamical models of other, entirely unobserved variables (such as the voltage in a Ca\textsuperscript{++} imaging experiment) and apply the same techniques. The probabilistic form of this approach also naturally allows combination of measurements from different sources, such as voltage and Ca\textsuperscript{++} imaging, done simultaneously.

Finally, we relax the assumption that the underlying kinetic model of the cell is entirely known to the case in which the true channel densities are unknown. The above procedure then becomes the E-step of expectation-maximisation, while the M-step reduces to a simple constrained linear regression.
Bayesian sampling techniques to combine physiological data with prior knowledge
Beau Cronin, James Schummers & Konrad Kording

Experiments in sensory electrophysiology typically aim to characterize the relationship between stimuli and neuronal responses. A sequence of neuronal responses, for example spikes, is recorded in reaction to a set of stimuli. This neuronal activity exhibits systematic variation between repetitions of the same stimulus, and it is therefore crucial that models of spiking behavior represent the probabilistic nature of the stimulus – response relationship. The task of data analysis in this setting is to convert the recorded data into a statement about the function of the sensory system. Two kinds of models are typically used. The first kind of model specifies the properties of the neuron with a large number of parameters, for example a space-time receptive field (STRF). This approach typically leads to large error margins about the parameters, but may in theory yield good fits to the firing responses. Alternatively, a low-dimensional description of the response properties is chosen. For example, the properties of orientation-selective neurons in the primary visual cortex are often quantified by a Gaussian tuning curve. This approach, because of the small number of parameters, typically leads to small error margins about their values, but may miss important properties of the response characteristics that can not be represented by the low dimensional model. Whichever kind of model is chosen, the main challenge of data analysis is characterizing the stimulus-response relationship to a high degree of precision, given only a limited amount of recording data.

Fortunately, data analysis does not take place in the absence of prior knowledge: decades of research in sensory systems provide two important kinds of constraints which are relevant when analyzing data. Firstly, we may have a qualitative understanding of the overall form of a response. For example we may know that at any delay relative to a stimulus presentation, the orientation response of simple cells in the primary visual cortex can be described by a circular Gaussian tuning curve. Secondly, we may have quantitative knowledge about the properties of neurons, for example the finding that the tuning properties of these cells change smoothly over the time-course of the response. This knowledge implies that a receptive field that changes smoothly is more likely than a receptive field that changes abruptly. Many neuroscientists make regular use of such pieces of knowledge in their data-analysis. Here we develop an approach that makes explicit this combination of new experimental data with known neuronal properties. This Bayesian framework not only considers the best parameter estimate, but also all potential alternative interpretations of the data. This approach leads to superior data analysis, while at the same time allowing electrophysiologists to make direct use of the intuitions obtained from extensive laboratory experience.

As some of the necessary computations are not analytically tractable, we apply Markov Chain Monte Carlo sampling methods to obtain numerical solutions. Because of the ability to include simple intuitive models as prior knowledge, the method leads to better estimates of the response properties with less data. It outperforms classical fitting methods because it considers each possible stimulus—response relationship as a potential explanation of the data. It thus also provides a direct quantification of error margins, given the experimental data. Applications to simulated data as well as data from an experiment recording neuronal responses in cat area 17 demonstrate the strengths of this Bayesian approach.
Learning Horizontal Connections from the Statistics of Natural Images

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A common assumption in neuroscience is that the visual system is adapted to the statistics of natural images [1]. Hence, by building probabilistic models of natural images, we can gain insight into how visual information is represented and processed in the visual cortex. For example, it has been shown that learning a sparse code for images predicts the shapes of simple cell receptive fields in V1 [4].

Here we develop a model of lateral connections in V1 that is based on the statistical dependencies among model V1 units in response to natural images. This work is related to [2, 4, 5]. We propose the following generative model: \( I = \Phi a + \nu \), where \( I \in \mathbb{R}^n \) is an image patch, \( \Phi \in \mathbb{R}^{n \times m} \) is an overcomplete transform, and \( \nu \sim \mathcal{N}(0, \epsilon^2 I_n) \) is Gaussian noise. We describe the unit coefficients \( a \in \mathbb{R}^m \) as a Gaussian scale mixture \( a = h \odot u \) (\( \odot \) is the element-wise product), where \( u \in \mathbb{R}^m \) has a Gaussian distribution \( \mathcal{N}(0, \Lambda) \) with diagonal covariance matrix \( \Lambda \), and \( h \in \{0, 1\}^m \) has a Boltzmann-Gibbs distribution \( p(h) = \frac{1}{Z} e^{-\frac{1}{2} h^T Th - b^T h} \). The statistical dependencies among units are modeled by the coupling matrix \( T \), which corresponds to the strength of horizontal connections, and \( b \) is a bias term that describes the sparsity of a given unit. This model does not make any assumption about which linear code (i.e. \( \Phi \)) should be used, and about which units should exhibit dependencies.

We learn the parameters of the model \( (\Phi, \Lambda, T, b) \) using a variational method that exploits the sparsity of optimal codes for natural images. As in [4], the learned basis \( \Phi \) is well described by Gabor filters. By analyzing the weights of \( T \), we find evidence for excitatory connections among Gabor filters at similar positions and orientations, as well as cross-orientation inhibition, which have been previously reported in primary visual cortex physiology.

Acknowledgments
This work was supported by NGA grant MCA 015894-UCB and NSF grant IIS-06-25223.

References
Higher Order Effects by Shunting Inhibition in Reduction of Conductance-Based Network Models to Rate Models
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Rate models have been widely used for understanding the collective behavior of large neuronal systems. However, the quantitative discussion of rate models has been limited because the biological interpretation of the parameters in rate models is unclear. Shriki \textit{et al.} derived a precise mapping between the parameters of the rate equations and those of biologically realistic conductance-based network models in condition that the network activity is not highly synchronized \cite{1}. Although the reduction at the single neuron level is easy, interaction terms make the reduction difficult. They solved the difficulty by including interaction terms in the leak current term. As a result, multi-neuron systems of the conductance-based model are transformed into the single conductance-based model and its leak conductance effectively increases by this operation. Therefore we need to evaluate how this effective increase of the leak conductance affects the \(f\)\(-\)\(I\) curve of the conductance model. This is equivalent to evaluating effects on firing rates by shunting inhibition. Shriki \textit{et al.} assumed that shunting inhibition modulates firing rates in a purely subtractive manner based on the model study \cite{2} and experimental evidence \cite{3}. More specifically, they made an assumption that the gain of the \(f\)\(-\)\(I\) curve is independent of leak conductance and the firing threshold of the \(f\)\(-\)\(I\) curve increases linearly with leak conductance. Because it has been shown that shunting inhibition affects the \(f\)\(-\)\(I\) curve subtractively in an integrate-and-fire model \cite{2}, their assumption means that the behavior of the \(f\)\(-\)\(I\) curve in the conductance-based model is approximated to that of an integrate-and-fire model.

However, we numerically found that the gain and the threshold of the \(f\)\(-\)\(I\) curve have second order dependence on leak conductance (See figure 1). Although this higher order effects deviated from subtractive effects by shunting inhibition has not been taken seriously at the single neuron level, we show that it is very important to take it into account in order to predict the network activity precisely over a broad range of leak conductance changes. Taking this higher order effects into consideration, conductance-based network models with second order interaction are reduced to a network of rate equations with higher order interaction, which has not been considered in conventional rate models. That means the conductance-based model has higher calculation capability because of the existence of active ionic channels than an integrate-and-fire model and a conventional rate model in terms of rate coding, too. We apply our reduction method to the conductance-based network models with Mexican-hat type interaction and Hebbian connection. And we analyze the reduced rate models by a statistical mechanics approach.

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{figure1.png}
\caption{Effects by shunting inhibition on gain and firing threshold of the \(f\)\(-\)\(I\) curve. Circles are gain and firing threshold of the conductance-based model for different values of leak conductance. Solid lines are quadratic function fitted to data.}
\end{figure}

Acknowledgments
Supported by JSPS (Nos. 14084212, 16500093, and 1770415).

References
Learning in a Generative Model with Competitive Combination Is Approximated by (Soft-)Winner-Take-All Networks

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In recent years, algorithms such as independent components analysis (ICA) [1] and sparse coding (SC) [2] have been used to describe the statistics of the natural environment, and the components extracted by these methods have been linked to sensory neuronal response properties. Stated in the language of probabilistic generative models (see e.g. [3]), ICA and SC describe sensory data as a linear superposition of learnt components. For many types of data, including images, this assumed linear cooperation between generative causes is unrealistic. Alternative, more competitive, generative models have also been proposed: in [4] hidden causes are combined by noisy-or, and in [5] a still more competitive scheme is described. Here, we formulate an extreme case of competition, in which the strongest generative input to an observed node alone determines its value. Thus, where ICA and SC use a sum, we use a max. Such a rule has the property of selecting, for each observed node, a single generative cause to determine that node’s value. In the case of image data, combination by occlusion shares this selective property.

Whilst exact maximum-likelihood learning of the parameters of such a model is intractable, we show that efficient approximations to expectation-maximisation (EM) can be found in the case of sparsely active hidden sources. One of these approximations is shown to be equivalent to a neural network model with a generalised soft-max activation function, and a simple Hebbian Δ-rule with divisive weight normalisation. Thus, we show that learning in winner-take-all (WTA) type networks, e.g. [6-9], may be interpreted as approximate maximisation of a data likelihood. In the limit of very sparse input, we recover the classical soft-max function, which is commonly used for clustering. This observation may help to explain how such WTA networks can successfully resolve components as well as determine clusters in data where appropriate [6-9].

Using the benchmark “bars test” [10], we numerically verify the accuracy of the approximate update rules and the corresponding neural network. These experiments show that the generative approach is competitive with results obtained by other methods.

Acknowledgments
This work was funded by the Gatsby Charitable Foundation.

References

Evoked brain responses are mediated by feedback loops

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Neuronal responses to stimuli, measured electrophysiologically, unfold over several hundred milliseconds. Typically, they show characteristic waveforms with early and late components. It is thought that early or exogenous components reflect a perturbation of neuronal dynamics by sensory inputs – bottom-up processing. Conversely, later, endogenous components have been ascribed to recurrent dynamics among hierarchically disposed cortical processing levels – top-down effects. However, no direct evidence has been provided that this is the case. Here we show that evoked brain responses result from a feedback loop and late components of event-related responses are mediated by backward connections.

We evaluated dynamic causal modelling (DCM) of mismatch responses, elicited in an oddball paradigm using electroencephalography (128 EEG scalp electrodes). In DCM, the brain is regarded as a deterministic nonlinear dynamic system that is subject to inputs and produces outputs. The aim of DCM is to model interactions among cortical regions, estimate and make inferences about its coupling and how this coupling is influenced experimentally [1]. Sources of cortical activity were modelled as equivalent current dipoles (ECD) [2]. Responses to deviant tones were explained by coupling changes among a network of sources which was motivated by a predictive coding framework [3]. We used Bayesian inversion of DCM to estimate the parameters of the models and Bayesian model selection to select the best of two models: with or without backward connections.

Bayesian model selection for models with and without backward connections provided very strong evidence that backward connections are necessary to explain late components (> 220 ms post-stimulus). Furthermore, the conditional contribution of backward connections to evoked responses at the source level becomes more important later in peristimulus time.

Crucially, these results link a generic feature of brain responses to changes in its sensorium and a key architectural component of functional anatomy; namely backward connections that are necessary for recurrent or re-entrant dynamics. Recurrent interactions among levels of cortical hierarchies are the theoretical cornerstone of most modern theories of perceptual inference and learning.

Acknowledgments
This work was funded by Wellcome Trust (JMK, SJK and KJF) and the Portuguese Foundation for Science and Technology (MIG).

References
Time scale dependence of neuronal correlations

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Correlated activity has been observed at a variety of signal levels (e.g. spike counts, membrane potentials, local field potentials, EEG, fMRI BOLD) in different areas of the brain. Many of these signals can be considered as filtered (superpositions of) spike trains. It is largely unknown how the spike train correlation structure is altered by this filtering and what the consequences for the dynamics of the system and for the interpretation of measured correlations are. In this study we focus on signals derived from spike signals by linear filtering. We particularly consider spike correlations caused by overlapping presynaptic neuron populations (common input correlations). We demonstrate that statistical second-order measures like variances, covariances and correlation coefficients generally exhibit a complex dependence a) on the statistics of the presynaptic spike trains and b) on the filter properties (e.g. time constants; see Fig.1A). We propose that these effects may be used in the brain to modulate the interaction strength between neurons or neuron populations. Furthermore, we show that for a large class of spike processes the high frequency coherences reflect the strength of common input. In our network models this allows a reliable estimation of the network connectivity from intracellular recordings of pairs of neurons (Fig.1B).

\textbf{Fig. 1:} Dependence of correlation coefficients (A) and average high frequency coherences (B) of input spike counts (circles, binsize 0.1 ms), synaptic currents (squares, time constant 0.5 ms), membrane potentials (diamonds, time constant 10 ms) and output spike counts (stars, binsize 0.1 ms) on the frequency $f_0$ of a global oscillation in a random network of excitatory and inhibitory model neurons (network connectivity 0.1). Plots illustrate numerical (symbols) and analytical results (gray curves).

Partially funded by BMBF-01GQ0420, BMBF-DIP F1.2 and GIF.
Analysis of a self-organizing system for visual correspondence

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Various aspects of brain structure and function have been modelled as self-organizing systems, using coupled nonlinear differential equations. Two typical examples are the ontogenesis of retinotopy (the ordered projection between retina and tectum) and the establishment of visual correspondence (projections that link corresponding points in two visual patterns) which is important for stereo matching, motion estimation and object recognition. Both concern the formation of connectivity patterns between two domains, their major difference being that retinotopy is spontaneous while correspondence is driven by external stimuli and the similarities between their features.

Spontaneous pattern formation is usually analyzed by methods developed for Turing instability [5], synergetics [1], and the like. However, computer simulation remains the method of validation of driven pattern formation systems. Feature similarities between visual patterns appear in the dynamics as a constant term [3], or a linear coefficient [4], which makes analysis difficult if not impossible. Methods to formulate and analyze driven pattern formation need to be developed.

We formulate and analyze a visual correspondence system by introducing feature similarities to a retinotopy formulation developed earlier [2]. That analytical treatment showed how a one-to-one retinotopic projection develops from an undifferentiated initial state. We present a method to incorporate feature similarity into the dynamics. Using numerical methods and addressing 1D patterns with shift and scale variations, we study how the system converges to the desired state, by following the analytical treatment in [2]: normal mode decomposition of the linearized system, and amplitude equations of unstable modes and their interactions.

Acknowledgements

Supported by EU project FP6-2005-015803 “Daisy”, the Hertie Foundation and the Volkswagen Foundation.

References


Learning Sparse and Invariant Features Hierarchies

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Understanding how the visual cortex builds invariant representations is one of the most challenging problems in visual neuroscience. The feed-forward, multi-stage Hubel and Wiesel architecture [1, 2, 3, 4, 5] stacks multiple levels of alternating layers of simple cells that perform feature extraction, and complex cells that pool together features of a given type within a local receptive field. These computational models have been successfully applied to handwriting recognition [1, 2], and generic object recognition [4, 5]. Learning features in existing models consists in handcrafting the first layers and training the upper layers by recording templates from the training set, which leads to inefficient representations [4, 5], or in training the entire architecture supervised, which requires large training sets [2, 3]. We propose a fully unsupervised algorithm for learning sparse and locally invariant features at all levels. Each simple-cell layer is composed of multiple convolution filters followed by a winner-take-all competition within a local area, and a sigmoid non-linearity. For training, each simple-cell layer is coupled with a feedback layer whose role is to reconstruct the input of the simple-cell layer from its output. These coupled layers are trained simultaneously to minimize the average reconstruction error. The output of a simple-cell layer can be seen as a sparse overcomplete representation of its input. The complex cells add the simple cell activities of one filter within the area over which the winner-take-all operation is performed, yielding representations that are invariant to small displacements of the input stimulus. The training procedure is similar to [6], but the local winner-take-all competition ensures that the representation is spatially sparse (and the complex-cell representation locally invariant). The next stage of simple-cell and complex-cell layers is trained in an identical fashion on the outputs of the first layer of complex cells [7], resulting in higher level, more invariant representations, that are then fed to a supervised classifier. Such a procedure yields 0.64% error on MNIST dataset (handwritten digits), and 54% average recognition rate on the Caltech-101 dataset (101 object categories, 30 training samples per category), demonstrating good performance even with few labeled training samples.

Figure (a) Architecture for recognition. (b) Some learned filters in the 1st and 2nd stages of simple-cell layers.

References
Dynamic causal modelling of fMRI with neural mass models

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INTRODUCTION
The aim of this work was to endow dynamic causal models (DCM) for fMRI time series with a greater biological realism. DCM is a natural extension of the convolution models used in the standard analysis of fMRI. DCM models neuronal dynamics in each region and the long-range interactions between different regions. We use a Bayesian inversion scheme to estimate the posterior distributions of the generating parameters. Currently, causal models for fMRI consider only one neuronal state per region. In this work we adopt a more biologically constrained and plausible model, using multiple neuronal sources (subpopulations) per region. Critically, this allows us to place positivity constraints on the connectivity such that the model conforms to the organisation of real cortical hierarchies, whose extrinsic connections are excitatory (glutamatergic). Consequently, we can also model changes in both extrinsic and intrinsic connectivity.

METHODS
Usually, DCMs for fMRI are based upon a bilinear approximation to neuronal dynamics with one state per region. In this work we extend this model to cover two states per region. These states model the activity of an inhibitory and excitatory subpopulation. This has a number of key advantages. First, we can relax the shrinkage priors used to enforce stability in single-state DCMs because the interaction of excitatory-inhibitory pairs confers dynamical stability on the system. Second, we can model both extrinsic and intrinsic connections. Third, we can enforce positivity constraints on the extrinsic connections (i.e., influences of excitatory sub-populations over regions). Finally, this reparameterisation enables one to model the effect of context or experimental changes, on the coupling as a proportional increase or decrease in connection strength (c.f., the additive bilinear effects used previously). The model and mathematical forms are provided in Figure 1.

EMPIRICAL DEMONSTRATION
We used this new model to assess the site of attention modulation during visual motion processing in an fMRI paradigm previously reported by Buchel and Friston. For the purpose of this experiment we considered three experimental inputs: A ‘photic stimulation’ variable indicates when dots are on a screen, the ‘motion’ variable indicates that the dots are moving and the ‘attention’ variable indicates that the subject is attending to possible velocity changes. We used Bayesian model selection to adjudicate between different two-state and one-state models.

CONCLUSION
Our results indicate that one can estimate area-intrinsic connection strengths using fMRI. On real data, we find that the two-state DCM is a better model than the standard single state DCM. The present analysis demonstrates the usefulness of adopting generative models for fMRI time series that are informed by anatomical and physiological constraints.
Multilinear neural encoding models capture nonlinearities and contextual influences in cortical responses

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We describe a class of neural encoding models that is expressed in multilinear form. Neural encoding models typically predict a neuron’s firing rate from a time-varying stimulus. The parameters of these models reflect the encoding properties of the respective neurons, which in turn may shed light on the function of the corresponding brain area.

We use multilinear methods to extend traditional neural encoding models in various directions: the linear encoding model is extended to include an “input nonlinearity” (a nonlinear transformation of stimulus value applied before temporal filtering [1]); such a nonlinearity is also added to the LNP model [2], resulting in the “NLNP model”. In the auditory domain, when STRF models [3] are extended with the input nonlinearity, the resulting structure allows for the identification of new inseparabilities in sound processing (such as inseparabilities in time and sound level) beyond the traditionally studied time-frequency inseparability.

A further multilinear extension to the auditory STRF model results in the “context model”, an easily interpretable model that includes context effects such as cross-frequency suppression and short-term stimulus-specific adaptation.

Due to their multilinear structure, these models benefit from a sound alternating-least-squares estimation procedure. We place the models in a probabilistic framework, so that the estimation procedure can be extended to include regularization methods, and methods for estimating error bars around the estimated parameters. Such error bars are important when interpreting the models and relating them to neural function.

Model fits on rodent somatosensory and auditory cortex data illustrate the interpretability and utility of the multilinear model. In somatosensory cortical neurons, fits of the simplest models show a bowl-shaped input nonlinearity, invariant to the direction of whisker displacement. More complex versions of the model augment this picture through the inclusion of a slower, direction-sensitive response. In auditory cortical neurons, the input nonlinearity models have an improved predictive power over STRF models. They reveal inseparabilities in time and sound level, and in frequency and sound level. The context model shows a strong dependency of firing rate on the context of a sound, i.e. on nearby frequencies and recent stimulus history; including these stimulus-stimulus interactions results in a substantial increase in predictive power. The multilinear models provide a powerful, rich and compact description of dynamic neuronal responses.

References


Nonlinear dynamics underlying slow oscillation in dopamine neurons of the ventral tegmental area

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Myriad theoretical and experimental studies have shed light on midbrain dopamine (DA) neurons as neural basis of reward, learning, and goal-directed behavior [1]. Particularly, the burst firing of DA neurons is thought to be neural coding of prediction error about future reward. The traditional criteria for burst firing were 80/160 ms; the initiation of a burst was identified when the interspike interval (ISI) of two consecutive spikes<80ms and the burst was terminated when the ISI>160ms. It was reported, however, that the criteria is not sufficient for intact description of firing patterns in DA neurons of the ventral tegmental area (VTA) using spectral analysis and single-unit recording [2]. In addition, slow oscillation (SO), rather than burst firing, was suggested to be a major firing patterns of VTA DA neurons.

To examine whether the slow oscillation of DA neurons is an important information carrier about reward signal, we estimated the amount of information content within the ISI sequences of 206 VTA DA neurons using an information-theoretic measure, Approximate Entropy (ApEn). The ApEn can quantify the complexity or irregularity of a time series [3]. We compared ApEn values of two DA neuron groups which were classified based on the spectral analysis [2] (SO neuron if mean power of 0.5-1.5Hz was greater than mean power of 0-3Hz; non-SO neurons otherwise). We found that SO neurons had significantly higher ApEn values than non-SO neurons (p=0.005). This indicated that SO neurons exhibited more complex dynamics. Furthermore, surrogate data analysis revealed that SO neurons showed more well-defined nonlinear temporal structure compared to non-SO neurons.

We suggested that the slow oscillatory firing of DA neurons play a role in information processing in terms of reward and learning. The future studies will have to investigate the neural mechanism underlying SO generation and its functional role in goal-directed behavior possibly by computational modeling in both cellular level and neural network level.

Acknowledgments
This work was supported by the Korea Science and Engineering Foundation (KOSEF) grant funded by the Korea government (MOST) (No. M10644000028-06N4400-02810).

References
A biologically realistic model of statistical inference applied to random dot motion

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We propose a model of basic motion perception consisting of a hierarchical non-linear state space model (NSSM) developed within a variational Bayes (VB) framework. Each level of the hierarchy is a ‘cause’ that generates a prior distribution on the level below via a generative function.

The temporal dynamics and generative functions between layers of the hierarchy are implemented as neural networks with non-linear activation functions. Optimization of model parameters and causes proceed concurrently as a combination of fixed-point rules and Gauss-Newton decent. To make the optimization problem tractable, the standard mean-field and Laplace approximations are employed. The precise factoring used in the mean-field approximation is designed to meet a balance between tractability, neurological plausibility and modeling power. In this approach inference and learning proceed concurrently, in an online and unsupervised fashion.

Other work has produced similar implementations of NSSMs that have been successful in predicting low-dimensional temporal signals, but with highly restrictive assumptions on the form of the posterior distributions and with learning done in batches instead of online [2].

Competing work has relaxed many of these implementation assumptions and achieved prediction of high dimensional input but at the cost of discarding VB techniques in favor of inefficient discrete state-space methods [1]. Moreover, such techniques have been demonstrated only with pre-learned weights and simplistic statistical models.

Our model is primarily tested on realistic high-dimensional input generated by randomly moving dots over a detection grid. The results from a spiking neuron implementation of the model based on the Neural Engineering Framework (NEF) are compared directly to single cell recordings in random dot motion perception and decision-making tasks.

References
Event driven transitions between attractors in spiking networks

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Many complex cognitive tasks require the animals to go through several processing stages, each one representing a inner mental state which contains the information about past experiences, and the “instructions” to parse new events and to generate the proper motor response. Language in humans is one of the highest expression of the ability to generate these complex sequences of mental states. In [1] the authors propose a simplified network of Hopfield like neurons in which the inner mental states are represented by attractors of the neural dynamics, and external or internal events induce transitions between attractors. Furthermore they show that the observed diversity in the neural response (e.g. mixed selectivity), can be effectively harnessed to increase the number of transitions between attractors.

Here, by using a mean-field approach and simulations, we provide evidence that networks of leaky IF neurons can realize arbitrarily complex schemes of attractors and transitions. We show that the network can implement a simple task switch protocol, often used in psychophysics experiments, to test the ability of the system to respond to the same external stimulus with different motor actions, depending on the rule notified in effect. The Figure illustrates the network behavior during the presentation of the same event \(A\) associated to the left (L) and the right (R) movement depending on the active context (attractor 1 or 2). The above heterogeneity is implemented considering subpopulations reacting if an inner state of the network is active and an external event appears (see the last four populations in the middle panel). Transitions between the high firing rate states of the populations 1, 2, L and R, was possible only considering a hierarchy of connections, as observed in biology where close populations have a stronger connectivity with respect to the coupling between distant sets. Such feature allows the coexistence of distributed attractors also in more simplified network models [2].


Figure 1: A sequence of four inner mental states driven by the same external event \((A)\) when different contexts are active, as coded by the persistent activation of the subpopulations 1 and 2. A context switch is implemented providing a “not reward” signal \((N\text{Rew})\), as sketched in the top panel. The middle and bottom panel show respectively a rastergram of a subset of neurons and the instantaneous firing rates \((\nu_x)\) of the relevant subpopulations involved. Different colors code different subpopulations, labeled on the left of the raster plot. External events are presented during the gray strips. \(Rew\) stay for “reward”. The network contains 40000 excitatory and 16000 inhibitory IF neurons.
Optimality of active sensing
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Active sensing via exploratory actions is an important yet little-understood aspect of motor behavior. It includes eye movements, exploratory finger movements, whisker and ear movements, vocalizations used for echo-location, command signals sent to muscle spindles via gamma motoneurons. Such actions do not normally have direct consequences in terms of rewards or punishments. Instead they enhance the flow and quality of sensory information, and thereby contribute indirectly, by improving the feedback control of “regular” actions. This contribution can be substantial – as for example in driving, where the wrong pattern of eye movements can have grave consequences.

Our goal is to develop a computational theory of active sensing in the broader context of sensorimotor integration. We consider active sensing to be a special case of stochastic optimal control combined with Bayesian inference. This general framework is becoming the theoretical framework of choice for studying perception and action. A growing body of evidence supports the view that sensory systems integrate all sources of information in a statistically-optimal manner, and send the resulting estimates to motor systems, which apply feedback control laws optimized to yield the best possible performance.

Despite the mathematical coherence of this framework, the sensory and motor aspects of sensorimotor integration are often studied separately, resulting in a gap which prevents the theory from reaching its full potential. This is partly because the information processing which the theory calls for is often beyond the reach of existing algorithms, forcing researchers to over-simplify their problems. In particular, existing models of motor control assume that motor commands are generated on the basis of point estimates, and ignore the uncertainty associated with those estimates. In special circumstances – involving linear dynamics, Gaussian noise and quadratic performance criteria – the optimal way to act is indeed independent of estimation uncertainty. But in general uncertainty is likely to matter. We need formal models which make such effects explicit. Active sensing is an ideal candidate in that regard, because reducing uncertainty is the only purpose of exploratory actions.

We have developed two formal models in which optimal control laws for active sensing can be efficiently approximated and their predictions compared to experimental data. The first model is a model of eye-hand coordination in the context of manual tasks involving multiple objects. Key to the model is the fall-off of visual acuity with distance away from the fixation point. We represent this with state-dependent sensory noise. Different patterns of eye movements cause different patterns of uncertainty in the estimates of object positions, and thereby affect the accuracy of the concurrent hand movements. The model yields concrete predictions which are in close agreement with data from eye-hand coordination experiments. In these experiments we manipulated the visual feedback available to the subject, in ways suggested by the model, and observed changes in eye-hand coordination as predicted by the model.

The second model addresses the tradeoff between exploration and exploitation. It applies to experiments where hand movements are mapped to screen cursor movements via a well-defined but unknown to the subject mapping. Even though the subject has a simple task – to track a moving target on the screen – this task imposes conflicting demands on the hand movement system: it requires both tracking (exploitation) as well as probing and learning the unknown mapping (exploration). We represent the online learning process in innovations form, which allows us to transform the partially-observed system into a fully-observed system whose augmented state incorporates the uncertainty about the hand-cursor mapping. The solution to the resulting stochastic optimal control problem is a control law which incorporates both exploration and exploitation, and achieves an optimal tradeoff between the two. Although this tradeoff has received a lot of attention in Reinforcement Learning, it has previously been resolved heuristically.
Statistics of irregular bursting

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We study dynamical mechanisms and statistical properties of irregular bursting oscillations arising in a class of neuronal models of Hodgkin-Huxley type with and without noise. Specifically, we consider a phenomenological model of a square-wave bursting neuron in the regime close to the transition from tonic spiking to bursting. We identify two distinct mechanisms for irregular bursting oscillations. The first mechanism is based on chaotic spiking dynamics arising near the transition to bursting, while bursting oscillations generated by the second mechanism are induced by small random perturbations. For each case, we present a (randomly perturbed) Poincaré map and analyze statistical properties of the trajectories of the discrete system. Our mathematical analysis suggests that the number of spikes within one burst are distributed geometrically in each case. However, the parameters of the geometric distributions are determined by different factors depending on the underlying dynamical mechanism.

Acknowledgments
This is a joint work with Pawel Hitczenko (Drexel University). This work is supported by NSF grant IOB 0417624.

References
How coupling affects the reliability of driven theta neurons

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For a neuron or neural network, the question of reliability can be formulated as follows: if an external stimulus is applied multiple times, will it elicit essentially the same response each time \textit{independent of the state of the system} when the input is received? The answer is fundamental to the ability of the system to encode stimuli, such as incoming sensory signals, in a repeatable way. It also determines whether an ensemble of such systems would synchronize if they receive the signal as a common input.

The reliability of isolated cells has been explored extensively in both experiment and theory. For example, single neurons respond reliably to fixed current signals in laboratory experiments (e.g., Bryant and Segundo 1976, Mainen and Sejnowski 1995). Theoretical studies have shown that reliability is typical for many neuron models, and is always the case for phase models.

The reliability of \textit{networks} of coupled cells is far less well understood. Here, we take a first step toward understanding how input stimulus and network architecture interact to determine reliability. We focus on a 2-oscillator pulse-coupled network with the following structure:

\[ \varepsilon I(t) \sim (\theta_1 \rightarrow a_{fg} \rightarrow \theta_2) \]

and adopt the standard 'theta neuron' model that characterizes spiking cells near saddle-node bifurcations.

Our main findings are: 1. Single cells that are reliable in isolation can become highly unreliable when coupled, depending on input amplitude and coupling strengths. The figure below illustrates this contrast: different initial conditions are converge to the same response for the (reliable) feedforward network (left), but fail to converge for the (unreliable) network with feedback (right). 2. Chaotic dynamics with a particular statistical property, random SRB measures, are a signature of unreliability. Such measures are typically supported on lower-dimensional strange attractors. A physical and biological consequence is that that phase relationships in unreliable networks are highly structured. 3. Parameters at which the two-cell network is especially susceptible to producing unreliable dynamics coincide with the onset of 1:1 phase locking for the system with zero input. This leads to a geometric explanation for unreliable vs. reliable network dynamics.

We conclude by noting implications of our results for larger networks, for predictions for slice experiments, and for the encoding of stimuli by spiking neural networks.
Learning Complex Structures of Images Through Recursive Independent Component Analysis

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It has long been hypothesized that the functional role of perception is to capture the statistical structure of the sensory stimuli such that corresponding actions could be taken to maximize the chances of survival (see [1] for a brief review). Attneave [2] pointed out that such statistical structure was measured by the redundancy in the sensory inputs. Barlow [3] further hypothesized that for a neural system one possible way of capturing the statistical structure was to remove the redundancy in the sensory outputs. Linear implementations of this hypothesis, such as Independent Component Analysis (ICA), has been used to explain the functional role of simple cells in the primary visual cortex [4, 5].

However, since ICA is intrinsically a linear method, there are inevitably some structures that cannot be captured by a linear ICA. This is reflected in the fact that there is residual redundancy in the ICA outputs when it is applied on natural image patches [6]. Residual Redundancy Reduction studies how to capture the structures not captured by a linear ICA. In this work, we propose to apply another layer of ICA to reduce the residual redundancy. This was inspired by the idea that different areas of cortex share similar anatomical structures and likely use similar computational learning principles. Also, by doing so we transformed a new and hard problem into an easier and previously solved problem. We derived a nonlinear activation function between layers which allows the higher layer of ICA to work efficiently. As a result, we get to a hierarchial recognition model in which the higher layers capture more complicated structures of images by pooling the simple structures learned at the lower layer.

Acknowledgments
We thank Eric Wiewiora and other GURU members for helpful discussions.

References


Modeling Neural Spiking with Point Processes Nonparametrically: A Convex Optimization Approach

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Characterizing neural spiking activity as a function of environmental stimuli, and intrinsic effects such as a neuron’s own spiking history and concurrent ensemble activity is important in neuroscience. Such a characterization is complex and there is increasing need for a broad class of models to capture such details. Point process models have been shown to be very useful in characterizing neural spiking activity [1]. The likelihood of a point process \( \{N(t)\}_{t=0}^T \) is completely defined by its conditional intensity function

\[
\lambda(t|x_t) \triangleq \lim_{\Delta \to 0} \frac{P(N(t + \Delta) - N(t) = 1|x_t)}{\Delta}
\]

where \( x_t \) corresponds to previous spiking activity, \( \{N(\tau)\}_{\tau=0}^t \), as well as any latent environmental stimuli. Most point process models are parametric as they are often efficiently computable, the parameters may be related back to physiological and/or environmental factors, and they have nice asymptotic properties when \( \lambda(t|x_t) \) lies in the assumed parametric class [1]. However, if \( \lambda(t|x_t) \) does not lie in the assumed class, misleading inferences can arise. Nonparametric methods are attractive due to fewer assumptions, but very few efficient methods for estimating \( \lambda(t|x_t) \) are known. We propose a computationally efficient method for nonparametric maximum likelihood estimation when \( \lambda(t|x_t) \) is assumed to be Lipschitz continuous [2].

We are given neural spiking activity observations \( \{N_i\}_{i=1}^M \) once every \( \Delta = 1 \) ms that result from \( \{x_i\}_{i=1}^M \), known stimuli and the neuron’s own spiking history. \( \hat{\lambda}_i \) is the estimate of \( \lambda(t|x_t) \) at millisecond \( i \). We minimize the negative log likelihood of the point process subject to the Lipschitz continuity constraints:

\[
\min_{\lambda} \sum_{i=1}^M -N_i \log(\hat{\lambda}_i) - \hat{\lambda}_i \Delta
\]

\[
\text{s.t.} \quad \|\log(\hat{\lambda}_i) - \log(\hat{\lambda}_j)\|_\infty \leq K \|X_i - X_j\|_\infty, \quad i < j, \quad j = 1, \ldots, M
\]  

(1a)

(1b)

We show that (1a) is convex, as are the constraints in (1b); so (1) is a convex optimization problem and thus efficiently solvable. We develop an equivalent problem with separable [3, Sec. 3] structure in (1a) and linear structure in (1b) to represent its dual in closed form. Thus (1) can be solved using very efficient unconstrained methods, such as gradient descent. We apply our method to goldfish retinal ganglion neural data and compare results to inhomogeneous Poisson and inverse Gaussian parametric models. We assess goodness-of-fit via the time-rescaling theorem and measure model uncertainty via bootstrapping [4].

References


Input-Driven Dynamic Attractors

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In traditional models of attractor neural networks, such as the Hopfield, Boltzmann, and analog-digital ring network, inputs are available to the network either once or continuously. The intrinsic dynamics cause the network activity to converge to a “stable” state which can be a fixed point, a limit cycle, or a chaotic attractor. We suggest to incorporate the timing of inputs as a crucial parameter of the neural dynamics. This leads to a novel paradigm to study dynamic input-driven attractors in recurrent neural networks. In this paradigm the network accepts inputs periodically as opposed to initially or constantly. In between iterations where inputs are accepted the network activity evolves according to the recurrent dynamics. This characterizes a number of perceptual systems including vision where visual scenes are processed and fed to downstream systems discretely at a rate of 10-50 Hz [1] and olfaction where 40 Hz gamma oscillations in the olfactory bulb/antennal lobe lead to a fixed point only for longer odorant presentations [2].

![Image of input-driven dynamic attractors]

Figure 1: (left) Periodic inputs create new attractors. The dotted line represents possible inputs. Only periodic inputs generate multiple attractors in the network attractor space. (right) An example for visual memory with two types of noisy inputs: correlated and uniform: (top) constant presentation, (middle) initial presentation, (bottom) periodic window.

We argue that applying our paradigm to existing network architectures allows networks that previously had a small number of available attractors (even none) to develop many dynamic attractors depending on the specific input patterns. We also demonstrate that the paradigm can suggest new architectures and introduce an attractor based network that accepts noisy inputs in a periodic window and uses competing excitatory and inhibitory dynamics to produce low noise models of the inputs which are input-driven stable states.

References
Correlation between neural spike trains increases with firing rate

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Populations of neurons in a variety of brain areas show temporal correlation between their spike trains. Correlated firing has been linked to stimulus encoding, attention, stimulus discrimination, and motor behavior. Nevertheless, the mechanisms underlying correlated spiking are poorly understood, and its coding implications are still debated. It is not clear, for instance, on whether correlations between the discharges of two neurons simply reflect the correlation between their afferent currents or whether they depend on other factors. We addressed this question by computing the spike train correlation coefficient ($\rho$) of unconnected pairs of \textit{in vitro} cortical neurons receiving correlated inputs (Fig. 1A). Remarkably, even when input correlation remained fixed, the spike train output correlation increased with the firing rate ($\nu$), but was independent of spike train variability (Fig. 1B). In the limit of white noise forcing and weak input correlation $c$ we derive the compact expression valid for any spiking neuron:

$$\rho = \frac{\sigma^2 \left( \frac{d\nu}{d\mu} \right)^2}{CV^2\nu}c.$$  

Here $\mu$ and $\sigma^2$ are the mean and variance of the driving current and $CV$ is the coefficient of variation of the ISI distribution. Our theory gives an excellent match to simulations of spiking LIF neurons (Fig. 1C) as well as the cortical data. A functional consequence of our relation is that, if the firing rate of a population of neurons is tuned to a stimulus feature, then so is the population correlation.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure1.png}
\caption{Relationship between output spike correlation and output rate. \textbf{A} \textit{In vitro} neurons were stimulated with Gaussian currents having both common and independent components, evoking correlated trains of action potentials. \textbf{B}, The spike train correlation coefficient (a normalized and zero mean corrected measure) increases with the discharge rate of the neurons as the input correlation remains fixed. \textbf{C}, Statistical theory (Eq. 1, curves) and simulations from pairs of LIF neuron models. Firing rate was ranged by increasing the mean input current $\mu$ (red curve) or the current fluctuations $\sigma^2$ (blue curve).}
\end{figure}

**Acknowledgments**

Funding was provided by the Spanish MEC (JR), HFSP (BD), Burroughs Welcome Fund (ESB), NSF (KJ, ESB) and NIH (AR).
Emerged Representation Invariance through Neuron Position and Dendritic Shape

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One of the challenges in neuroscience is to understand how invariances of sensory inputs are learned, represented and used. We report on a theoretical and computer model exploration of the hypothesis that invariances can be represented by the spatial position of the neurons, and exploited by using a prior, or constraints, on the shape of the dendritic tree. The basic assumption is that neurons which represent features with similar semantics are likely to be in a proximate spatial position in the cortex. For instance two simple cells in V1 that are tuned to different but parallel proximate bars are semantically similar. “Similar semantics” implies that the neurons are expected to have a similar effect on the higher layers of the processing hierarchy, and not necessarily that they overlap receptive fields or have correlated outputs. We formulate the expectation of a “similar effect” as a prior on the weights, i.e. the synaptic strength, between these neurons and a neuron in the next level of processing. The prior encourages the weights to be similar while learning. Mathematically, we define the weights of synapses as a function, \( g \), of the pre-synaptic neuron position in the cortex \( u_i \), i.e. \( w_i = g(u_i) \). Then, instead of learning each weight independently, we define a prior on \( g \) that encourages this function to be smooth, i.e. achieve similar weights in adjacent positions\(^1\). Biologically, this kind of prior can be implemented by a prior on the shape of dendrites, e.g. a dendrite is more likely to interact with neurons which are in the neighborhood of other neurons that are connected to the same dendrite.

Note that the semantics or invariances are represented by spatial position and not necessarily by invariant neurons. In other words, the invariance depends on the shape of the dendrites in the next processing level, and can go beyond the invariance of each individual cell. For example, the organization of simple cells in V1 can be used to achieve invariance, even without translation invariant cells. For sensors, the organization of receptors “by semantics” follows from the geometry of the sensor (e.g. retina). For higher layers it can be achieved by self-organization based on input statistics and the organization of the previous layer.

The idea that the topography is useful for computation has been proposed before (see e.g., [1]). Here we formulate and study how this can be done in practice to improve pattern recognition. The theoretical approach is based on a recent work [2, 3] in statistical learning theory, where a prior is constructed using the properties of features, called meta-features. These concepts can naturally be applied to biological neural networks, where spatial position represents meta-features and the prior is applied by dendritic tree shape. Our framework is simulated by a simple network for handwritten digit recognition. We study the recognition accuracy with several methods for self-organization based on variants of previous work (e.g., Kohonen’s SOM and topographic ICA), and several types of smoothness priors on the distribution of weights. We compare the methods, and discuss the biological plausibility of the priors in the context of dendrite shape.

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\(^1\)A more biological plausible prior might be on the smoothness of variance of weights as a function of the spatial position.
\(^2\)A manuscript can be found in http://www.cs.huji.ac.il/~eyalkr/
Innate Visual Learning Through Spontaneous Patterns of Activity

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Patterns of spontaneous activity in the developing retina and LGN are necessary for the proper development of visual cortex in many animals, permitting newborn V1 to share many of the response properties of adult V1 without the “training” benefit of visual experience. We contend that these spontaneous patterns can be analyzed as a possible “innate learning” strategy which is simple to implement biologically by making use of the same adaptive efficient coding strategy as the adult animal. Our abstract patterns are generated through simple, local interactions and form random structured patterns resembling retinal waves and hypothesized “LGN waves”. An efficient sparse coding of these patterns resembles a 2-D Gabor code with many of the same properties as stimulus filters found in V1.

Instead of empirically studying the statistics of spontaneous activity in the developing visual system, we ask a more theoretical question: what properties would be ideal in an “innate visual learning” strategy?

1) Theoretical and physiological simplicity: Tractable analytical statements within a plausible framework.

2) Consistent efficient coding algorithm: The same algorithm used for efficient encoding of natural scenes and adult experience-based refinement of the visual code is also applied to the prenatal activity patterns.

3) Physiological receptive fields: Patterns encoded by the above algorithm produce V1-like Gabor filters. We show how patterns from a simple threshold percolation network, along with ICA coding, satisfy these criteria. The theoretical simplicity allows scale invariance and fractal dimension variation of the edges in a manner consistent with analytical calculations and necessary for generating the proper efficient code. The parameters of the model – p, the percolation probability; r, the neighborhood radius; and t, the active neighbor threshold – have rough physiological analogies in the Butts et al. \[1\] retinal wave model - fraction of recruitable amacrine cells, dendritic arbor size, and neural pooling threshold, respectively.

But independent of how the patterns are generated, our results show that simply generated patterns are capable of producing a Gabor code with physiologically relevant filter properties, with an example below; This shows that simple patterns of activity are capable of “innately training” the early visual system.

\textbf{Figure 1: Orientation bandwidths of Gabor filters derived from a sparse coding of patterns from the three parameter (P, R, T) model.} In the graphs to the right, The median physiological orientation full bandwidth is represented by the vertical line, whereas the bandwidths of the Gabor filter fits from each set of patterns are represented by the histograms.

\textbf{Acknowledgments}

Work supported by grants from the National Geospatial-Intelligence Agency to DJF and the NSF to MVA.

\textbf{References}

Inferring the Structure of Populations of Neurons using a Sequential Monte Carlo EM Algorithm

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A fundamental goal of neuroscience is to be able to construct models of a population of neurons acting in concert to perform nonlinear operations. A primary difficulty hindering progress towards this goal is the paucity of computational tools designed with population data in mind. Cross-correlation based ideas become computationally intractable due to the combinatorial explosion. Fitting phenomenological models to multicell data has received some attention, but we take a more biophysically realistic approach. Our models have two distinguishing features to this effect. First, we consider experimentally derived noise distributions act on the neurons, which can be non-Gaussian (e.g., synaptic failures). Second, we assume the existence of unobserved data (i.e., hidden states), in addition to the observed data (or states). These qualities naturally lead to a Sequential Monte Carlo Expectation-Maximization approach (SMC-EM). The expectation step requires computing the likelihood of the joint probability of both the hidden and observed state trajectories. By assuming that the hidden states are Markov, these distributions are approximated using SMC. The maximization step requires computing the maximum likelihood estimates (MLEs) of the model parameters. By choosing models with likelihood functions that are jointly convex in the parameters, we can guarantee convergence. The MLEs for those parameters for which no closed-form solutions exist are determined using standard convex optimization tools.

We apply this approach to data assumed to have been acquired using one of two population recording techniques: i) arrays of extracellular electrodes, or ii) 2-photon microscopy (2PM). When using electrodes, the observed states are spike times, and the hidden states are voltages of each neuron and conductances of each synapse. Each neuron is modeled with stochastic-leaky-integrate-and-fire (IF) dynamics, with noisy conductance-based synapses (noise due to failures or number of neurotransmitters released). When using 2PM, the data are noisy images of calcium signals, which are themselves noisy low-pass filtered versions of the spike times. Neurons in this case are modeled as Linear-Nonlinear-Poisson (LNP) functions, such that the external stimulus is linearly filtered, its output is exponentiated giving firing rate, and spikes are generated with Poisson statistics according to that rate. Presynaptic spikes operate on postsynaptic firing rate via linear filters.

Figure 1: Mean particle hidden state trajectories (gray lines) coincide well with actual hidden state trajectories (black lines). \(\text{Left: voltage for IF model.}\) \(\text{Right: calcium concentration for LNP model.}\)

Acknowledgments: This work was supported by NIH grant DC000109.
Towards real-time, mouse-scale cortical simulations

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Neurobiologically realistic, large-scale cortical and sub-cortical simulations are bound to play a key role in computational neuroscience and its applications to cognitive computing [1]. The mouse cortex has roughly $8 \times 10^6$ neurons and 8000 synapses per neuron. Modeling at this scale imposes tremendous constraints on computation, communication, and memory capacity of any computing platform. For example, assuming an average firing rate of 1 Hz, the entire memory must be refreshed every second, each neuron must be updated at every simulation time step, and each neuron communicates to each of its targets at least once a second.

We have designed and implemented a massively parallel cortical simulator. The simulator is designed for low to moderate complexity spiking neurons, for example, [2]. The state of each neuron is updated synchronously at a user-specified resolution, say, 1ms. Each neuron can be presynaptic to a realistic number of target neurons. Each synapse can implement STDP [3]. The simulator also incorporates axonal conductance delays ranging from a low of one time step to a model-defined maximum. To realize mouse-scale simulations, we have made several key novel technical contributions as briefly discussed below.

1. In previous simulators (e.g., NCS [1]), each neuron, upon its firing, sends an individual message to each of its target neurons. This becomes a bottleneck. We observed that, in a massively parallel implementation each compute node will house and process several neurons, and, hence, each neuron can group messages to all targets that reside on a single compute node into a single message. This idea drastically reduces the communication complexity from order of synapses to order of neurons.

2. In STDP, when a neuron fires, each excitatory synapse is examined for LTP, which appears to require a computation proportional to the number of synapses in that neuron. Instead, we maintain all synapses that were activated since the last neuronal firing on a recently-fired list. Since, typically, the size of this list is far smaller than the number of synapses, this leads to a significant computational benefit.

We deployed the simulator on a 4096-processor BlueGene/L supercomputer with 256 MB per CPU. Using spiking neurons [2], we were able to represent $8 \times 10^6$ neurons ($80\%$ excitatory) and 6300 synapses per neuron in the 1 TB main memory of the system. Using a synthetic pattern of neuronal interconnections, at a 1 ms resolution and an average firing rate of 1 Hz, we were able to run 1s of model time in 10s of real time. On other (smaller) models, we have observed biologically consistent dynamical properties such as spontaneous formation of neuronal groups and synchronous/asynchronous firing patterns. Our goal is to continually refine the computational architecture and to add neurobiological details such as macro and micro neuroanatomy, neuromodulators, and more detailed neuron and synapse dynamical equations.

References

Bayesian Reinforcement Learning and Sensory Decision-making

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We present a new model of LIP dynamics in which firing rate during a decision-making task is proportional to the predicted reward gained by gathering more sensory evidence. We develop a normative Bayesian framework that shows how the speed-accuracy tradeoff in the LIP could be set to maximize expected future reward (which if there is no incremental reward is just the reward rate (Gold & Shadlen 2002)). In particular we show how a population of “stopping” cells in LIP could predict the optimal time to stop accumulating evidence in a sensory decision-making task. These “stopping” cells would have a firing rate proportional to the predicted amount of reward gained by gathering more information about the stimulus and would interact with another group of neurons which estimate the reward rate. When the firing rate of reward rate driven neurons exceeds that of stopping cells, no more evidence is gathered.

In an environment filled with uncertainty, the best we can do is use a policy based only on noisy sensory observations to select actions that maximize reward (Kaelbling et. al. 1998). Since each observation is by itself unreliable, the optimal policy derived from Bayesian reinforcement learning is to gather a fixed-length history of observations, decode from these the state of the world using Bayesian inference, and use the MAP state estimate for action selection. The number of observations we decode the state from determines the speed/accuracy tradeoff, assuming that gathering more observations improves accuracy. To find the optimal speed/accuracy tradeoff, we find the optimal length for the observation history using Q learning and optimal stopping theory (Tsitsiklis & Van Roy 1999).

Within this framework we derive a model for LIP firing rates over a broad range of stimulus conditions and reward regimes. This model has testable physiological predictions. The first physiological prediction is that if no incremental reward is given during the trial for gathering more evidence, LIP firing rate ramps to an upper bound up until right before the decision is made, which is consistent with current experimental results (Roitman & Shadlen 2002). If on the other hand a small incremental reward is given during the trial, LIP firing should ramp until it reaches a peak and then decrease to a stereotyped value right before the decision is made. Other models of LIP firing rates exclusively emphasize the log-odds or a function of the posterior probability ramping to an upper bound (Gold & Shadlen 2001, Ma et. al 2006), and thus make a different prediction than our model for incremental rewards. Additional predictions include that compared to standard free-response TAFC tasks, LIP firing rate ramps to a lesser bound for decisions about mixed-stimuli (such as dots with coherent motion in multiple directions), and n-choice tasks (n > 2). LIP firing is also expected to ramp to a higher bound when substantial time penalties are added to error trials. Finally, this model can be used to estimate the set of weights on a dynamic prior which maximizes reward rate. The weights are shown to increase with time, predicting that prior information is integrated more as time elapses, which is consistent with current experimental work on how prior information is used in sensory decision-making tasks (Shadlen et. al. 2006).

Acknowledgments
Thank you to Mike Shadlen for discussions and Peter Dayan for suggesting the connection between optimal stopping theory and LIP.
Computations underlying decisions between multiple directions of motion

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While first theoretical attempts have been made to study possible decision making mechanisms underlying choices between multiple alternatives (e.g., [1][2]), most behavioral and neurophysiological studies have so far focused on choices between two alternatives. The available data sets from choice experiments between multiple alternatives are largely not quantitative enough to address the underlying computational mechanism. The 2AFC version of the random dot motion direction discrimination task has been very helpful in advancing our understanding of the neural and computational mechanisms underlying choices between two alternatives.

Here we present behavioral data from a new version of the random dot motion discrimination task. Subjects are presented with a random dot stimulus containing up to three coherent motion components with different directions. They are asked to pick the dominant direction of motion out of three alternatives. The viewing duration is controlled by the subjects (reaction time task). Response times (RTs) and the subject’s choice are measured. The advantage of this task is that it provides the experimenter with full control over the sensory evidence provided for each of the alternatives. Thus, for example, situations with equal amounts of sensory evidence for each of the alternatives can be created at different levels and the behavioral (and, in the future, also neurophysiological) responses can be studied.

In the 2AFC version of the task both the behavioral as well as neurophysiological data recorded from the parietal cortex of monkeys performing the task could be explained by a computational model based on the idea of a race to threshold between two integrators accumulating the net sensory evidence for a particular choice [3]. Here we show that the behavioral data (probabilities of particular choices as well as RT distributions) from our new 3-choice task are quite well explained by a computational model assuming a race to threshold between three integrators, one for each alternative. Each integrator accumulates the net sensory evidence for a particular alternative. The net sensory evidences are calculated as linear combinations of the activities of three relevant pools of sensory neurons with a positive weight assigned to the pool providing evidence for a particular choice and negative weights assigned to the pools providing evidence against a particular choice. Overall, the model turns out to be consistent with Multialternative Decision Field Theory [1].

Tuning ramping neuronal activity and reaction time by balanced synaptic input in a decision making circuit

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Neurophysiological studies on nonhuman primates have discovered that in some brain areas such as lateral intraparietal (LIP), single-neuron activities correlated with time integration of sensory information during perceptual decisions. To study the mechanism of the decision related neural activity, we have previously proposed a spiking neural network model [1] which exhibits ramping neuronal activity with reaction times in the range of hundreds of milliseconds and approximately Gaussian reaction time distributions, consistent with the behavioral data from the monkey experiment. In the present study, we show that our model can be extended to produce reaction times longer than one second and asymmetrical reaction time distributions with a broad exponential tail, as observed in some human studies of simple decisions.

The main idea is that ramping activity in a decision circuit (like LIP) is under the influence of top-down signals, presumably from the prefrontal cortex. One candidate mechanism that instantiates gain modulation assumes that noisy excitatory and inhibitory synaptic inputs to a neuron covary in a balanced configuration. On the single neuron level, theoretical and experimental works have shown that the balanced synaptic input modulates the gain of a neuron in response to external drives [2]. How a balanced synaptic input affects a highly recurrent neural network is unknown. We implemented a balanced synaptic input in our attractor decision-making model, and tested the possibility that such a gain modulation provides a mechanism to dynamically adjust the rate of ramping activity, thereby determining a desired range of reaction times as well as the shape of reaction time distribution.

We found that the balanced input significant slows down the ramping activity. While the mean reaction time can be extended to about two seconds, the distribution of reaction time follows a broad exponential tail with a maximum reaction time close to five seconds. This is because a decreased gain of single cells leads to a weakened competitive interaction between neural pools selective for different choice alternatives. Long reaction times and skewed reaction time distributions can be produced by the linear ramp-to-threshold (diffusion) model, a popular cognitive model for simple decisions. However, whereas in the diffusion model a lower drift rate required for a longer reaction time leads to poorer performance, in our neural circuit model the addition of a balanced synaptic input improves the decision performance.

We further show that by changing the balanced input strength, we can switch the network between different states: quiescence, competition (decision making) and bistability. Thus the balanced input indeed can serve as a mechanism that dynamically tunes the network behavior without the need of changing intrinsic properties of the network such as synaptic strength or membrane conductance.

This work is supported by Swartz Foundation.

References

Temporal integration of balanced excitatory and inhibitory inputs

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Temporal integration of information plays a pivotal role in a variety of cognitive processes, such as sensory discrimination, decision-making or interval timing. However, neural mechanisms of this computation remain to be elucidated. In previous models of temporal integration by recurrent neuronal networks \cite{1} or single neurons \cite{2}, neurons integrate a constant external input. Recent lines of evidence, however, suggest that activity of in vivo cortical neurons is generated through balanced excitation and inhibition \cite{3}. Here we propose a recurrent neural-network model that integrates balanced excitatory and inhibitory synaptic inputs. We show that the temporal integration in this network is more accurate when it integrates the fluctuating component of these inputs rather than the mean value.

We consider a uniform recurrent network of $N$ excitatory leaky integrate-and-fire neurons. All the neurons are initially in the resting state (‘off’ state); if a neuron discharges a spike, it moves to another state (‘on’ state) where constant depolarizing current is active, which promotes regenerative spike discharges. Each neuron receives an external input that consists of excitatory and inhibitory bombardments, which generates a rapidly varying postsynaptic current $I_{\text{in}}(t) = \mu + \sigma \xi(t)$. Here $\mu$ and $\sigma^2$ are the mean and the variance of this current, respectively; $\xi$ denotes fluctuation with zero mean, which is approximated by Gaussian white noise.

It is analytically or numerically shown that, if the strength of recurrent connection is properly tuned, the number of neurons in the ‘on’ state, say $n$, grows with time at an exact-constant rate. We found that, when $\sigma^2$ is varied while $\mu$ is constant (i.e. the excitatory and inhibitory inputs are balanced), the constant growth is kept, with its rate scaling linearly with $\sigma^2$ (Fig. 1). In contrast, the constant growth is not kept when $\mu$ is varied while $\mu$ is constant. These results indicate that $n$ represents temporal integration of the variance but not the mean of an external input. The final question is how to decode $n$. We propose that $n$ is decoded by the firing rate of a downstream neuron that has afferent inputs from the recurrent network, which are mediated by NMDA current or depressing synapses \cite{4}.

References

Optimal decision-making with probabilistic population codes
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We are constantly faced with situations in which we have to decide which action to perform given unreliable sensory information. Most of these decisions involve continuous variables with non-stationary statistics, i.e., variables whose reliability changes over time. For instance, a tennis player must decide when and how to hit the ball based on its continuous motion. The motion of the ball must be obtained from its image whose quality varies over time: it is hard to see when it is on the other side of the court, but it becomes easier to discern as it moves closer to the player. None of the current neural models (diffusion to bound, point attractor networks) can deal with this general setting because they are designed for binary targets with stationary statistics.

We present the first neural model of decision-making that can perform the integration of the sensory evidence and the selection of motor response optimally for continuous and discrete variables with non-stationary statistics. As an example, we use a standard task in which subjects are asked to discriminate motion direction in a random-dot kinematogram in which a fraction of the dots move coherently in the same direction. Subjects respond with a saccadic eye movement in the perceived direction of the dots. This decision-making process consists of two stages: the accumulation of motion evidence and the selection of a saccade. The Bayes-optimal strategy in this case is to first compute the posterior distribution over saccades given all sensory evidence available since the start of the trial, and then collapse this distribution onto the maximum-a-posteriori (MAP) estimate.

We show that given the Poisson-like nature of response variability in the cortex, both integration and action selection can be implemented optimally in neural networks. For the integration, neurons (possibly in LIP) need to compute the temporal sum of the spikes generated in MT (assuming that MT provides the sensory evidence). This automatically generates a probabilistic population code representing the posterior distribution over saccade direction given all spikes from MT since the start of the trial. This neural integration remains optimal even when the coherence of the dots changes during the course of a single trial or across trials. For action selection, the MAP estimate can be recovered by a two-dimensional attractor network. In general, attractor networks cannot extract the MAP estimate from a probabilistic population code but for Poisson-like variability, optimality is guaranteed. This works for arbitrary correlations and arbitrary tuning curves.

We have implemented this model and found that it captures the speed accuracy trade-off that has been reported in humans and monkeys. It also accounts for the temporal evolution of neural activity in LIP and SC during decision-making. In addition, our framework predicts that LIP encodes a posterior distribution over motion direction at all times. We have tested this prediction on LIP data and found that it is indeed the case. This result is particularly surprising because, according to the diffusion to bound model of decision-making, LIP activity does not and cannot encode a posterior distribution. Yet, our analysis strongly suggest that it does, lending strong support to our approach. Finally, we predict the evolution of LIP activity for experiments involving 4 or more discrete targets, a continuous variable, or stimulus with non-stationary statistics.

Acknowledgments
This work was supported by ONR, NSF, NIDA and the James S. McDonnell Foundation.
Decoding the outcome of free decisions before they reach awareness

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There has been a long debate whether subjectively “free” decisions are determined by brain activity ahead of time \cite{1-3}. When humans are asked to execute simple movements at a time they freely choose, brain activity over motor regions is elevated a few hundred milliseconds prior to the subjective awareness of their decision \cite{1}. This has often been taken as evidence that an unconscious “decision” to act is initiated by the brain a few hundred milliseconds before this decision reaches awareness. However, it has remained unclear whether the intention to act is initiated in motor-related brain regions, or if high-level brain areas in prefrontal cortex are involved. Furthermore, it has been highly criticized that the short delay between brain activity and awareness could reflect inaccuracies in the participants’ subjective reports \cite{3}. Here we show that the outcome of “free” decisions is encoded in brain activity at much longer timescales of up to several seconds before they reach awareness. We measured brain activity using functional magnetic resonance imaging (fMRI) and trained a support vector pattern classifier \cite{4} to predict the outcome of a free decision from brain signals recorded several seconds before a decision was made. The outcome of the decision was encoded in brain activity in prefrontal cortex and parietal cortex even up to ten seconds before the decision was made. This delay is too long to be accounted for by inaccuracies in measuring the onset of conscious intentions. Instead it presumably reflects the operation of a network of areas that begin to prepare an upcoming decision long before it enters awareness. The findings suggest that our free choices are determined by brain activity much earlier than commonly appreciated.

Figure: Information about the outcome of a decision that can be decoded in periods before (“PRE”) and after (“POST”) the decision has reached awareness (FPC: fronto-polar cortex; PC: precuneus).

Acknowledgments
We thank Dick Passingham, Hakwan Lau and Niko Kriegeskorte for helpful discussions. This work was supported by the Max Planck Society and the German Federal Minstry of Education and Research.

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Uncertainty Representation in Orbitofrontal Cortex during Decision-Making in Rats

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Uncertainty has long been studied in economics, psychology and behavioral ecology as a decision variable critical for understanding behavior. More recently, several computational schemes have been proposed for how populations of neurons might be able to represent not only a value of interest but also the uncertainty associated with it. However, despite the recognition of uncertainty as a pivotal variable for decision-making and neural coding, little is known about how and where it is represented in the brain.

We explored this question in rats by recording neural activity from the orbitofrontal cortex during an odor-mixture categorization task. Rats were trained to report the category (dominant component) of binary mixtures of two odors and were rewarded either at the left or the right choice port for correct decisions. Discrimination accuracy for pure odors was close to 100% but for the most difficult mixtures performance dropped to almost 60%. Since reward was always provided for correct choices, the outcome was uncertain only because sometimes rats were not able discern and/or remember the correct category of the odor mixture.

The orbitofrontal cortex (OFC) has been implicated in representing reward value, and insofar as discrimination difficulty affects reward probability, OFC firing would be expected to vary with the odor mixture ratio. Indeed, a large fraction of OFC neurons showed mixture-ratio dependent firing. Such firing rate modulation could emerge through learning, by associating particular stimuli with the average experienced reward probability. In contrast, we found that ~30% OFC neurons predicted not only the average reward outcome, but trial outcome before reward feedback was provided. How could neurons predict trial outcome after making a choice—an event beyond the animal's control? This could occur if during the decision process, in addition to the choice, a degree of uncertainty or confidence associated with the choice is also estimated. If this estimate is veridical then on average it will predict choice accuracy and hence trial outcome. Moreover, a good estimate of uncertainty will reflect the stimulus difficulty when the choice is correct. Consistent with this, the firing rates of outcome selective neurons varied systematically with stimulus difficulty in correct trials.

Previous modeling studies suggested that while the value of a variable is represented by the mean firing rate of a neuron, the degree of uncertainty about that value may be encoded by the variance of the firing rate. Instead we found that orbitofrontal neurons provide an explicit firing rate representation of uncertainty. Nevertheless, it may be that during the decision process other brain areas employ implicit representations, which are then converted into a firing rate in the OFC. Our results emphasize that uncertainty is a fundamental quantity for decision-making, one that is easily and most likely automatically computed during the decision process and represented across multiple brain areas, similar to other key decision variables such as choice probability and reward value.
Flexible Shaping
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Cognitive flexibility, the ability to acquire, adapt, combine and recombine behaviors appropriate to ever-changing tasks, is a hallmark of intelligent behavior. In mammals, flexibility is likely to depend crucially on mechanisms and representations within the prefrontal cortex (PFC), and on the PFC’s extensive connections with structures such as the basal ganglia (BG) and hippocampus. To study flexibility, it is necessary at the very least to present collections of related tasks; unfortunately, most experimental, and almost all computational, approaches have hitherto focused on learning single underlying tasks, albeit with subtly changing contingencies. In this work, we consider a foundational form of flexibility – the way that separate behavioral components can be acquired through shaping and then combined to solve an overall task.

We study the 12-AX task, which was proposed and then modelled by O’Reilly et al [2] as a rich test bed for analysing PFC-PFC and PFC-BG interactions. Subjects are presented sequentially with letters or the digits ‘1’ or ‘2’. If the most recent digit they have seen was a ’1’, they have to provide a non-default response only to the sequence segment ‘AX’; if it was a ’2’, then they must react only to ‘BY’. Storing ’1’ or ’2’ is an outer working memory loop defining a cognitive context; storing either ‘A’ or ‘B’ is an inner loop. O’Reilly et al modeled a complex reinforcement-based learning process for this task, and showed that it out-performed a standard architecture for learning to use working memory in tasks. However, in both cases, the networks had to learn the full task monolithically, in one fell swoop. Instead, we considered the consequences of shaping, by training individual subcomponents separately, and learning their combination. We performed our shaping in an LSTM [1] network.

We first confirmed that it is substantially easier to learn to combine partial competences than to learn from scratch. However, if we include the time taken to learn the components the overall benefit is a little less evident. Nevertheless, shaping leads to more abstract representations with better generalization. For instance, if training involved restricted numbers of inner loops per outer loop, then the shaped network, with its more abstract inner-loop storage, generalized more proficiently to larger numbers. Shaping also helps learning when there are so many inner loops that the credit assignment path for the outer loop is very extended.

Shaping is only one simple aspect of flexibility. However, it already poses issues such as neural modularization, and also even more evanescent structure in ongoing behaviors, that we are starting to address.

Acknowledgments
Thanks to Randy O’Reilly for discussions and software. Support from the Gatsby Charitable Foundation.

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Simultaneous recording of single units from the primate amygdala and midbrain dopamine neurons during probabilistic appetitive and aversive conditioning

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Midbrain dopamine (DA) neurons are well characterized during appetitive conditioning procedures as encoding errors in reward prediction. Recent work from our laboratory has shown that during interleaved appetitive and aversive conditioning neural correlates of both positive and negative value exist in the amygdala across roughly half of all cells isolated for study\textsuperscript{[1]}. In addition, we find that responses to appetitive and aversive reinforcement reflect whether reinforcement was expected, a hallmark of prediction error signals. Theories of reinforcement learning (RL) posit that value signals and error signals interact reciprocally to promote learning. That is, if a subject has not learned to accurately predict reinforcement, then reinforcement should produce an error signal which feeds back onto a representation of value such that the subject can make a more accurate prediction in the future. As the amygdala and midbrain DA neurons are reciprocally connected anatomically, we seek to determine whether the time course of changes in DA and amygdala neuron responses during learning is consistent with the type of functional interaction proposed in RL models. In addition, we seek to determine whether DA neurons encode punishment prediction error signals in addition to reward prediction error signals.

On each trial of an experiment, monkeys were presented with one of three abstract images (fractal patterns), which were new to the monkey each session. After a delay, each image was followed by the presentation of a large reward, a small reward, or an air-puff directed at the face with a probability of 0.8. Monkeys learn to lick at a reward delivery tube in anticipation of a reward, and blink in anticipation of an air-puff directed at the face. In fact, positive and negative CS values are defined operationally here as licking in anticipation of liquid reward or blinking in anticipation of an air-puff, respectively, and these two behaviors were used to assay learning as it was occurring. At some point after a monkey demonstrated learning of the CS-US associations, the CS-US contingencies for the large reward and punishment conditions were reversed such that the image paired with reward was paired with air-puff and vice versa. Here we present very preliminary findings from a small population of simultaneously recorded amygdala and putative DA neurons that suggest two findings. First, amygdala and DA neuron response dynamics both appear to be correlated with the time course of behavioral learning. Second, at least some putative DA neurons appear to respond to punishment with a phasic increase in firing. We are also exploring whether there are differential effects on tonic vs. phasic dopamine firing depending upon the valence of reinforcement. The criteria used for isolation of DA neurons were threefold: 1) spike waveforms > 2ms; 2) low spontaneous firing rates of less than 10 Hz; 3) phasic response to unpredicted reward. Future experiments will seek a more definitive DA neuron categorization scheme by presenting DAergic antagonists during recording. DA neurons, because they express autoreceptors for DA, should be inhibited by such pharmacological interventions.

Acknowledgments
This work supported by Gatsby, Culpeper and James S. McDonnell awards to CDS. JJP supported by NEI.

References
Encoding of stimulus value in primate orbitofrontal cortex and amygdala during reinforcement learning.

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The amygdala and orbitofrontal cortex (OFC) are often thought of as components of a neural circuit that assigns affective values to sensory stimuli, and uses these values to anticipate future events and adjust behavioral and physiological responses. We have recently shown that individual amygdala neurons encode the positive or negative values of visual stimuli during reinforcement learning[1]. But the amygdala does not function in isolation; interactions between limbic structures, such as the amygdala, and cortical areas, such as the OFC, are almost certainly important for motivated behavior. We hypothesized that the OFC may contain a similarly dynamic representation of value that changes with learning. We were also interested in comparing neural signals in the OFC and amygdala during appetitive and aversive classical conditioning.

We therefore recorded simultaneously the activity of individual OFC neurons and amygdala neurons while monkeys performed a trace-conditioning task. During each session, a monkey learned the values of three novel abstract images (CSs): one associated with large reward, one with small reward, and one with punishment, each of which occurred after a CS with a probability of 80%. We assessed monkeys’ learning by monitoring two behaviors: licking in anticipation of reward, and blinking in anticipation of punishment (which consisted of an aversive air puff to the face). After monkeys learned the initial image values, we reversed the values of two of the images in an un-cued manner, and monkeys learned the new values through experience. We found that monkeys’ licking distinguished among all three trial types, with licking durations correlated with the size of the reward. Monkeys’ blinking distinguished between punished and rewarded trials.

We also found that the responses of a significant portion of OFC neurons, primarily recorded in area 13, were modulated by image value during one or more periods of the task. Consistent with previous results, about half of amygdala neurons also encoded image value. Responses in both areas were also modulated by image identity. As populations, both amygdala and OFC neurons encoded gradations of value (i.e., strong positive and weak positive). Finally, as we previously showed for amygdala neurons, OFC neurons changed their activity at about the same time that monkeys’ behavior changed in response to image value reversal. Across the population of neurons, the time course of this change was similar for neurons from the OFC and the amygdala. In future experiments, we will seek to determine whether and how the flexible representations of value in the these areas are interdependent.

Acknowledgments
This work supported by Gatsby, Culpeper and James S. McDonnell awards to CDS. S.E.M. received assistance from an NSF Graduate Research Fellowship.

References
Synaptic models for slow memory decay

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A longstanding hypothesis in neuroscience is that learning involves changes in synaptic efficacies. As synaptic efficacies are bounded, the flip side of this hypothesis is that learning one thing necessarily involves forgetting another. The problem of forgetting is especially severe if synaptic efficacies take on a discrete (or even binary) set of values, something that has been suggested for theoretical reasons (e.g. \cite{1}) and for which there is some experimental evidence \cite{2}. In this regime, past memories fade exponentially fast, and memory capacity is only logarithmic of the number of synapses.

Recently, a potential solution, using what is known as the Cascade Model, was proposed \cite{3}. In this model, the synapse has many discrete internal states but only two efficacies. The synapse switches between the internal states in a stochastic fashion (assuming some Hebb-like learning rule), with switching rates that are different for different states. This mechanism results in power-law decay of the memory trace and, therefore, a much higher memory capacity.

In the work we report here, we have studied the family of such possible models. Our aims are: (1) analyze the performance of these models, and in particular determine if the internal states are used in an optimal way. And, (2) ask how likely these models are. In particular, can the original model be generalized into a broader class of models, and does the model demand fine tuning of its parameters, or is it robust to small parameter changes?

This work is divided into two parts. First we present an analytic solution for the original Cascade Model. Applying that analysis, we calculate the memory decay rate and the resulting memory capacity. Next, we introduce a framework for the analysis of generalized Cascade Models. Within this framework, we derive conditions for both power-law memory decay and its robustness to small changes in parameters, and describe several representative examples.

Acknowledgments
This work was supported by the Gatsby Charitable Foundation and the Center for Neural Computation.

References
Optimal Eye-Movement Paths Emerge as Monkeys Perform a Free-Viewing Scan Task

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In our daily lives, we develop habitual ways of completing series of movements that we perform repeatedly. We developed an experimental paradigm to determine whether macaque monkeys, without prior or explicit instruction, develop such habits. It was found that they do, and we show that the scanning paths that develop during the course of training take on patterns that successively approach, and then settle, at the optimal solutions for minimizing path length and time per trial. We trained two monkeys to perform a free-viewing scan task in which the monkey was presented, depending on the stage of training, with a square grid of either 4, 9, or 16 identical targets. While the targets were presented, the monkey's sole task was to constrain its eye position to be within the region of space bounded by the grid. After a variable delay (1-2s when the animal was well-trained), reward was randomly assigned to one of the grid targets, and the trial would end in reward when the animal captured that target. Training consisted of ca. 1000 correct trials per session for a given target array size and continued until the monkey reached a criterion of ≥80% rewarded performance. In one monkey, criterion was achieved after session 13 for the 4 target grid, session 21 for the 9 target grid and session 38 for the 16 target grid. Monkey 2 reached criterion on the 4 target grid in 42 sessions, and is currently training on the 9 target grid.

As the monkeys performed this task, they developed repetitive, habitual patterns of eye movements. The set of repeated patterns of eye movements performed varied throughout training, with some coming into use and falling into disuse across sessions. Additionally, as training progressed, fewer and fewer eye movement patterns were necessary to describe the contents of an increasingly larger fraction of individual correct trials in a given session. For example, in monkey 1, it required tallying all of the trials that contained any of the 19 5-fixation eye movement patterns performed at least twice to account for >70% of the correct trials in 9 target scan task during session 20. By session 60, only 2 patterns accounted for >80% of correct trials. These specific sequences were often members of a larger repeated sequence that could be identified if start and stop positions on the grid array were disregarded. Monkey 1 performed her “habit” of making successive clockwise saccades around the 4 target grid array on 100% of the trials by session 30. Monkey 2 reached a similar, but counter-clockwise, pattern of sequential saccades around the same grid on >75% of correct trials by session 54. In monkey 1, we observed a dynamic change in the saccade patterns as the monkey was presented with the 9 target grid after the 4-target grid initial exposure. The monkey again adopted repeating patterns that were briefly expressed and then were replaced, until the monkey settled on a contour-plus-center path that covered all the targets on >70% of correct trials by session 60. We used an exhaustive search algorithm to determine the optimal solutions to minimize path length and scan time for each grid pattern. Remarkably, both the final scan-path pattern in the 9 target task for monkey 1 and the final scan-path patterns in the 4 target task for both monkeys proved to be optimal solutions for minimizing path length and path time. The temporary scan-paths that occurred transiently during training grew successively closer to these optima. We suggest that the formation of habits may not necessarily be arbitrary, but rather, could reflect neural mechanisms evolved to achieve optimal behavioral control under varying behavioral contexts.

Acknowledgments Supported by NEI EY12848, NDSEG Fellowship and ONR N00014-04-1-0208.
Shape your liquid with plasticity!

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Cortical networks involved in coding and processing of information are constantly shaped by a large variety of plasticity mechanisms. But how do different forms of plasticity interact to shape the structure, dynamics and computational properties of recurrent spiking networks? We use a simple recurrent spiking neural network made of threshold units that allows us to look at the network structure and dynamics in a detailed fashion. Two forms of neuronal plasticity are considered: spike timing dependent plasticity (STDP) that changes synaptic strength and intrinsic plasticity (IP) that changes the excitability of individual neurons to maintain homeostasis of their activity. In analogy to liquid state machines\([1]\) we analyze the ability of such networks to exhibit a fading memory of external inputs and study the extent in which they may discover structure in non-random, predictable time series.

We find that STDP and IP interact in non-trivial ways such that the effect of one of them on network behavior can be substantially altered by the presence of the other (also see \([2,3]\)). Specifically, autonomous networks without input shaped by a combination of STDP and IP lead to many limit cycles with stable network behavior in the presence of small perturbations. When we study input driven networks, the "causal" nature of the STDP rule allows the reservoir to learn structure in the time sequences corresponding to likely sequences of external inputs. The intrinsic plasticity enforces "balanced" dynamics that utilizes all resources in the network. Together, these mechanisms allow recall (t<0) and prediction (t>0) with a performance that was similar to that of randomly structured reservoirs, while networks trained with just STDP or IP separately perform on average significantly worse (see figure). These differences may be explained by our finding that the two forms of plasticity keep the dynamics of the network at the edge of chaos.

Our results underscore the importance of studying the interaction of different forms of plasticity on network behaviour.

Acknowledgments
This work was supported by the Hertie foundation and grant EC MEXT-CT-2006-042484 (PLICON).

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Perceptual learning as improved Bayesian inference in early sensory areas

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Extensive training on simple tasks like 2-AFC orientation discrimination results in large improvements in performance, a form of learning known as perceptual learning. Psychophysical experiments manipulating external noise strongly suggest that perceptual learning is due to improved decision-making. In contrast, single cell recordings have demonstrated that the response properties of neurons in early sensory areas are modified by training, suggesting a change in early sensory representations as opposed to decision making. No model has successfully managed to reconcile these contradictory conclusions.

We believe that the problem stems from the fact that all models treat sensory processing and decision making as different types of computations: nonlinear filtering (or feature extraction) for sensory processing and Bayesian inference for decision making. We propose instead to consider both sensory processing and decision making as instances of Bayesian inference. Indeed, in both cases, the goal of the computation should be to infer a probability distribution over the variable of interest, say orientation, given the statistics of the incoming spikes. The main difference is that sensory processing should keep the posterior distribution while decision making should collapse the distribution onto an estimate. If we are correct, the two processes are exceedingly difficult to tease apart with behavioral methods alone. Any change that improves Bayesian inference in early sensory area will appear to affect decision making and vice-versa.

We apply our approach to the case of orientation selectivity. We show that it is possible to derive an analytical expression for Fisher information in a network of spiking neurons receiving input spikes—a difficult problem that had eluded a solution until now. This expression allow us to determine the impact of any network parameters on Fisher information and, therefore, on the efficiency of the Bayesian inference. It reveals in particular that increasing the amplitude of feedforward connections in early sensory areas, along with specific changes in lateral connectivity, can increase Fisher information and change the tuning curves of sensory neurons in a way consistent with what has been found experimentally. Importantly, we also show that, at the behavioral level, the system behaves as if the decision stage had been improved, even though the changes took place early in the model.

In addition, this work sheds new light on the nature of noise in the nervous system. The main source of variability in the nervous system is believed to be the Poisson-ness of firing in cortex. We show that in our model, this factor barely contributes. Instead, the main factor is the suboptimal nature of the inference performed by cortical circuits due to incomplete knowledge of the statistics of incoming spikes.

Acknowledgments
This work was supported by ONR and NSF.
Differential effects of aging and learning processes on cortical interaction

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Using fMRI we show the co-existence of two different forms of cortical reorganization in elderly subjects: an age-related and a learning-related cortical map expansion. The age related expansion of the finger representation in somatosensory cortex (SI) was accompanied by a significant decline in the tactile discrimination performance. To show that the observed age-related changes are not irreversible, we applied a tactile coactivation protocol of Hebbian learning. In young subjects this procedure induces perceptual learning leading to an improvement of tactile acuity parallel to an enlargement of cortical representations of the coactivated finger. Applying this approach in elderly we found that after coactivation the tactile performance improved thereby ameliorating the age-related deterioration in tactile performance \cite{1}. The perceptual improvement was accompanied by a further enlargement of the cortical representation indicating that coactivation is similarly effective in elderly subjects. To understand both the process of aging and the process of two-point discrimination performance and its reverse effect on the size of the cortical representation we here use a mean-field approach to model cortical population activation.

In the model tactile stimulation evokes either single peaks of activation, which code for the subjective experience of a single point on the skin, while bimodal activations are read out for perceiving two points. The activation profile arising from stimulus inputs depends not only on the distance between inputs on the skin, but also on interactions within the cortex, which is depicted by Mexican-hat interaction characterized by local excitation and a broader range inhibition. In the “young” model both the excitatory and the inhibitory interaction components are sharp leading to focused representations. The “aging” model has a broader interaction consistent with broader, more distributed representations in aged subjects.

In the aging model, the cortical representation is larger than the representation in the young model due to the broader range of interaction resulting perceptually in an impaired discrimination performance. In contrast, coactivation-induced plasticity is modeled through a weakening of inhibitory interaction. Although this modification also expands the cortical representation of single fingers, it leads to an improvement of two-point discrimination ability both for the young and the old model as it weakens the strong inhibitory winner-takes-all component. According to our simulations the fine structure of excitatory and inhibitory interaction is differentially affected by aging and learning and thus explains the size of cortical maps and discrimination abilities.

References
Neural signals in primate amygdala discriminate among gradations of value

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We have recently discovered that the primate amygdala contains two populations of neurons that encode the positive and negative values, respectively, of conditioned visual stimuli [1]. For neurons encoding positive value, responses to an image associated with reward were stronger than responses to the same image when it was associated with a punishment; neurons encoding negative value had the opposite response profile. We have now investigated how the amygdala encodes gradations of values assigned to visual stimuli. We recorded single units in the amygdala while monkeys performed a trace-conditioning task in which 3 novel abstract visual stimuli were paired with either large reward (2 large drops of water), small reward (one smaller drop of water) or an aversive air-puff directed at the monkey’s face. The reinforcements were delivered on 80% of trials and were omitted on 20% of trials. After the initial associations were learned, we reversed the assignments without warning, delivering air-puffs instead of large rewards after the image that was initially paired with large reward and vice-versa for the image initially associated with air-puff. The image paired initially with small reward was never reversed. We monitored two behavioral parameters, anticipatory licking and eye closure, that demonstrated monkeys’ leaning. Monkeys typically closed their eyes, in anticipation of aversive air-puff, and licked a reward delivery tube in anticipation of rewards, with licking durations correlated with the size of rewards.

We recorded neural activity from 85 cells in 2 monkeys. About 50% of these cells encoded either positive or negative value of the conditioned images during either the visual stimulus or trace intervals. The majority of these value-coding cells also differentially encoded value gradations of visual stimuli. We defined the trials with large reward as having a strong positive value. Trials with smaller rewards were defined as having a weak positive value, and the trials with air-puffs were defined as having a negative value. Monkeys’ behavior, over the population, reflected that they had learned the association and gradations of value. They licked most on large reward trials, less on small reward trials and almost not at all on negative trials. Blinking behavior reflected learning about negative association, as monkeys closed their eyes anticipating air-puff, but not on either of the two positive trial types.

Across the population of neurons, responses to the image associated with a small reward (weak positive trials) were intermediate to the responses to images associated with strong rewards or aversive air-puffs, especially during the trace interval immediately preceding reinforcement. This finding held whether neurons fired most strongly to images associated with aversive air-puffs (negative value-coding neurons) or to images associated with large rewards (positive value-coding neurons). These data suggest that neurons in the amygdala provide a graded representation of the learned values of visual stimuli. Moreover, the differential responses to images associated with strong and weak rewards demonstrate that the changes in response properties of amygdala neurons during reinforcement learning do not reflect the formation of an association between images and the sensory properties of rewards. The sensory properties of the rewards were identical in the two trial types, and the rewards only differed in quantity. Across the population the graded representation of value is a sustained signal that extends from shortly after the presentation of an image predicting reinforcement and is temporally extended until reinforcement.

References:
Induction and binary expression of LTP/LTD in a minimal model of the CaMKII kinase-phosphatase system

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The calcium/calmodulin-dependent protein kinase II (CaMKII) plays a key role in the induction of long-term post-synaptic modifications following calcium entry. Experiments suggest that these long-term synaptic changes are all-or-none switch-like events between discrete states [1]. The biochemical network involving CaMKII and its regulating protein signaling cascade has been hypothesized to durably maintain the evoked synaptic state in form of a bistable switch [2,3]. However, it is still unclear whether different experimental LTP/LTD protocols lead to corresponding transitions between the two states in realistic models of such a network. Furthermore, the biochemical mechanisms giving rise to the non-linearities exhibited during LTP/LTD induction remain elusive.

Starting from a detailed biochemical model, a reduced model of the CaMKII autophosphorylation and the protein signaling cascade governing CaMKII dephosphorylation is presented. Dephosphorylation is mediated by protein phosphatase 1 whose activity is indirectly regulated by a calcium-dependent balance of kinase (protein kinase A) and phosphatase (calcineurin) activity.

As previously shown [2], two stable states of the CaMKII phosphorylation level exist at resting intracellular calcium concentration and high calcium transients can switch the system from the weakly- (DOWN) to the highly-phosphorylated (UP) state of the CaMKII (similar to a LTP event). We show here that increased CaMKII dephosphorylation activity at intermediate Ca$^{2+}$ concentrations can lead to switching from the UP to the DOWN state (similar to a LTD event). This can be achieved if protein phosphatase activity promoting CaMKII dephosphorylation activates at lower Ca$^{2+}$ levels than kinase activity. Finally, it is shown that the CaMKII system can qualitatively reproduce results of plasticity outcomes in response to spike-timing dependent plasticity (STDP) protocols, presynaptic stimulation protocols and pairing protocols. We also address the question to which extent such a biochemical realization of bistable synaptic plasticity can account for the non-linearities exhibited during LTP/LTD induction by pre- and postsynaptic spikes. Our investigations show that a reduced model of the CaMKII protein network can account for both induction - through LTP/LTD-like transitions - and storage - due to its bistability - of synaptic changes.

Acknowledgments
Supported by the French Ministry of Research, ACI Neurosciences intégratives et computationnelles and the ANR (Agence Nationale de la Recherche).

References
Tuning for Criticality: A New Hypothesis for Sleep

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We propose that the critical function of sleep \cite{3} is to prevent uncontrolled neuronal feedback while allowing rapid responses and prolonged retention of short-term memories. The goal of learning is optimal behavior, and this sometimes requires the integration of sensory stimuli that are widely separated in time. At a neuronal level, this corresponds to persistent activity in local networks. Unfortunately, when a network exhibits persistent activity, small changes in the parameters or conditions can lead to runaway oscillations. Thus, the very changes that improve the processing performance of the network can put it at risk of runaway oscillation. To prevent this, stimulus-dependent plasticity should only be permitted when there is a margin of safety around the current network parameters. We propose that a critical role of sleep is to establish a margin of safety by exposing the network to a variety of conditions and inputs, observing for erratic behavior, and adjusting the parameters accordingly. During wakefulness this margin of safety is gradually consumed, ultimately requiring refreshment by another period of sleep. When sleep is not possible, an emergency mechanism comes into play to prevent runaway oscillations; this is done at the expense of processing efficiency, and constitutes tiredness. We contend that this theory matches the phenomenology of sleep and tiredness better than do alternative theories, such as the memory consolidation theory \cite{1, 2, 5}. This theory also makes a number of novel testable predictions.

The most direct prediction is that different plasticity regimes should operate during wakefulness, tiredness and slow-wave sleep. Some experiments that relate to less direct predictions have already been conducted for other purposes. For instance, we would expect that the impulse response of cortex during wakefulness would be near the boundary of criticality, and that during slow wave sleep the impulse response would be moved closer to the boundary, which is consistent with the experimental data of Massimini et al. \cite{4}. One success of this hypothesis is that it explains tiredness as an emergency mechanism. If this is true, then combating the symptoms of tiredness should increase the risk of suffering epilepsy. An increased risk of epilepsy would also be expected as a consequence of regular sleep deprivation, particularly among babies and children.

Acknowledgments
Supported by Science Foundation Ireland grants 00/PI.1/C067 (BAP) and 06/RFP/BIM020 (CJH).

References


Neuromodulation and plasticity of the adult auditory cortex

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Cortical networks are highly dynamic and labile. In large part, these qualities reflect the ability of cortical synapses to be rapidly modified in a way that depends on the patterns of experience, activity, and neuromodulation. However, the rules of cortical synaptic plasticity and neuromodulation remain unclear, especially in the intact brain, where cortical circuitry is under the powerful influence of a diverse set of subcortical systems.

To understand how neuronal activity and neuromodulation lead to changes in cortical synapses in vivo, we have used a combination of approaches, including in vivo whole-cell recording, electrical stimulation of the cortex, thalamus, and subcortical neuromodulator nuclei, and telemetric recording and stimulation in the behaving animal. In the experiments reported here, we have focused on the organization of receptive fields in the primary auditory cortex (A1) of adult rats, and the control of cortical responses by modulatory inputs from the basal forebrain.

Our whole-cell recording experiments first showed that sensory stimulation alone does not lead to long-term changes in synaptic receptive fields, suggesting that repetitive pre- and postsynaptic spiking (such as that which drives spike-timing-dependent plasticity) are not sufficient for long-term synaptic modification in adult A1 in vivo.

However, pairing sensory stimulation with electrical stimulation of the basal forebrain, containing the major cholinergic input to the cortex, reliably produced large long-term changes in the synaptic receptive fields of A1 neurons. Excitatory currents were enhanced concomitantly with suppression of inhibitory currents, and these effects were specific to the paired stimulus. While the potentiation of excitation persisted for the duration of the recording, the suppression of inhibition recovered in an activity-dependent manner over a few hours, eventually increasing to ‘re-balance’ the excitatory and inhibitory synaptic receptive fields. Simultaneous monitoring of cortical and thalamic inputs via electrical stimulation revealed that these changes are intrinsic to the cortex.

Parallel studies using wireless recording and stimulation in the behaving animal have shown the effects of basal forebrain stimulation on auditory discrimination. Our results explain how neuromodulation can change spike rates and cortical maps, can boost attention and behavioral performance, and account for the necessity of neuromodulation to drive long-term cortical plasticity in the adult brain.
Capacity enhancing mechanisms in a hippocampal online learning model

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The hippocampal formation is involved in the online storage of episodic memories. The challenge for such a memory is to encode a continuous stream of patterns presented only once, while retaining a high-fidelity trace of each stored pattern for the longest possible holding time. Using a simplified model of the CA3-CA1 Schaffer collateral pathway, we set out to identify (or propose) circuit, cellular, and synaptic properties that help maximize the system's online storage capacity. Three principles have guided our search, and have suggested capacity-enhancing strategies. They are: (1) The principle of uniform trace strength, which favors the use of binary-valued synapses, uniform subunit thresholds, and normalization circuitry to ensure that a constant number of subunits is devoted to the storage of each pattern; (2) The principle of trace resource minimization, which leads to an LTP variant requiring that synapses be strengthened only in cohorts of sufficient size; and (3) The principle of trace resource synchronization, where through the use of synaptic tagging and age-ordered synaptic depression, the system can synchronously recover the resources consumed by patterns that have reached the end of their storage lifetimes. Each of these mechanisms has been tested in our model (representing a 2.56 million synapse chunk of the hippocampus), and has led to substantial increases in storage capacity. We will discuss the biophysical mechanisms that could contribute to these capacity enhancing strategies.
Noise based memories

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Long term memories are widely believed to be stored in the pattern of synaptic couplings. In order to retrieve a memory the synapses are probed by pre-synaptic activity, which, weighted by the synapses, generates a current driving the post-synaptic neuron. By looking at the activity of post-synaptic neurons, it is possible to read out the information stored in the synaptic couplings. In classical neural network models (e.g. the Hopfield model), the mnemonic trace is assumed to be in the average value of the total synaptic currents. Usually neurons partition in two or more groups, each group being characterized by a different average synaptic current, and hence by a different mean activity. For example certain neurons will be considered ‘active’ because their activity is above some threshold, and others will be ‘inactive’ in response to the input which triggers the process of memory retrieval. The pattern of activities of all neurons represents a readout of the information stored in the synaptic efficacies. Here we investigate whether the variance of the synaptic currents across different neurons can also carry information about memories. Previous attempts \cite{1} considered the efficiency of encoding information in the second order statistics of population responses. We study the case of on-line learning in binary synapses which is known \cite{2} to be difficult because the mnemonic trace contained in the average synaptic currents decays exponentially fast. We show that there is a component of the variance which depends on the correlations between synapses which are on the same dendritic tree. Such a correlation is always present, even in the case of random uncorrelated pre- and post-synaptic patterns of activity. This component of the variance contains a mnemonic trace which also decays exponentially, at the same rate as the mnemonic trace contained in the average synaptic currents. Such a mnemonic trace can also be harnessed to retrieve information about past memories.

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure.png}
\caption{(A) Ratio between the mean synaptic currents (named $h_1$ and $h_2$) of two groups of neurons whose activity should be different when the specific memory that we are tracking is retrieved. As soon as $h_1 = h_2$, the memory is forgotten. $h_1/h_2$ is plotted against the number of new experiences which overwrite the old ones and disrupt the memory (we assume that there is constant rate $r$ of new experiences, $t$ is time). The tracked memory is stored at time zero. Different curves correspond to different statistics of the input patterns (sparse random uncorrelated patterns with an average fraction $f$ of active neurons). (B) Dynamics of the ratio of the standard deviation of the two distributions $h_1$ and $h_2$. The memory is not forgotten as long as there are detectable differences between the two standard deviations. Lighter lines correspond to decreasing coding levels: $f = \{0.30, 0.19, 0.11, 0.07, 0.04\}$.}
\end{figure}

\textbf{Acknowledgments} We thank W. Bialek and L.F. Abbott for interesting discussions. Supported by the SNF grant PP00A-106556 and by NIH-2R01 MH58754.

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Working memory associated differential inhibitions describe categorized negative priming effects

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A broad range of neural and behavioral data suggests that planning complex behaviors, cognitive control, and social behavior has been shown to depend on prefrontal cortex (PFC) [1]. The negative priming (NP) effect is characterized by the apparent slowing down of response time to a stimulus if it has been previously ignored. We differentiated the negative priming effects in the Stroop Task, depending upon the characteristics of two consecutive stimuli into three subgroups, NP1, NP2, and NP3 respectively.

A computational model we constructed in this study, which was refined version of the Parallel Distributed Processing (PDP) model [2], includes compartmentalized prefrontal system functioning. Our model was tested with the Stroop Task to characterize heterogeneity in reaction times in NP1, NP2, and NP3, which was not feasible with previously proposed PDP model. Our model is composed of prefrontal functioning unit that includes additional temporally storage nodes which resemble the working memory aspect of prefrontal cortex functions in addition to PDP model proposed previously [2].

Here, we present a computational model that provides an explanation for the differences in the reaction times for NP effects according to their proportionate stimulus sequences and directions. We propose that the difference in the NPs account for the plurality of PFC functions in human cognitive control, PFC-specific differential inhibitions, and PFC-gating mechanism via dopaminergic innervations. Current computational model is able to capture the extent of categorical differential inhibitions in the working memory to model devoted PFC-specific neural mechanism.

Acknowledgments
This work was supported by “Investigation for brain dynamics on emotion-based human decision-making using fMRI and EEG” Grant Number M10644000028-06N4400-02810

References

Caching and replay of place sequences in a Temporal Restricted Boltzmann Machine model of the hippocampus

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The hippocampus is thought to be critical for the rapid formation and cued recall of complex event memories. For example, a set of hippocampal place cells that fires in a particular sequence during exploration may fire in the same sequence during sleep [1]. We propose a novel model of the hippocampal memory system that reconciles a wide range of neurobiological data. Here we address the question of how the hippocampus encodes sequences rapidly, and what is the function of sequence replay.

Our model draws upon two recent developments of the Restricted Boltzmann Machine (RBM): 1) a hierarchy of sequentially trained RBM’s [2], and 2) the extension to sequential inputs employed in the Temporal RBM [3]. The top two layers of the model, representing the dentate gyrus (DG) and CA fields, are connected via undirected links to form an autoassociator, allowing the model to generate memories of coherent events, rather than generating top-level unit states independently. The CA region also has directed connections from previous CA states, representing the CA3 recurrent connections. Thus the probability distribution learned over the visible and hidden units is conditioned on earlier states of the autoassociator. The model is trained by contrastive Hebbian learning, with data-driven and generative phases providing the statistics for the positive and negative Hebbian updates respectively. This is broadly consistent with Hasselmo’s proposal that the hippocampus oscillates between encoding and recall modes within each theta cycle [4]. When trained on traversals along a linear track and broadly place-tuned inputs (Fig 1a), the hippocampal units develop place fields (Fig 1b), while the CA time-delayed recurrent collaterals encode the sequential structure of the data. It has been widely assumed that sequence replay is required for memory consolidation, in which rapidly stored hippocampal memories are gradually transferred to cortex. Alternatively, the hippocampus may always be required to recall complex associative memories, while replay allows the brain to maintain consistent forward and generative models in the hippocampal-cortical system [5].

Figure 1: Raster plots of 10 repetitions of a) 10 input and b) 20 CA units’ responses across space (abscissa)

Acknowledgments
This work was supported by funding from NSERC (S.B., G.E.H.) and CIAR (G.E.H.).

References
Memory Traces in Normal Neural Networks

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Critical cognitive phenomena such as planning and decision making rely on the ability of the brain to hold information in short-term memory. Many proposals exist for the maintenance of such short-term memories in persistent activity that arises from stable fixed point attractors in the dynamics of recurrent neural networks. However such fixed points are incapable of storing temporal sequences of recent events. An alternate, and relatively less explored paradigm, is the storage of arbitrary temporal input sequences in the transient responses of a recurrent neural network. In this paradigm, short-term memory reconstructs the past input history from the network’s current dynamical state$^{1−3}$. Such a paradigm raises important theoretical questions about the memory capacity of a generic recurrent network to store information about past inputs. How does this capacity scale with the number of neurons $N$? How is it affected by noise? How does the memory for past inputs degrade as a function of time? Prior work has addressed these theoretical questions primarily within the restricted class of linear neural networks whose connectivity is given by an orthogonal matrix$^3$. Here we address these questions for a more general class of matrices known as normal matrices, i.e., matrices that have an orthogonal basis of eigenvectors. This class of matrices includes symmetric and antisymmetric as well as orthogonal matrices.

We develop a general mean field theory to compute the memory capacity of a linear recurrent network with a normal connectivity matrix. Focusing on fully connected random symmetric matrices, we find that the memory trace for past inputs decays exponentially as function of time. The rate of decay is inversely related to the degree of stability of the network. At the boundary between stability and instability, this memory trace decays as a power law. The predicted power-law is verified in numerical simulations. The total capacity is, however, sensitive to noise. The strength of the noise must be exponentially small in $N$ in order for the capacity to be extensive, i.e. scale linearly with $N$. This result contrasts with the orthogonal case in which extensive capacity only requires the strength of noise to scale as $1/N$. We have also studied numerically short-term memory properties of classes of nonrandom connectivity matrices including asymmetric sparse matrices. This work highlights the architectural constraints imposed on recurrent networks that subserve short term memory functions, yields a theoretical understanding of the decay of memory traces in them, and provides a basis for further studies of more biologically realistic dynamical models of short term memory in cortical networks.

Acknowledgments
HS thanks O. White for very helpful discussions. Supported by the Swartz and Israel Science Foundations.

References
Sensory-to-motor transformation: temporal coordination in dual tasks

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For a coordinated and consistent goal-directed behavior, the human brain has to constantly control spatial as well as temporal accuracy of all movements made by an individual. This is a challenging task when a movement pattern comprises both concurrent oculomotor and manual (either bi- or unimanual) motor actions. On the other hand, the brain is engaged not only in the movement control but also in sensory-to-motor translation processes which precede motor responses (an eye movement examples an outcome of such a transformation). What happens when two sensory-to-motor processes (a periodic and a discrete, for example) have to be completed in parallel? The temporal accuracy of motor responses under these highly demanded conditions of a dual task paradigm was the subject of our experimental investigation.

The continuation tapping paradigm (1) was employed to establish a periodic task: in the continuation phase, subjects tapped at a rate given by an auditory signal in the preceding synchronization phase. In the first experiment, while tapping with the index finger of the dominant hand, the subjects responded as fast as possible to a discrete stimulus by their non-dominant index fingers (a discrete task). In the second experiment, in response to the discrete stimulus subjects have to quickly saccade: first, to the right side and then back. Phase resetting curves (2, 3) showing the temporal relationship between both actions were constructed. It was evident that, in the temporal domain, there is an interference between these concurrently performed motor tasks. For the saccades, we found mutual interactions similar to Stuyven et al (4), but also a novel type of interference: the phase entrainment as well as phase hastening effects describing the mechanism of synchronization between finger tapping and eye movements.

Acknowledgements
This work was supported by DAAD fellowship to M. Sharikadze.

References


Bayesian integration of motor plans across multiple reference frames predicts eye-centered reach errors

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The search for the neural representation of movement plans in primate cortex has revealed that a wide range of putative “reference frames” are used across sensorimotor circuits. This finding appears difficult to reconcile with psychophysical studies showing that a single reference frame can often explain the spatial patterns of movement error. Here we show how a model that uses multiple weighted representations of the planned movement vector can explain a widely-observed retinotopic pattern of reach errors, the “peripheral exaggeration effect” in pointing to non-foveated visual targets. This effect has been used by many researchers to argue that reach planning is retinotopic. We show that a similar but reversed pattern is observed when reaching to peripheral proprioceptive targets. We argue that both of these error patterns can be explained by the Bayesian integration of neural representations in multiple reference frames and by the presence of biases in the transformations between them.

Our model is based on three main ideas: there are multiple simultaneous representations of a planned movement vector, there is a statistical cost for performing coordinate transformations, and these transformations are biased due to the presence of non-uniform spatial priors. The model supposes that the spatial location of reach targets and effectors are represented in multiple reference frames regardless of the sensory modality in which they are perceived (see Figure). Computing these representations requires transforming visual and proprioceptive signals into each coordinate frame. These transformations are assumed to inject both bias and variance into the transformed signals. Bayesian integration occurs at two levels: for each representation, vision and proprioception are optimally combined, taking into account the transformation-derived variance, and the multiple resulting movement vector plans are similarly combined. In order to explain the “peripheral exaggeration effect”, the model must include a bias in the transformation between body-centered and retinotopic transformations that pulls the computed retinotopic location towards the fovea. This bias could be explained by assuming a non-uniform prior on the distribution of retinotopic locations. In particular, the data are well-modeled by a mixture model in which locations are equally likely to be drawn from a Gaussian distribution about the retina (“fixation engaged”) and a uniform distribution (“fixation not engaged”). We show that this bias arises in a network model of sensory integration (Deneve et al., *Nat. Neuroscience*, 2001) if Hebbian learning is introduced into the network and the model is exposed to this same prior distribution of retinotopic locations. The model predicts a (nearly) retinotopic pattern of reaching errors that qualitatively matches those observed for pointing to visual and proprioceptive targets in both the presence and absence of visual feedback from the hand.
Integrating sensory integration and adaptation: statistical and network models

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We present a model for the integration and adaptation of visual and proprioceptive sensory signals in eye-hand coordination, as well as psychophysical data to support the model. Sensory integration and adaptation are viewed as a coupled process, analogous to the Expectation Maximization (EM) algorithm for performing statistically optimal parameter estimation. In the model, visual and proprioceptive signals of the position of the arm are integrated in a Bayesian optimal fashion, where more reliable signals get higher weights (the E-step). The combined estimate then drives adaptation in each sensory modality, acting as a reference for determining the apparent bias in each modality (the M-step).

We focus on the case of integrating visual and proprioceptive feedback of the hand in a Virtual Feedback environment with shifted visual feedback. Since the variability of each sensory modality is non-isotropic, the combined estimate is not necessarily collinear with the two unimodal estimates (see Figure at right). The model predicts that the resulting visual and proprioceptive adaptation vectors will therefore not be collinear with the visual shift. Using a virtual reality setup we designed an experiment to test this hypothesis. As in our previous work, errors aligning the right and left hands were used as a measure of proprioceptive adaptation, and errors in aligning the left hand to visual targets were our measure of visual adaptation. As predicted, both adaptation vectors deviated from the direction of the visual shifts. The model was able to provide an account of both the direction and magnitude of these adaptation effects.

Lastly, we show that this algorithm can be implemented in a network model based loosely on that of Deneve at al. (Nat. Neuroscience, 2001). Adaptation is achieved via Hebbian learning between the primary and secondary input layers (see Figure below).
Diverse and precise tuning of neuronal activity in serotonergic brainstem nuclei

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Serotonin is an important neuromodulator implicated in diverse range of physiological functions as well as psychiatric disorders. It is released in the forebrain by neurons in a set of brainstem nuclei called the raphe nuclei. Dorsal raphe (DR) and median raphe (MR) nuclei send divergent ascending projections in the forebrain. Our current understanding of serotonin function is mostly gained from pharmacology and lesion studies. Neuronal recordings in animals performing specific behavioral tasks have greatly increased our knowledge of other neuromodulatory systems e.g. dopamine. There has been no report of recordings in raphe neurons during behavioral tasks. We believe such study will give us novel insights about raphe function at fast time scales.

In this study, we recorded from DR in rats performing a two-alternative choice odor discrimination task. Rats were trained to associate single odors to availability of water at one of two choice ports. Rats sampled odor by poking into the center port and responded with a poke into a choice port. Correct responses were rewarded probabilistically after a variable delay. Well-trained rats performed at more than 80\% in 100 - 300 trials per session. This paradigm allowed us to study sensory, motor and reward related responses with high temporal precision. After training, rats were chronically implanted with a 6-tetrode recording drive targeted to the DR using a guide cannula. 54 neurons were recorded in 7 rats over an average of 4-8 sessions per rat. Recording locations were verified histologically. Raphe neurons showed diverse firing properties with respect to waveform characteristics, firing rate, sleep state modulation. By conventional criteria, 10\% of neurons were putative serotonin neurons.

Neuronal responses were analyzed with respect to four behavioral epochs: odor sampling, movement, reward anticipation and reward consumption. Firing rates of >70\% neurons were specifically modulated during at least one epoch, many tuned to multiple epochs. Many neurons responded to behavioral events within 100 ms. A subpopulation of neurons were even more precisely time locked (~20 ms), with a very strong (> 40 sp/s) phasic response, apparently to the water valve click. During odor sampling, approximately one third of units showed decrease in firing rate while a subset also showed odor-induced activation, in rare cases, stimulus selective. During movement, equal proportion of neurons showed enhancement and suppression of firing. A large proportion of neurons (~ 40\%) were inhibited during reward anticipation while a subset (10\%) showed changes in firing rate around time of expected reward. Putative serotonin neurons showed no obvious association with a specific response profile.

These recordings demonstrate that, like neurons in other neuromodulatory nuclei, raphe neurons are rapidly and precisely modulated by various behavioral events. The functional diversity of raphe responses likely reflects in part diversity of intrinsic properties and synaptic connectivity of neurons and is consistent with the possibility that significant information processing may occur within the raphe. This study highlights the need for methods to relate firing patterns to precise identification of neuronal cell types.

Acknowledgments
We thank Adam Kepecs for help with software. This work was supported by USAMRAA NETRP.
A second-order maximum entropy model predicts correlated network states, but not their evolution over time

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Highly correlated network states are often seen in multielectrode data, yet are predicted to be rare by independent models. What can account for the abundance of these multi-neuron firing patterns? Recent work [1, 2] has shown that it is possible to predict over 90% of highly correlated network states, even when correlations between neuron pairs are weak. To make these predictions, both groups used a maximum entropy model that fit only the firing rates and the pairwise correlations (a second-order maximum entropy model), and which was maximally uncommitted about all other model features. This new work raises several questions. First, how general are these results? Both previous reports largely used retinal data. Could this maximum entropy approach also succeed when applied to cortical slices? Although the original model explained correlations among spikes, could it also be used to explain the abundance of correlated states of local field potentials (LFPs)? A second issue concerns the abundance of correlated states over time. Can a second-order maximum entropy model predict sequences of correlated states?

To examine the generality of this approach, we applied a second-order maximum entropy model to a variety of in vitro cortical networks, including acute slices from rat (n = 3) and human epileptic tissue (n = 1), as well as organotypic (n = 3) and dissociated cultures (n = 3) from rat. We explored its effectiveness in predicting correlated states of both spikes and LFPs at one time point. On average, the model accounted for 76 ± 34% (mean ± s.d.) of the available multi-information, slightly less than reported in previous studies. But in all cases, the maximum entropy model significantly outperformed an independent model, demonstrating its effectiveness in explaining correlated states in cortical spikes and LFPs at one time point. We also explored how well the maximum entropy model predicted sequences of correlated states over time. Here, the model often failed to account for the observed sequence lengths. In 7/10 preparations, the distribution of observed sequences was significantly longer (6: p < 0.001, 1: p < 0.05). We conclude that a second-order maximum entropy model can predict correlated states, but not their evolution over time. This suggests that higher-order maximum entropy models incorporating temporal interactions will be needed to account for the sequences of correlated states that are often observed in the data.

Acknowledgments
This work was supported by NSF grant number 0343636 to JMB.

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Are Cortical Networks Balanced?

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In the last 10 years or so there has been a lot of work exploring the idea that cortical circuitry in vivo is in a state of nearly-balanced excitation and inhibition, with neuronal firing largely driven by fluctuations in the synaptic input. Simple models, treated in a self-consistent mean field theory, show how this balance can be achieved dynamically, and simulations confirm that irregular firing at low rates is a robust property, in agreement with decades of single-cell recordings. Can we thereby understand the cortical states observed in typical single- or multiple-cell recordings as essentially such balanced states?

I argue here that we cannot. The reason is that the balanced-state hypothesis is not consistent with the observed size of neuronal cross-correlation coefficients, which is about 0.1. A self-consistency argument relating neuronal input and output correlations predicts cross-correlation coefficients either of order 1/N (where N is the size of the network) or nearly 1 (almost complete synchrony). Intermediate values are not stable. I have also carried out simulations of the standard model of a generic cortical column with N ranging from 500 to 5000 and synaptic concentrations up to 30%. For all cases where irregular asynchronous firing is observed, the cross-correlation coefficients are of order 1/N. For all cases where irregular asynchronous firing is observed, the cross-correlation coefficients are of order 1/N. It is not clear exactly what N to use in comparing these results with experiments, but it is hard to argue that it should be of order 10, which is what would be needed to match the measured values. At the least, such a small N would invalidate the popular and appealing mean-field picture, which requires large N because it employs a central-limit theorem.

The most frequently-cited cross-correlation measurements [1,2] were mostly performed in area MT of monkeys viewing irregularly-moving stimuli. In these conditions, spikes occur most frequently when the stimulus starts to move rapidly in the cell’s preferred direction. These responses can be very strong because they are caused directly by excitation from lower areas, and the feedback inhibition from the local circuitry (which is what would maintain a balanced state) has not kicked in yet. Of course the network will re-balance itself quickly if the stimulus motion doesn’t change too rapidly, but by then the neuron will already have spiked. It will also spike some when it is better balanced, but the firing statistics are dominated by the spikes during the brief unbalanced periods.

I tested this picture by stimulating the generic column model with a simple kind of time-dependent input suggested by the experimental paradigm: a firing rate in the external driving population which flips between low and high values at intervals whose duration is exponentially distributed. (Most simulations were done for a mean on-duration (and mean off-duration) of 50 ms.) I found that very typically neurons tended to fire synchronously (within a time window of 5-10 ms) in fast response to off-on stimulus flips, in clusters with a distribution of sizes ranging up to several hundred. The average cross-correlation coefficients were of order 0.1, in agreement with the experiments. Thus, the neuronal activity is not characteristic of a steady balanced state. Rather, it reflects firing in response to rapid changes in the external excitation of the network during brief periods when the balance is strongly upset.
Illuminating cell identity during in vivo recordings

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Tell us your favorite brain region. Whatever area you pick, we will be able to tell you a lot about it, like its inputs or the stimuli that optimally drive its activity. If your goal is to understand the function of neuronal circuits in vivo, you will need to see what each of the individual neurons in the circuit is doing. However, as soon as you stick your electrodes in, you will face the same problem that most neuroscientists do: a huge diversity of neuronal responses.

Part of the response diversity arises from the fact that neuronal circuits are made up of a heterogeneous mixture of neurons with different intrinsic properties, input and output connections. We hypothesize that we can explain much of this apparent diversity by identifying the nature of the cells we record from. The problem of characterizing neurons in a circuit becomes particularly difficult when the goal is to do extracellular recordings in freely behaving animals. In this kind of experiment, one can rely on methods like antidromic stimulation or the shape of the recorded spikes to tease apart the identity of some of the elements in the circuit, but these methods have limited application.

We are addressing this issue with a system based on the ability to target and remotely control the activity of specific populations of neurons. This can be achieved with the help of light-gated ion channels whose expression is genetically restricted to the intended target neurons, so that only they have a built-in capacity to respond to light. For this, we are using the photo-triggered ion channel ChannelRhodopsin-2 (ChR2), an algal protein that can be genetically targeted to the cells of interest, and whose activity can be reliably controlled at the millisecond timescale with blue light: activation of the channel leads to precise control of activity in the designated neurons [1].

We are combining expression of this photoreceptor in specific cell types with extracellular tetrode recordings in freely behaving animals: ChR2 is expressed in vivo in a particular cell type, using viral systems; during extracellular recordings a large number of single units is observed; in the end of the experimental session light is shined over the recorded area; only the cells expressing ChR2 respond to the light stimulus, allowing us to identify the nature of the cell we recorded from.

We are testing this strategy using cell connectivity as a way of defining neuronal types in the auditory cortex (ACx) of rats. ACx neurons pyramidal neurons project to multiple brain regions, including the amygdala or the posterior parietal cortex, and presumably carry different information about auditory stimuli to these centers. To specifically target ACx cells based on their projection pattern we are making use of herpes simplex virus (HSV), which can retrogradely travel through the axons of infected neurons. So, by infecting the axon terminals of ACx pyramidal neurons that project to these different brain regions we hope to be able to identify cells based on their acquired capability to respond to light. Our first results, expressing ChR2 ubiquitously in the ACx of the rat, show that we can reliably control the activity of neurons in the cortex of the rat, in vivo, using light. Through a combination of a variety of different but complementary tools, we hope to get new insights about neuronal circuits, more complete than what was possible by solely using electrophysiology.

Response variability of type-1 neurons to periodic and random pulsatile input

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Globus pallidus (GPe) and subthalamic nucleus (STN) neurons of the basal ganglia communicate with inhibitory and excitatory efferents respectively, but individual cells are not necessarily reciprocally connected [1]. Examining previous models [2] reveals that neurons with both type-1 and type-2 phase response curves (PRCs) could be involved in the GPe-STN circuitry. In vivo and in vitro GPe recordings show spike time variability that may be due to stochastic external synaptic input, periodic input, or intrinsic membrane noise. In an effort to systematically understand the variability caused by various intrinsic and extrinsic factors (including periodic and stochastic [3]), we report here some modeling work on response properties of type-1 neurons (with period $T_0$) to periodic ($T_f$) and random (with Gaussian noise $\eta$) external pulsatile input by using piece-wise linear approximations to the corresponding typical PRCs. 1:1 phaselocking is achieved for $r (= T_f / T_0) < 1$, but large enough that $r > 1 - A$, where $A$ is the maximum phase advancement of the PRC. The stability of this state depends also on the skewness of the PRC (parametrized by $M$). PRCs with right skewness allow synchrony for stronger stimuli, but left skewed PRCs limit the stability region to $A < 2(1 - M)$. Thus left skewed PRCs can show a bigger parametric region displaying a variable spike output. The neuron’s desynchronizing mechanism and the firing rate variabilities are studied around but outside of 1:1 locked state. For $r$ close to unity, the coefficient of variation (CV) of the interspike intervals is a sensitive function of the skewness factor $M$. But for weaker stimuli or for $r \ll 1$, CV is high but confined to a narrow range. The results are extended to two and large number of uncoupled neurons with type-1 PRCs that are receiving common periodic and/or random inputs.

References


Oscillatory circuits underlying the retinal detection of temporal periodic pattern

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It is observed that retinae subjected to periodic patterns of light flashes in the range of 6-20 Hz can respond to an omitted flash by ganglion cell spikes after a precisely fixed amount of time [1]. We explore the mechanism underlying the omitted stimulus response (OSR) with emphasis on the function of ON bipolar cells. We model ON bipolar cell terminals with LRC circuits in which an inductor represents the voltage-dependent conductances. Two models are developed and tested: a single adaptive oscillator model and a resonator bank model. In the former there is only one LRC oscillator whose inductance is determined by calcium concentration which effectively leads to the dependency of oscillator’s resonant frequency on stimulus frequency. In the latter multiple oscillators are involved which individually dominate the response at each stimulus frequency. The matching of terminal oscillation frequency with flash stimuli frequency implies a fixed latency from OSR to omitted flash as observed in experiments (See Fig. 1). For the resonator bank model the effects of gap junction coupling and synchronization are examined. We also compare model predictions and empirical observations in term of OSR size and latency when flash number and duration vary. We find that the adaptive oscillator model is more robust and can better encompass the frequency range in which OSR is observed, suggesting that calcium dynamics and the nonlinear conductance-voltage relation play important roles.

![Graph](image)

Figure 1: Predicted delays from OSR to omitted flash using single adaptive oscillator model (black triangles) and resonator bank model (red circles). Dashed line shows average latency observed [1].

Acknowledgments
This work is supported by PHS grants MH58480 and MH62196 (Cognitive and Neural Mechanisms of Conflict and Control, Silvio M. Conte Center). J. G. is supported by The Britt and Eli Harari Fellowship.

References
Coupling inhibitory populations: from phase-locking to chaos

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Synchronization of neural oscillations has been hypothesized to play an essential role in the large-scale integration of the activity of distinct cell assemblies in brain. Experiments consistently show that synchronous periodic rhythms emerge, disappear and organize themselves spatially across multiple local areas, oscillating coherently with dynamically evolving phase relations [1]. The strong irregularity of cortical neurons response \textit{in vivo} combined with a significant degree of synchrony in the temporal fluctuations of neuronal activities hints as well to the existence of less regular oscillatory episodes, possibly associated to intrinsically chaotic dynamical states [2]. In this work we explain in a unified way the generation of local oscillatory activity in inhibitory interneuronal networks, the spontaneous development of phase-locked configurations in networks with patchy connections, and, finally, the transition from periodic to aperiodic oscillatory regimes [3, 4].

We first studied a simplified model in which a local network of neurons is represented by a threshold-linear firing rate variable inhibiting itself with a delay [4]. Delayed inhibition leads to oscillations of the firing rate, provided that the self-coupling is strong enough. Two such oscillating units are then coupled together symmetrically. Periodic in-phase and out-of-phase oscillations as well as bistable states can be obtained if there is reciprocal inhibition between the units. On the other hand, when the reciprocal interaction is excitatory, two regimes can be identified: (I) For strong self-inhibition, the system spontaneously breaks its symmetry and undergoes phase-locked periodic oscillations with an intermediate phase-shift. Increasing gradually the excitatory coupling, the laggard unit activity becomes more irregular. Only for stronger excitation the symmetry is restored and both populations become chaotic. (II) In the case of weaker local inhibition, the system develops aperiodic oscillations which are initially quasi-periodic and becomes chaotic only for stronger excitatory coupling.

The phase-diagram for the delayed rate model can be in part determined analytically. The predictions are then compared with extensive simulations of an associated conductance-based model [4]. Each population is now modeled as a randomly connected network of inhibitory interneurons and some diluted long-range excitatory connections are drawn at random between the two populations. The different dynamical states of the rate model, including asymmetric chaos, symmetric chaos, quasi-periodic oscillations and bistabilities, are found when maximal conductances and the probabilities of establishing internal inhibitory and external excitatory connections are varied.

Acknowledgments
This work was supported by UniNET-NEST EU FP6 research grant.

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Parallel Hopfield Networks

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There is a growing body of evidence for the existence of precisely timed spikes in the brain. This idea has led to the development of a plethora of computational models exploiting precise spike timing (e.g. [1]). One such model is the Concurrent Recall Network (CRN) model of Wills [2]. In these networks, memories are represented by asynchronous firing patterns that are stored in the system by making use of variable axon delays between neurons to ‘resynchronize’ the otherwise asynchronous input to each neuron, a concept known as Polychronization [3]. In addition, the network employs conjunction detectors on each neuron which are simplified models of spiking dendrites [4]. These novel elements vastly improve the performance of the CRN by reducing the interference between different memories allowing multiple memories to be recalled simultaneously - hence the name Concurrent Recall Networks.

A limitation of the CRN model is that the memories are binary in that they are either activated or not. A different approach is to allow memories to be partially activated with only a subset of neurons spiking at the specified time. By creating these different sub-patterns ‘within’ each CRN memory, the memory capacity of the system expands rapidly.

In particular we choose to store random patterns of activity in these ‘sub-networks’ in a prescription similar to the Hopfield model [5]. In this case, each CRN style memory acts as an independent attractor network implementing a noisy approximation to the usual Hopfield dynamics. In addition, the network retains the concurrent recall ability and is able to simultaneously enact the dynamics of multiple Hopfield networks in parallel in the same network; therefore we term these networks Parallel Hopfield Networks.

It is possible to study these networks analytically and we have obtained mean-field equations for the order parameters of the Hopfield sub-networks. Solution of these equations allows the computation of the memory capacity of each of the Hopfield sub-networks as a function of the number of stored CRN memories and the amount of background activity (caused by recall of other CRN memories or neuronal noise) in the network. Predictions from this theory are in agreement with initial simulations on networks with large numbers of neurons.

Acknowledgments
We thank D. J. C. MacKay, S. Wills and L. H. Finkel for helpful discussions.

References
Behaviors emerge from computations distributed across many neural circuits. How are these neural circuits joined together into systems? How much does one neural circuit need to know about the dynamics of another to properly interpret its output? At one extreme we might imagine that each brain area must in some sense reverse engineer the circuit that generated its input in order to engage in further computations. On the other extreme, we might imagine a highly plug-and-play system in which individual brains areas know little about each other’s dynamics, and instead merely use some simple agreed upon code to transmit information. In this work, we use the prey capture behavior of the salamander as a model system in which to address these questions. Salamanders are predatory amphibians that catch rapidly moving insects. At the forefront of this behavior, nonlinear circuit dynamics in the retina transform the image of a moving target into a complex pattern of electrical impulses distributed across thousands of ganglion cells. The stimulus which drove the responses of a single ganglion cell is not easily inferred from these spike patterns. Here we demonstrate experimentally that despite these complexities, the position of a small rapidly moving target may be tracked with close to photoreceptor precision by calculating the center-of-mass of the ganglion cell population activity (Fig 1), a quantity that can be estimated with the well known population vector average (PVA). PVA tracking works only for cell types whose response dynamics are characterized by the motion anticipation circuit described by [1]; cell types lacking these dynamics generate noisier estimates with substantial delays to the true target position.

Our results show that a highly complex and nonlinear circuit effectively generates a low-dimensional output that may be decoded with linear methods. Such a simple and fast algorithm is well suited to the task of real-time target tracking. A downstream decoder needs to know only the receptive field center of each ganglion cell -- a parameter easily learned during development. In contrast the temporal dynamics and nonlinearities inherent in retinal encoding may be ignored. However, there is a price to be paid -- we show that this algorithm is robust only for a range of target sizes and speeds that are commensurate with that of the prey captured by the salamander. This suggests that specializations in the salamander for catching moving insects begin in the retina itself, where particular dynamical regimes of individual neural circuits ultimately constrain the sizes and speeds of prey that the salamander can catch most effectively.

Figure 1. Photoreceptor-precision target tracking using populations of ganglion cells. Spike rate data from a population of off-type ganglion cells is used to track a target moving at ~10 deg/s via the population vector average. The population estimate (red) has zero delay with respect to the true position (black), and an RMS error of ~5 photoreceptors (PR). The estimate from the model (blue) has ~1 PR error, representing the noise-free case. Note the characteristic overshoots in the estimate during rapid turns.

Layer 2/3 Is A Neural Multigrid: Information Maximization In A Local Network Explains V1 Hypercolumn Formation

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One of the most striking feature of primate V1 is a topographic ordering of receptive fields. Previous models of topographic map formation (e.g., [1]) pose topography as a constraint on receptive-field formation. Optimization techniques maximize information between visual inputs and outputs [2], and produce receptive fields strikingly similar to those in V1, but not topography. Neural network implementations of infomax [3] require fully connected lateral networks, which the cortex does not possess. While the density of lateral connections in layer 2/3 surpasses all other connection classes [4], a local, patchy connectivity pattern is still observed [5]. A model of infomax in 2/3 must therefore explain how this optimization can be implemented in a local network. We hypothesized that topography might emerge naturally from such a model.

Here we present a neural multigrid that approximates infomax in a locally connected network, and embeds optimal receptive fields in a phase-independent topographic map. Our approach allows for a 66% reduction in the density of lateral connections, and yields a network topology similar to that observed in layer 2/3. We conclude that two key features of layer 2/3, 1) local, patchy synaptic connectivity and 2) topography, together serve the same goal: information maximization in a biologically constrained network.

Figure 1: A. Neural multigrid maps optimal filters. B. Local network yields hypercolumns.

Acknowledgments
We thank Ralph Linsker and John Wagner for many helpful discussions.

References
State-dependence of sensory-evoked responses in neocortex

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The neocortex typically operates in one of two states. The activated (desynchronized) state, typical of alert wakefulness and REM sleep, is characterized by a high-frequency, low amplitude local field potential (LFP). The inactivated (synchronized) state exhibits high low-frequency power, and spontaneous transitions between UP states of widespread depolarization and spiking, and DOWN states of generalized silence.

Cortical responses to sensory stimuli exhibit enormous trial-to-trial variability, much of which is state-dependent. This presents a problem for averaging in order to find the “typical” response. One solution is to classify trials (repeated presentations of the same stimulus) into categories depending on the cortical state at the time of the stimulus (activated vs. inactivated, UP vs. DOWN, etc.). In this work, we are more interested in understanding how the intrinsic dynamics associated to different states controls population activity.

We investigated the state-dependence of sensory-evoked responses using a dynamical systems approach. Cortical LFPs and population spike trains were recorded from the auditory cortex of urethane-anesthetized rats using multi-site silicon microelectrodes. 5ms noise click stimuli were presented, and intervals of silence were used to investigate spontaneous activity. Activated states were induced by electrical stimulation of the pendunculo-pontine tegmental nucleus (PPT).

We quantified the strength of “initial” and “persistent” network responses using multiple unit activity (MUA). In the activated state, initial responses were more or less consistent, whereas persistent network activity merely reflected a return to baseline. In contrast, the inactivated state exhibited greater variability in initial responses, and persistent activity which often reflected transitions between UP and DOWN states. We found that a “past activity” variable, which summarizes recent network activity, is highly correlated to persistent network activity after a stimulus presentation. In the activated state, the correlation was strongly positive, whereas in the inactivated state, the correlation was strongly negative.

By viewing the MUA as the output of a dynamical system driven by external sensory stimuli, we constructed a simple nonlinear model which captures the essential dynamic differences between the activated and inactivated states, and explains much of the trial-to-trial variability of sensory-evoked responses. By fitting the model to data, we were able to determine the phase diagram associated to each kind of activity, and the bifurcation which transitions from activated to inactivated state. Furthermore, using the model we made predictions for initial and persistent responses which were better than those using past activity alone.

Acknowledgments
This work was supported by NIH grant R01MH073245, and the Alfred P. Sloan Foundation.
A Continuous Attractor Model for Grid Cell Activity

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Measurements in the dorsolateral band of the medial entorhinal cortex (dMEC), an input to hippocampus, reveal that neurons in this area selectively fire when a rat, moving around in an enclosure, visits any vertex of an imaginary regular triangular lattice that tiles the plane \(^1\). In this work we consider continuous attractor models as a possible description of this neural activity: Symmetric mexican-hat synaptic connectivity leads spontaneously to the formation of a static triangular lattice pattern within a two-dimensional neural layer. Because all phases (translations) of this pattern are equivalent attractor states of the network, it is possible to induce rigid translations of the pattern by including a fraction of neurons with weak asymmetric synaptic connectivity, and driving them selectively with inputs that represent rat velocity as the rat moves around in real space. Such continuous attractor models, in the context of grid cells, were suggested very recently by us and other authors \(^2\)-\(^4\).

To test whether a continuous attractor model could provide a realistic explanation for the experimental observations, we simulated such models using network sizes constrained by counts of neural number in EC. We find that in a finite network with non-periodic boundary conditions, a grid-cell firing pattern typically does not emerge in the single neuron response as a function of rat position, even when a regular triangular grid is robustly present in the neural population \(^3\). To actually reproduce grid cell firing, stringent requirements must be met, which we enumerate and discuss in detail. We show that if the network is finite and has non-periodic boundaries, there are fundamental reasons tied to the structure of the attractor manifold for why it is difficult to meet these requirements.

We next show that a continuous attractor model may nevertheless yield grid cell firing patterns, in either of two possible ways. First, with proper choice of weights and inputs at the network boundary, the accuracy of the network’s response to velocity inputs can be dramatically improved, and produce grid-cell firing. However, the accumulation of errors with rat movement cannot be eliminated altogether even in a noise-free network. Second, a network with periodic boundary conditions can have an extremely accurate velocity response, limited in practice only by intrinsic noise or uncertainty in the velocity input. We suggest specific experimental tests to distinguish between these distinct possibilities – an important step in moving continuous attractors from the metaphorical to the concrete realm in explaining neural activity.

Acknowledgments

We thank Torkel Hafting and Mehran Kardar for helpful discussions. This work was supported in part by NSF grant PHY99-07949.

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Neurally Plausible Sparse Coding via Competitive Algorithms

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Recent evidence indicates that many sensory systems employ sparse population codes [1]. However, neurally plausible mechanisms capable of efficiently finding sparse approximations are currently unknown. Signal processing researchers often employ suboptimal greedy sparse approximation algorithms [2] that iteratively select the single best vector. Though these algorithms work well in practice, they have two significant drawbacks making them implausible for neural systems: they would be difficult to implement in parallel architectures, and they have erratic temporal variations when coding smooth time-varying stimuli.

We have developed and studied a new class of neurally plausible sparse approximation algorithms based on thresholding and one-way lateral competition. In our Competitive Algorithms (CAs), a neuron with receptive field \(\phi_i\) has internal state \(u_i(t)\) that charges up like a leaky integrator in response to a stimulus \(x(t)\). Thresholding functions ensure that only units with significant activity induce competition through lateral inhibition. Specifically, each unit’s internal state is described by the ODE

\[
\dot{u}_i(t) = \frac{1}{\tau} \left[ \langle \phi_i, x(t) \rangle - u_i(t) - \sum_{j \neq i} (\phi_i, \phi_j) T_\gamma(u_i) \right],
\]

where \(T_\gamma(\cdot)\) is a thresholder. CAs descend energy functions combining reconstruction MSE and a sparsity-inducing penalty,

\[
E(t) = \frac{1}{2} \left\| x(t) - \sum_i T_\gamma(u_i) \phi_i \right\|^2 + \gamma \sum_i \Lambda(c_i(t)).
\]

The form of \(\Lambda(\cdot)\) is determined by \(T_\gamma(\cdot)\), and can include \(\ell^1\) or \(\ell^0\)-like penalties (corresponding to soft and hard thresholding).

In addition to being neurally plausible, CAs can produce coefficients with approximately the same sparsity as greedy algorithms. CA coefficients also display inertia, with the coefficients contributing to the representation changing smoothly as the stimulus changes. Figure 1 illustrates that on a standard video test sequence, greedy algorithms used virtually a new set of active coefficients on each frame whereas CAs reused most of the same coefficient locations. This regularity of the CA coefficient sequences reduced the conditional entropy of the coefficient activity states by a factor of two over greedy algorithms. By capturing the smoothness and predictability inherent in the natural video sequence, CA coefficients make it easier for higher-level structures to identify and understand the changing content in the time-varying stimulus.

References
Intrinsic basis of gain modulation and adaptive neural coding

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In some forms of sensory adaptation, the neural gain curve scales rapidly with the standard deviation of the randomly varying input [1,2]. Further, the linear filters of a linear/nonlinear model may also change. While this form of adaptation has been addressed as a learning problem [1,3,4], in some systems, this change is so fast that it has been proposed that it may be a result of intrinsic nonlinearities [5,6,7,8,9]. A related issue is the observation of gain control by background noise in cortical neurons [10,11]: the slope of the firing rate vs current (f-I) curve can be changed by changing the variance of background random input. In this work, we will put these results in the perspective of neural encoding of random inputs with varying mean and variances, and will show how a given neuron’s encoding behavior with respect to mean and variance is influenced by the static parameters of the underlying dynamical system.

Using the Hodgkin-Huxley model, we construct a linear/nonlinear model using white noise covariance analysis. We show that different choices of the maximal conductance parameters lead to distinct gain modulation, such that a static neural model may implement gain control in the sense of the LN model. For a class of simple models we also derive the form of changes in the spike-triggered average and covariance modes as a function of the variance of the input.

Finally, we are able to analytically relate variance-dependent changes in the gain of f-I curves to an underlying LN model. Under the assumption that the LN model is fixed, we derive a series of equations relating the local change of the gain to white noise analysis. First of all, the gain with respect to the mean is proportional to the time integrated spike triggered average (STA). The spike triggered covariance, with the STA, determines the slope of the gain with respect to the mean, and also the gain with respect to the variance. In a particular case when the encoding depends on a single feature, the last two quantities are proportional to each other, which leads to a simple result: the firing rate satisfies a diffusion equation in a space spanned by the mean and the variance. We test these equations using the HH model neuron.

References

Distance Measure in Probability Space and Correct Measure of Variability

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In many experiments, spike times are recorded under several different conditions and the major goal of the experiments is to describe the statistical difference between the spike sequences under different experimental conditions such as different sensory stimuli. For a stationary Poisson Process, the firing rates would measure the statistical difference of spike sequences reasonably. However, non-Poissonian features as well as non-stationarity of spike sequence may make this measure of the statistical difference very wrong. Statistical features of spike sequences from a real neuron is not easy to be reproduced by a simple model. For example, Shinomoto et. al. found that a simple LIF neuron or Ornstein-Uhlenbeck process does not reproduce spiking statistics of neurons in prefrontal cortex. The inconsistency between the model and the data was mainly due to large skewness values of the data which may be caused by anomalous long intervals embedded in spike sequences. An important question is whether the statistical features that we fail to reproduce is significant in terms of information within spike times.

Here we study how the error of discrimination based on spike times depends on higher order moments of the ISI distribution than first two moments: mean and variance. We calculated Chernoff distance for spike sequences generated by two different renewal processes where the probabilities of generating spike sequences are determined by ISI distributions. Chernoff distance measures the discrimination capability between a pair of distributions and has an exponential relation with maximum-likelihood discrimination error in small-error limit. We consider a pair of ISI distributions with the same coefficient of variability (CV) and different means. Then, Chernoff distance between the corresponding distributions of spike sequences is calculated. We do this for several analytical models such as gamma, inverse Gaussian (IG) and exponential with absolute refractoriness period (ER) ISI distributions and ISI distribution of LIF neuron. We found that high variability in terms of CV does not necessarily mean low information in spike times. This means that the information within spike times strongly depends on higher moment than the mean and the variance. This explains why Manwani et. al. found that the estimation error based on spike times is not necessarily bigger with spike sequences with larger CV. Refractory period is very important for spike sequences to have large discrimination capability. Spike sequences from LIF neuron are more informative than that of IG and gamma distribution renewal processes when stationary voltage level is close to threshold value. We also discuss the error of assuming Poisson distribution in estimating discrimination capability based on spike times.
Burst spiking as a neural code in insect auditory receptors

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Based on the characteristics of the ionic channels that compose the cellular membrane, some neurons have a tendency to alternate high frequency periods with silent intervals. This is called burst firing. In order to characterize the type and amount of auditory information transmitted through burst firing in insects, the activity of grasshopper acoustic receptor neurons was recorded, for several stimulating sound waves. The analysis of these data reveals that the probability of generating bursts is strongly influenced by the statistical properties of the acoustic stimulus. Hence, the tendency to burst is not only determined by intrinsic neuronal properties, but also by the way in which those properties interact with the temporal structures in the stimulus.

These findings imply that there is a selective correspondence between specific stimulus features and particular response patterns. We characterized this correspondence, showing that bursts containing a specific number of spikes are usually found shortly after stimulus segments that share common features. Reciprocally, bursts containing different number of spikes are associated with stimuli that are qualitatively different from each other. Hence, the number of spikes in a burst conveys information about specific characteristics of the stimulus. In addition, the time at which a burst is initiated allows one to locate the relevant stimulus in time. In order to provide a quantitative measure of the relevance of burst firing in information transmission, we developed a new method to quantify the mutual information rate between stimuli and responses. We find that bursting grasshopper receptors encode 47% of the total information they transmit in burst-like patterns.

Acknowledgments

This work was supported by the Alexander von Humboldt foundation, the Consejo de Investigaciones Científicas y Técnicas, the Deutsche Forschungsgemeinschaft (SFB 618) and the Secretaría de Ciencia y Tecnología.

References


Deciphering correlations: Bayesian decoding of multi-neuronal
spike trains in primate retina

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Groups of neurons are known to exhibit correlated spiking activity, but the relevance of correlations for information processing is a topic of much current debate. We examine this issue by developing an optimal decoder for reconstructing a visual stimulus from the observed spike trains of a population of retinal ganglion cells. The decoder is based on a generalized linear model (GLM) that accurately represents the probabilistic encoding of stimulus information in the spiking responses of the population. The model for each cell consists of a bank of linear filters that capture stimulus dependence, spike history dependence, and dependence on the spikes of other cells, followed by an exponential nonlinearity and instantaneous (Poisson) spike generation. The filters operating on spike trains of other cells serve as “coupling terms” that capture interactions between cells, allowing for time-varying correlations (and anti-correlations) beyond those induced by the stimulus.

We fit this model to a population of several dozen simultaneously-recorded macaque retinal ganglion cells (ON and OFF parasol cells), whose receptive fields completely covered several square degrees of visual space. We used a regularized maximum likelihood fitting procedure to determine functional connectivity, and found strong positive coupling between pairs of ON cells and pairs of OFF cells, and negative coupling between ON-OFF pairs, with the strongest coupling occurring between nearby pairs of cells. We also fit a version of the model in which coupling filters were eliminated, making the response of each model cell conditionally independent of its neighbors (i.e., dependent only on the stimulus and its own spiking history).

We then used the model to perform optimal Bayesian decoding (reconstruction) of a novel stimulus from a set of observed spike times. By comparing the performance of the uncoupled model and with that of the full (coupled) model, we assessed the importance of correlated spiking for encoding and decoding. We found that: (1) spatial receptive fields are significantly smaller under the coupled model, suggesting that some portion of the classical receptive field can be more accurately explained in terms of the spiking activity of nearby cells; (2) the coupled model provides significantly more accurate predictions of multi-neuronal spike trains, faithfully accounting for second and higher-order correlations; (3) model-based decoding was significantly more accurate than optimal linear decoding; and (4) stimuli can be decoded $\sim 10\%$ more accurately using reconstruction based on the coupled model compared to the uncoupled model. These results indicate that correlations in retinal spiking activity cannot be ignored without losing information.

Acknowledgments
Funding was provided a Royal Society USA/Canada Research Fellowship (JP); NSF IGERT DGE-03345 (JS); NEI grant EY018003 (EJC, LP, & EPS); Gatsby Foundation Pilot Grant (LP); US National Science Foundation grant PHY-0417175 (AML); McKnight Foundation (AML & EJC); and HHMI (EPS).
Application of multiple generative models for identifying and decoding spatial memory in the hippocampus

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Generative models have been used to explain observed neural activity in terms of neural representations and the neural computations associated with information processing. The application of generative models has typically sought to identify a single information coding scheme and estimate its parameters. While potentially valid within early sensory systems, the assumption of a single information coding scheme or representation type is unlikely to be completely valid within more classical memory systems.

Neural representations within memory systems are derived from two primary sources, incoming sensory-based information that will potentially be encoded \textit{and} retrieval-based memory information that has been encoded. While the represented class of information is the same, regardless of its source, the dynamics of these representation types may be very different. Indeed, hippocampal representations of space display very different dynamics when driven by sensory information during awake behavior and when driven by previously stored, presumably memory, information during rest and sleep.

We investigated spatial information processing within the rodent hippocampus during navigation by comparing the performance of multiple generative models with explicitly defined different dynamical behaviors. We used a predictive filter-based decoding method to transform hippocampal neural activity, $s_t$, into a probabilistic representation over space, $x$. The iterative decoding algorithm employs a prediction step based on the model of representation dynamics $p(x_t|x_{t-1})$

$$p(x_t|s_{t-1}) = \int p(x_t|x_{t-1})p(x_{t-1}|s_{t-1})dx_{t-1}$$

(1)

and a correction step based on the observed spiking activity $s_t$ at time $t$

$$p(x_t|s_t) = \frac{p(s_t|x_t)p(x_t|s_{t-1})}{p(s_t|s_{t-1})}$$

(2)

where $p(x_t|s_t)$ is the probabilistic neural representation of space. Multiple dynamical models $p(x_t|x_{t-1})$ based on Brownian motion with different velocities were compared. For time interval, $t$, the explanatory power of the of each dynamical model was assessed by finding the probability that decoded neural representation [the posterior distribution of model $p(x_t|s_t) \rightarrow p(\hat{x_t})$] generated the observed neural activity

$$p_G(s_t) = \sum_x p(s_t|x_t)p(\hat{x}_t)$$

(3)

This method detected flexible use of multiple well-organized representation dynamics during awake behavior that often deviated from the animal’s position to reflect memory-based processing and included route replay and novel spatial decision-making processes. The use of multiple generative models provided a normative approach to identifying the contributions of experimentally observable sensory processes, experimentally covert cognitive (memory) processes, or other (noise) processes within the hippocampus.

Acknowledgments

We thank Edvard Moser for helpful discussions. This work was supported by a Fulbright scholarship to AJ, the Center for Cognitive Sciences (UofM) and the Centre for the Biology of Memory (NTNU).
Olfactory Coding and Discrimination in Drosophila

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In the adult Drosophila, odor molecules bind to the olfactory receptor proteins on the surface of the first order sensory neurons, the olfactory receptor neurons (ORNs). Each ORN expresses, out of a large family, only a single olfactory receptor protein. The axons of the ORNs expressing the same olfactory receptor converge onto a single glomerulus in the Antennal Lobe and target a few excitatory projection neurons (PNs). The PNs subsequently project to higher order areas such as the Mushroom Body and the Protocerebrum. A large amount of physiological data, both from this lab and other labs, has recently emerged, utilizing two-photon calcium imaging and direct electrical recording of genetically engineered animals. PNs coming out of distinct glomerulus are differentially activated by dissimilar odors, and in turn generate a combinatorial code.

How such a code is interpreted in the higher areas of the fly brain remains mysterious. Here we present a model of higher order neurons targeted by PNs that can discriminate individual odorants based on existing electrophysiological data. In particular, this model draws upon ideas from Claude Shannon’s principles of information transmission through noisy channels and estimates the discrimination capacity of such a system. Somewhat surprisingly, the number of odors that can be confidently discriminated, even in the presence of noise, grows exponentially with the number of distinct glomeruli present. The model also predicts the connectivity patterns from the PNs to the higher order neurons based on the ORN activity profiles. Finally, it proposes a hypothesis explicating the elusive, transformative function of the Antennal Lobe that would enhance discrimination of real odorants.
Isotropic preferred-torque distributions explain anisotropic preferred-direction distributions and population vector/reach direction relationships

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A simple model describing the relationship between neural activity in MI and corresponding two-dimensional arm motion in the horizontal plane is examined, wherein contributions to torques \((\tau_1, \tau_2)\) at both shoulder and elbow by each neuron are assumed proportional to the firing rate. Individual cell activity is assumed to increase as the direction of the \((\tau_1, \tau_2)\)-vector approaches that of the corresponding (constant) torque-per-firing-rate vector \((u_j, v_j)\) generated by the jth neuron. For example, if cosine tuning is assumed on the \((\tau_1, \tau_2)\)-plane, and a continuous isotropic gaussian distribution \(N(u,v)\) is assumed, then a neuron’s activity is given by

\[
r_i = \frac{8\sqrt{\pi}}{N_{tot} \rho} \sqrt{\tau_1^2 + \tau_2^2} \cos(\phi - \phi_j)
\]

where \(\phi = \tan^{-1}(\tau_2 / \tau_1)\), \(\phi_j = \tan^{-1}(v_j / u_j)\), and \(N_{tot}\) are the total number of neurons in the distribution and the r.m.s. norm of the \((u,v)\)-vector. Due to torques required to decelerate the arm after reaching peak velocity, cell activity as a function of reach direction tends to be bimodal (maxima 180 degrees apart) when the ratio of frictional to inertial torques is small. Such bimodality has been observed, particularly when monkeys move manipulanda of appreciable mass (cf. [1]). In the presence of substantial viscous friction, activities become unimodal, preferred directions (PDs) are meaningful, and population vectors as defined by Georgopoulos can be constructed. Applied to linear reaching tasks originating from a common point, results show (1) systematic deviations between reach directions and population vectors (Fig.1), (2) large variations of population vector magnitudes with reach directions (Fig.2), and (3) anisotropic distributions of PDs, all of which are very similar to those observed by Scott et al. [2]. Because the assumed distribution \(N(u,v)\) is isotropic, it is clear that anisotropic distributions of PDs can be artifacts of the task set, and not necessarily fundamental properties of neural ensembles. Using synthetic ensembles with torque-tuning properties selected randomly from \(N(u,v)\), the pseudo-inverse method was employed to reconstruct torque trajectories from cell activities, resulting in sets of filter coefficients that were compared against the known synthetic cell properties. These experiments suggest that in order to extract approximate torque-tuning characteristics of neural ensembles, more than 1000 neurons are probably required.

Acknowledgments
I thank Nicho Hatsopoulos for helpful discussions and review of this work.

References
REVERSE CORRELATION ANALYSIS OF THALAMIC RESPONSES TO DYNAMIC WHISKER STIMULATION

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A major function of the whisker thalamus (ventro posterior medial nucleus, VPM) is to transmit signals about surface texture to the barrel cortex. Different textures are known to induce characteristic “kinetic signatures” of whisker vibration, which are transduced as corresponding temporal sequences of precisely timed spikes by mechanoreceptors in the whisker follicle. However, it is not known how dynamic whisker vibrations are encoded by neurons in the thalamus.

In this study, we performed extracellular recordings from single VPM neurons in anaesthetized rats. To study how VPM neurons encode dynamic whisker vibrations, we recorded their response to mechanical stimulation of the contralateral whiskers with Gaussian white noise and analysed stimulus-response relationships using reverse correlation methods.

We found that many VPM neurons responded in a highly reproducible manner, with mean spike timing jitter of 0.4 ms. The most common type (~50% of our sample) had a velocity-sensitive spike-triggered average (STA), and an input-output function where firing rate increased monotonically with velocity. Other neurons had either monophasic position-sensitive STAs or more complex, polyphasic STAs sensitive to higher derivatives of the whisker signal.

To test the completeness of this stimulus-response description, we fit a maximum likelihood “generalised linear model” (GLM) to the data [1]. In this model, the instantaneous firing rate depends not only on an afferent input (convolution of the stimulus with a filter) but also on a spike-feedback term (convolution of spike train with a second filter). In our case, the stimulus filter typically captured velocity-sensitivity, the spike-feedback filter refractoriness. We found a good match between the time-varying firing rate predicted by the model and that recorded experimentally. Thus, stimulus-response relationships of these VPM neurons were well-captured by a single filter model. Consistent with this, the most informative kernel resulting from spike-triggered covariance analysis added at most 20% to the mutual information conveyed by the STA.

Our results indicate that neurons in the whisker thalamus encode surface texture by spike timing that is precise to at least 1ms and that the stimulus-spike relationship can be well-described by a generalised linear model dependent on a single stimulus feature – typically velocity.

Acknowledgments
This work was supported by: International Human Frontier Science Program Grant (to MM) and Long-term Research Fellowship (to MAM); UK MRC Neuroinformatics Fellowship (to MAM), EC Marie Curie International Reintegration Grant (to MM), Royal Society Joint Project Grant (to MM and RSP).

References
Adapting to a changing world.

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The relevance of synchrony in neural computation can be explored by investigating which classes of computation can, in principle, be readily achieved through the development of synchrony. For instance, in a series of papers, Hopfield and Brody have explored[1] a model network for olfaction using a biologically realistic architecture, where integrate-and-fire neurons with similar sensory stimuli synchronize their spike times, thereby achieving the recognition of a single, static olfactory pattern – odor. In their many are equal paradigm, the development of synchrony in a particular subset of neurons is readily identified by the spiking of higher level (‘cortical’) neurons.

We extend their approach to achieve odor separation[2] – the ability to detect the simultaneous presence of multiple odors, with different odor sources, and which therefore have different intensity fluctuations in time. We incorporate a simple model of adaptation that allows the network to be sensitive to components in the stimuli that change together, rather than the overall static characteristics of the stimuli. The collective response binds objects in the stimuli in terms of their common variation.

The interplay between cohering and decohering effects allows for rich dynamic responses that include reliable transient synchronous firing patterns that are readily detected by higher level cortical model neurons. The success of this algorithm for dynamic pattern recognition suggests that understanding the regulation of adaptation may be very important for processing dynamic stimuli.

Acknowledgments
We thank J.J. Hopfield for introducing us to this problem and for many very helpful discussions. This work was supported by ICAM.

References

Spatial organization of large-scale synchrony in primate retina

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Understanding the large-scale activity of a complete network of neurons is a central challenge in systems neuroscience. For any given circuit, a full understanding of network interactions requires (a) the ability to record from most or all neurons in the circuit, and (b) analytical methods to examine all possible interactions, a computationally daunting task. We apply powerful new experimental and analytical approaches to understand the complexity of network interactions in the primate retina.

Large-scale multi-electrode recordings were used to measure electrical activity in nearly complete, regularly spaced mosaics of several hundred ON and OFF parasol (magnocellular-projecting) retinal ganglion cells (RGCs) in macaque monkey retina [1]. The completeness of the mosaics indicates that we recorded from nearly every cell of both types in a 4x8 degree region of the visual field. In the presence of uniform, constant photopic illumination, pairs of RGCs fired synchronously (± 5 ms) much more often then expected by chance, indicating significant network interactions. Furthermore, synchrony declined systematically with distance indicating that correlated activity is spatially localized and universal among cells of the same type. Importantly, however, synchronized firing between pairs of neurons may fail to reveal more complex network interactions between larger collections of cells.

Previously, we showed that firing patterns in up to 7 parasol cells could be explained on the basis of interactions between neighbors in the mosaic [1]. Here we test whether this adjacent coupling can also explain large-scale firing patterns in the entire population. We examined the large-scale structure of network interactions by measuring the size and spatial configuration of synchronized firing patterns in populations of several hundred RGCs. We demonstrate that the structure of these firing patterns can be described accurately by local pairwise interactions, which is equivalent to a local neighborhood Ising model [2-3]. Examination of the parameters of the Ising model highlights the striking homogeneity and scaling properties of the population of RGCs: interactions between neurons are sparse and exhibit highly stereotyped dependence on distance and cell type. These results suggest that the entire population code can be characterized in a parsimonious manner. We have begun to extend these results to determine how the structure of large-scale correlations is influenced by visual stimuli.

Acknowledgments
Supported by NSF IGERT DGE-033451 (JS), NSF grant PHY-0417175 (AML), a Sloan Research Fellowship, and National Institutes of Health Grant EY13150 (EJC) and the McKnight Foundation (AML, EJC).

References
Population coding of song element sequence in the songbird brain nucleus HVC

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Birdsong is a learned complex vocalization, composed of various song elements aligned according to sequential rules. In Bengalese finches, the rules follow individually distinctive finite state syntax. Songbirds have a specialized brain area ‘song system’ for generating and learning complex vocalizations. Because of the importance of the auditory feedback in song learning and maintenance, there have been various studies to reveal the auditory neural representation in the song system. HVC is one of the sensory-motor integration sites for song learning, especially for the song element sequence. Although it has already been reported that some neurons in the zebra finch HVC selectively respond to typical element sequences included in their own song, stimulated element pairs in an experiment were only partial sequences of the entire sequence, such as ‘aa’, ‘ab’, ‘ba’, and ‘bb’ in ‘abcdefghi’. In order to know the neural representation of song element sequences fully, we have to evaluate the activity in response to all song element sequences, that is, ‘aa’, ‘ab’, ‘ac’, …, ‘gi’, ‘hi’, and ‘ii’ in ‘abcdefghi’.

In this study, we recorded the single-unit activities of HVC neurons driven by all possible song element pair stimuli in anesthetized Bengalese finches. Most of the neurons responded not only to sequences included in their own song, but also to the sequences that were not included. The sequence selectivity of each neuron was not rigid, but was broad. Each neuron had a response distribution property that is different among neurons in the same individual. Therefore, the information on song element sequence might be encoded by many neurons with broad but different response distributions to the element sequences.

In order to evaluate the information coding at a population level, we calculated the time course of population activity vectors for HVC neurons, and showed that each cluster corresponding to the present element strongly influenced by the previous element. We also calculated the time course of mutual information between the neural activities and stimuli (Fig. 1). The mutual information of present elements significantly increased. In addition, the confounded information, which is represented by the relation among present and previous song elements, also increased significantly after the presentation of element pairs. These results showed that the information of song element sequence encoded in a neural ensemble in HVC as a population coding.

This distributed representation of song element sequences might be important for generating complex sequential song in Bengalese finches. Since the Bengalese finch song is a good model of human language in terms of syntactical properties, these results might give useful insights for biology of language.
The Importance of Noise in Strongly Coupled Small Inhibitory Neuronal Networks: Theoretical Effects in the *Hermissenda* Eye.

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Neural information processing may depend importantly on the ability of a network to vary its firing rate continuously in response to continuous changes in its input. In strongly inhibitory networks of oscillating neurons, subsets of neurons that are intrinsically more active can silence the rest of the neural population. If excitatory drive is increased to the whole network, the silenced neurons may become active and inhibit the silencing neurons, thereby slowing the firing rate of the silencers. This leads to a non-monotonic relationship between excitatory input and output firing rate of the network. The presence of noise in the network can disrupt this non-monotonic relationship by disallowing the more active subset of neurons from completely silencing the rest of the network, thereby producing continuous responses in network behavior.

To study this problem, we analyzed a family of integrate-and-fire (IF) type neuronal models in response to stochastic inhibitory input times \([1, 2]\). We derived the Markov operator for the family and found the limiting invariant density of the operator and the average firing rate as a function of the inter-input time distribution. As the excitatory drive is increased, the average firing rate increased as expected. If the inter-input distribution was relatively variable or “noisy,” the average firing rate increased relatively linearly; in contrast, if the inter-input distribution was less variable, then the firing rate jumped up quickly from zero at a particular excitatory input level.

Along with other potential mechanisms of noise effects \([3]\), this phenomenon has potential applications to the functioning of the eye of the marine nudibranch mollusk *Hermissenda crassicornis*. With its five inhibitorily coupled and repetitively firing photoreceptors, the *Hermissenda* eye is an attractive model system in which to evaluate this phenomenon. Simulations of a five-photoreceptor inhibitory IF model network eye revealed that sufficiently strong white noise is required to produce a smooth response to changes in excitatory drive. These preliminary simulation results and the above results from the Markov chain analysis suggest that noise could play an important role in *Hermissenda* network function. Comparable physiological experiments on the biological eye are in progress.

Acknowledgments

WHN is supported by NIMH R01-MH068392 and RTG 0354259. PCB is supported by DMS 0515725. GAC is Supported by NIH R01-MN068392.

References


Point process models of the neural response to inter-vibrissae interactions.

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Cortical representations of natural stimuli are contextual, depending on both the ongoing stimulus pattern and the ongoing state dynamics. Clarifying the role of such interactions is challenging because of the potentially high dimensionality of natural stimuli spaces and the potentially strong non-linear interactions between dimensions of that space. Our approach is to parameterize the stimulus space and fit models of the history dependent spike rate using point process maximum likelihood estimation \cite{1}. The advantage to this approach is that statistical fit can be rigorously assessed, and a suitable model choice can lead to a substantial reduction in the number of stimulus dimensions while still accounting for the spiking statistics.

During active exploration, rodent vibrissae undergo highly complex patterns of movement with strong temporal and inter-vibrissa correlations, imposed by search strategy, by biomechanical properties of the sensory and by surface statistics. We explored one part of this stimulus space, the interaction between center and surround vibrissae. Using a novel multidirectional piezoelectric stimulator with attachments designed to independently and simultaneously manipulate all nine vibrissae \cite{2}, we deflected the D3 and eight surrounding vibrissae of isofluorane anesthetized rats in 8 cardinal directions. The spiking of multiple neurons was simultaneously recorded using a four tetrode array located in either layer II/III or IV of the D3 barrel. We defined a parametric model which expanded the directional dependence of the evoked spiking in terms of sinusoidal basis functions and also included the effect of a neuron’s previous spiking history. Fits of this model to a preliminary data set of 12 layer II/III neurons via maximum likelihood estimation accounted for the observed spiking statistics to within 95\% confidence intervals as defined by a Kolmogorov-Smirnov test statistic. Tuning curves derived from this model revealed that the direction tuning of the surround vibrissae transitions from being collinear with the tuning of the center vibrissa to opponent to the direction of the center vibrissa as the number of surround vibrissae being deflected is increased. These modeled tuning curves demonstrate the contextual nature of the center-surround interactions. We are in the process of applying this analysis to 77 (73) neurons recorded in layer II/III (IV). We have also begun to apply maximum likelihood techniques to spikes recorded in awake, freely behaving rats, and to anesthetized rats for which more naturalistic stimuli have been applied, and to compare these data with those obtained using our 9-vibrissae stimulator.

Acknowledgments
This work was supported by NIH grants R01-DA015644 and R01-NS045730-03.

References
Neural Representation of Sequential States within an Instructed Task

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In the study of the neural basis of sensorimotor transformations, it has become clear that the brain does not always wait to sense external events and afterwards select the appropriate responses. If there are predictable regularities in the environment, the brain begins to anticipate the timing of instructional cues and the signals to execute a response, and even the consequences of actions. An organism’s ability to anticipate events reveals an internal representation of the sequential progression of behavioral states within the context of the task being performed. Using the same eye movement tasks while recording neural data from two cortical oculomotor areas in the rhesus monkey, we found complementary spatial and sequential state representations of the Lateral Intraparietal Area (LIP) and the Supplementary Eye Field (SEF). While both areas encoded the position of eye movement targets, this spatial encoding was more consistently found in single neurons of LIP. In addition, the neurons of the SEF were found to collectively encode the progression of behavioral states of the task, with individual neurons detecting and/or anticipating different events or sets of events in the task or becoming tonically activated or depressed from one event to another and thus encoding states in an event-based manner. The entirety of responses from SEF was used to decode the current temporal position within the context of the task. Since LIP neurons were found to respond similarly when encoding an eye movement plan (saccade period) or the location of brightly flashed stimulus (cue period), the temporal information provided from SEF could be used to imply the significance of the spatial representation found in LIP.

Acknowledgments
This work was supported by ONR grant N00014-04-1-0523.
Temporal Sound Processing by Cochlear Nucleus Onset Neurons

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The human auditory system codes sound signals using the well-known rate-place principle but also preserves temporal information with very high precision. In this paper we investigate the processing principles of onset neurons located in the cochlear nucleus. These neurons reject steady-state excitation and fire on signal onsets with extremely high temporal precision.

For our study we have developed a detailed model of the human inner ear, which codes sound signals into trains of action potentials of the auditory nerve. These spike trains excite a model of so-called onset neurons located in the cochlear nucleus. We use a point model with the five major Hodgkin-Huxley type conductances the found in these neurons [1].

Spike-triggered reverse-correlation analysis revealed that octopus neurons fire preferentially if coincident input spikes follow a short interval of relative low excitation. The frequency spectrum of the reverse-correlation revealed that octopus neurons perform a band pass analysis of the incoming signal, with the pass band ranging from about 110 to 650 Hz. The low-frequency slope was approximately 6 dB/octave, which indicates that octopus neurons process the first derivative of the input signal. This mechanism suppresses steady-state activity and accentuates onsets, but also enhances amplitude modulation in the frequency region of voiced speech sounds.

Acknowledgments
This work was supported by the German Federal Ministry of Education and Research (01GQ0443).

References
HVC carries information of low frequency power in bird’s own song: possible neural correlates of bone conducted sound in zebra finch singing

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Auditory feedback is necessary for normal development and maintenance of learned vocalizations in human and songbirds. Humans perceive autogenous speech differently from playback of recorded speech mainly because low frequency power is transmitted principally via bone conduction to the middle ear. Results in songbirds indicate that low frequency components of auditory feedback may be particularly salient cues for song learning and maintenance. In zebra finches, both in vivo and in vitro evidence suggests that the sounds generated at the vocal organ (syrinx) include greater power at low frequencies than in the air borne (broadcast) song. In Bengalese finches, it has been shown that high frequency components of auditory feedback are not necessary for normal song maintenance. Here, we explore physiological manifestations of these auditory feedback-related phenomena. In adult birds, neurons of the avian forebrain nucleus HVC exhibit selective auditory response to the bird’s own song (BOS) under sleep or anesthesia. We examined HVC auditory responses in urethane-anesthetized adult zebra finches to broadcasted BOS (BBOS) and its low frequency amplified version (LBOS). Songs for auditory stimuli were recorded in a sound-attenuation chamber and digitized at 20k Hz sampling rate. BBOS stimuli were made by band-passing recorded songs between 200 Hz and 10 kHz, and LBOS stimuli were made by amplifying the power of BBOS syllables between 200 Hz – 1000 Hz (Figure 1). All stimuli were scaled to 70 dB root-mean-squared amplitude. Of 40 HVC neurons recorded from 7 birds, 9 cells (23%) evoked significantly higher mean firing rate during the stimulus presentation to BBOS than LBOS, while 12 cells (30%) evoked significantly lower mean firing rate (one-sided t-test, p<0.05). We also used a metric-space analysis [1] to quantify how much information is carried by differences in the temporal pattern of spike trains to discriminate between BBOS and LBOS. Most cells (n=36; 90%) displayed a significant amount of the mutual information, with the peak of the averaged information (0.266 bits) at a temporal precision (1/q) of 25.1 ms. This suggests that the temporal structure of spike trains in HVC neurons can carry information about the relative frequency power composition of BOS. This may provide for robust detection of self-generated sounds similar to what is known for mammals, e.g. echolocating bats.

References

Acknowledgments We thank Daniel Baleckaitis and Pete Rauske for technical assistance.
Biophysical determinants of single neuron computation
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Single neurons can perform a range of computations, including integration, coincidence detection or differentiation [1,2,3], and gap detection [4]. A central goal of neurophysiology is to understand how the information processing of a neuron is influenced by its biophysical properties. Recently, it has been suggested that the maximal conductances of a neuron affect its response in non-trivial ways [5,6]. This presents a challenge in understanding not only how a neuron’s computation depends on its conductance parameters but also how its computational role is maintained or altered during active regulation of its biophysical properties. Here, we examine two different characterizations of the neuron’s coding strategy: the neuron’s mean firing rate as a function of input statistics, and its linear filters and threshold functions. For both measures, we found that the parameter space of Hodgkin-Huxley conductance-based model neuron can be parsed into distinct regimes of computation.

First, with respect to the neuron’s mean firing rate response, these computational regimes are characterized by either repetitive firing or isolated bursts in response to noiseless inputs. We find that these regimes are separated by a planar boundary in the multi-dimensional parameter space of conductances. We show the basis for this change in computation by analyzing the dynamical system of a reduced model; we find that channel conductance parameters affect the position and geometry of a voltage-dependent threshold.

From the coding perspective, we employed white noise analyses to derive a linear-nonlinear cascade model. We show that two components of the model, the linear features and nonlinear threshold functions, behave differently: as conductance parameters vary continuously, the features barely change, suggesting that this characteristic of computation is almost insensitive to change in maximal conductances. However, the nonlinearity undergoes a rapid change at a linear boundary, and is otherwise almost invariant. We show a theoretical derivation of these properties in terms of the underlying dynamical system. Using a reduced model derived directly from the neuronal dynamical system, we derive the predicted linear filters and show that a change in shape of the voltage dependent threshold drives change in the patterns of threshold crossing, which in turn changes the nonlinearity.

These results help to bridge the gap between the dynamical system description of a neuron and its function in information processing, and suggest ways in which slowly adapting channels may modulate channel conductances as means of altering computation or as a homeostatic mechanism to preserve a particular computational strategy.

Acknowledgments
This work was supported by a Burroughs-Wellcome Careers at the Scientific Interface grant. BNL was supported in part by an ARCS fellowship.

References
Synchrony & Location Dependent Effects of Inhibition in a Pyramidal Neuron Model

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Inhibitory interneurons shape the functioning of the cortical circuit in myriad ways, though their precise roles in neural information processing remain poorly understood. A key feature used to classify inhibitory interneurons is the spatial distribution of their synaptic contacts on the dendrites (or soma or axon) of their pyramidal neuron targets. How do these different patterns of inhibitory termination affect a pyramidal neuron's integrative behavior, or alter its firing rate or firing pattern? Using a compartmental model of a layer 5 pyramidal neuron, we studied the arithmetic of excitatory-inhibitory interactions as a function of several variables, including location (dendritic vs. somatic vs. axonal inhibition), temporal structure (asynchronous vs. synchronous inhibition), and the measure of excitatory stimulus intensity (firing frequency vs. synapse count). Despite our attempt to arrive at broad generalizations about the data set as a whole, we found that the excitatory-inhibitory interactions were highly variable in nature, depending in complex ways on the various parameters we tested. A few interesting generalizations emerged, however, including the finding that synchronous inhibition (regardless of location) led to a division of OUTPUT firing rates, whereas asynchronous inhibition (regardless of location) acted divisively on INPUT firing rates. A number of more limited generalizations held as well and will be discussed. Our findings are consistent with the view that individual neurons have access to a rich palette of arithmetic operations.

Acknowledgments
This work was supported by NIH grant MH065918-03.
NMDA-Rich Dendritic Subunits as a Substrate for Divisive Arithmetic

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Many models of neural processing include division (e.g. divisive normalization) as a common and important neuronal computation, presumably mediated by synaptic inhibition. Yet the details of its neuronal substrate: the "where" and "how", are far from answered. If the output function of a neuronal unit is an expansive nonlinearity approximating an exponential function, then, to divide its output by a factor D is simply a matter of subtracting \( \log(D) \) from its input. Dendritic sub-units of pyramidal neurons are known to generate NMDA spikes, which provide a nonlinear input/output function. To investigate the divisive competence of this nonlinearity, we used a model pyramidal cell populated with active conductances and AMPA/NMDA type excitatory synapses stimulated by 50 Hz poisson spike trains. We found that the nonlinear function relating peak membrane potential to stimulus intensity provided a relatively poor approximation of the divisive operation. This was due in part to the very short range of inputs over which the NMDA nonlinearity accelerates and then saturates. In contrast, we found that the nonlinear function relating the time-averaged membrane potential to stimulus intensity provided a reasonably high level of divisive competence. This was explained in part by our finding that this nonlinearity exhibited a two-tier acceleration: firstly, the NMDA spike mechanism itself and secondly the acceleration from individual spikes to a plateau potential. We conclude that time averaged currents sourced from NMDA-rich subunits may provide a viable substrate for neural division.

Acknowledgments
This work was supported by NIH grant MH065918-03.
Transformation of Olfactory Representations Across Morphed Odor Conditions in the Antennal Lobe and the Mushroom Body

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In nature, animals rarely encounter stimuli in isolation and must often extract meaningful information from complex odor mixtures. And unlike vision, where we can easily parse out the individual lines in a Kandinsky painting, in olfaction, we typically perceive odors as single entities. Behaviorally, it has been shown that human subjects can rarely identify the individual components within a mixture when there are 4 or more components present [1]. On the other extreme, the female malaria mosquito can detect a single chemical 4-methylphenol, that is present in our sweat. How then, does the brain achieve these two seemingly contradictory tasks? We begin to address these questions using electrophysiological approaches, by recording from principal neurons of the antennal lobe (Projection neurons, PNs) and the mushroom body (Kenyon cells), the first and second relays of the locust olfactory system.

Individual PNs respond with characteristic epochs of excitation and inhibition that are both neuron- and odor- specific [2]. And because not all responding neurons express the same patterns at the same time, the state of the network is dynamic, carried by an assembly of neurons that evolves in a stimulus-specific manner over time. Neural representations can thus be described geometrically as stimulus-specific trajectories reflecting the state of the PN network [3]. How do these trajectories change with small changes in the stimulus? Do the trajectories change progressively to reflect changes in the stimulus, or are there abrupt discontinuous transitions from one trajectory to another? We addressed this question by first probing the PN network with small changes to the input that varied progressively along a continuum. By varying the ratio of concentrations of two components within a binary mixture, we effectively morphed one unique odor to another. We observed a progressive rather than abrupt transformation from one odor-specific trajectory to another.

To observe the transformation across a more broad range of stimulus space, we systematically increased the complexity of the mixture by adding single odorants in a stepwise manner from 2 to 8 (e.g., AB, ABC, ABCD, → ABCDWXYZ) and presenting different combinations that overlap by varying amounts (e.g., ABCD, ABCX, BCWX, BDWX, DWXYZ, WXYZ). To test the linearity of mixture representation, we estimated the ensemble PN response vectors to odor mixtures by adding the response vectors corresponding to the mixture components. We then examined the degree of deviation between these estimated response vectors and the experimentally observed response vectors. We find that for binary mixtures, there is good approximation between the estimated and experimental response vectors, but this approximation degrades rapidly when more odorants are added to the mixture. Finally, we examine the degree to which these representations mirror the responses of the targets of the PNs in the mushroom body, the Kenyon Cells.

Categorization and decision making in monkey auditory cortex

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The sequential patterning of frequency steps (upward, downward, flat) is the most important feature that humans use to memorize and recognize melodies. Because human lesion studies suggest an important role of auditory cortex in the categorization of frequency steps we recorded single and multieunit activities in primary (AI) and a secondary auditory field (CM) with a multielectrode array from two monkeys while they categorized frequency steps.

A trial always started with 3 identical tones. They were followed by 3 identical tones of lower frequency, either directly (down sequence with a downward step on the 4th tone) or after 3-5 identical tones of higher frequency (up-down sequence with an upward step on the 4th tone and a downward step on the 7th, 8th, or 9th tone). There were 'flat' frequency steps after the 1st and 2nd tone and after the 4th and 5th tone. After correct release of the bar upon a downward step the monkeys were rewarded with a drop of water.

We found that phasic responses of neurons in auditory cortex provided categorical information on the direction of frequency steps while slow modulations of tonic firing reflected procedural aspects of task solution. Many neurons increased their firing to frequency steps, but only to downward steps and not to behaviorally unrewarded upward steps. This was largely independent of the frequency composition of sequences and whether or not monkeys correctly identified downward steps. It also occurred when monkeys were passively exposed to the sequences. Such binary response differences to upward and downward steps and their independence from best frequency of neurons have not been observed in naïve monkeys. In contrast, the slow modulations of tonic firing, which did not occur during passive presentation of tone sequences, marked frequency steps that required categorical decisions and subsequently predicted correct behavioral responses and errors. Tonic firing level rapidly decreased shortly after the 4th tone and decreased significantly faster after downward steps than after upward steps and dissociated ~350 ms after the 4th tone. Opposite behaviors of firing changes were observed in error trials. Change rates thus predicted whether the bar would be released several hundreds of milliseconds later.

Our results demonstrate that neuronal mechanisms for categorical stimulus identification and for decision making can coexist in trained sensory cortex.
Decoding neural responses in macaque primary visual cortex

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One of the main questions in computational and systems neuroscience is how the responses from a population of neurons are combined to decode sensory signals. To address this question, we recorded from the superficial layers of primary visual cortex of opiate anesthetized, paralyzed macaque monkeys using a 10 x 10 electrode array with 400 µm spacing between adjacent electrodes. We presented sinusoidal grating stimuli of fixed spatial and temporal frequency drifting in 72 different directions. We recorded reliable responses which exceeded a threshold and sorted these waveforms offline, resulting in a population of between 44 and 86 simultaneously recorded cells. We constructed population neurometric functions using the spike counts collected over the stimulus period of 1280 ms to measure how well the neurons could discriminate between different stimulus directions.

We considered two decoding strategies. First, we used a likelihood ratio (LR) decoder which compares the likelihood of two stimuli from the underlying neural responses, assuming that the responses are statistically independent. After exploring different approximations, we concluded that Poisson statistics adequately described our spike count distributions. In this case, the LR decoder is linear: it separates the neural response corresponding to two stimuli by computing the weighted sum of the neuronal spike counts, with the weights given by the difference of the logarithms of the two tuning curves [1]. Second, we used a machine learning method to discriminate the population responses. We used a linear Support Vector Machine (SVM), which estimates a separating hyperplane in a space whose dimensions correspond to the neural response. The hyperplane maximizes the distance between classes of neural response and minimizes misclassified patterns [2]. Unlike the LR decoder, the SVM method can take advantage of neuronal correlations.

We explored the impact of correlations on both decoders by comparing raw with trial-shuffled responses; shuffling removes interneuronal correlations. The LR decoder performed better on the shuffled data than on the raw, which is presumably due to the fact that the LR decoder assumes independence between neurons. The SVM however, performed better on the raw data, showing that it can make use of correlations to improve decoding performance. Notably, the performance of the SVM progressively increased when pairwise, triple and multi-neuronal correlations were considered. Furthermore, low signal-dependent correlations (for widely different preferred orientations) and high signal-independent correlations tend to improve the performance of the SVM.

The LR decoder that ignores neural correlations is appealing because of its simplicity and biological feasibility. However, our results provide evidence that more sophisticated linear classifiers such as the SVM, while keeping the simplicity of a LR decode, can take advantage of neural correlations to improve decoding efficiency of sensory cortical neurons.

References
Multi-Layer Tempotrons

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The recently developed single-layer tempotron model has demonstrated the high capacity of neurons to read out information that is encoded in the relative timing of action potentials across populations of afferents[1]. However, because of the simplicity of this architecture, the tempotron performance is inherently limited. Since the model neuron relies on spatio-temporal representations, processing of stimulus time-dependencies requires their prior transformation into spatially distributed patterns of afferents[2]. Additionally, the tempotron cannot combine high temporal resolution with long time integration. In contrast, sensory systems can be sensitive to fine temporal structures of input signals even when the computation of perceptual decisions requires the integration of such signals over long times (e.g. [3]).

Motivated by these challenges, we extend the tempotron model to multi-layer architectures. We derive a learning rule for multi-layer integrate-and-fire neurons adapting previous learning algorithms based on the Minimum Disturbance Principle[4]. The resulting learning algorithm combines tempotron learning with backpropagation of the target decisions into the hidden-layers. We show that this algorithm can successfully train a hidden layer of tempotrons to recode temporal information that arrives on a single input channel into a spatio-temporal spike pattern. This allows a subsequent output tempotron in the network to discriminate between incoming spike sequences. We study the coding principles that underly the emerging internal representations. This model is applied to the problem of learning interval discrimination tasks[2].

Two processing time scales are incorporated in the two-layer tempotron. Fast synapses in the input layer allow the hidden-layer tempotrons to learn to detect fine spatio-temporal features such as patterns of synchronous spikes. Slow synapses in the output layer enable the output neuron to integrate in both space and time the activity of these feature detectors. We show that this architecture leads to a considerable enhancement in discrimination accuracy particularly for noisy input patterns. Applying this model to specific examples of discrimination tasks yields optimal synaptic connections. These results demonstrate that our learning rule uncovers some of the powerful computational capabilities of multi-layer spiking networks.

Acknowledgments
This work was supported by the Minerva Foundation and the Israel Science Foundation.

References
Irregular persistent activity induced by synaptic excitatory feedback

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Neuro-physiological experiments on monkeys \cite{1} have reported highly irregular persistent activity during the performance of an oculomotor delayed-response task. These experiments show that during the delay period the ISI’s coefficient of variation (CV) of prefrontal neurons is above 1, on average, and larger than during the fixation period, regardless of whether the cue is preferred or nonpreferred.

Previous models \cite{2-3} of spontaneous and selective persistent activity in the cortex based on excitatory synaptic feedback do not reproduce this feature because the excitatory feedback during persistent activity brings neurons in a region of the f-I curve in which the firing is relatively independent from fluctuations and hence the CV is small.

To overcome this problem, we introduced two ingredients: (1) a high post-spike reset potential (close to threshold), (2) a non-linear relationship between synaptic efficacy and pre-synaptic firing rate via a short-term depression (STD) mechanism. We show that when the reset potential is close enough to the threshold, the CV-I curve has a maximum above 1 for a sub-threshold mean current. The range of the mean synaptic input values for which the CV is greater than 1 is always in the sub-threshold regime in which firing is dominated by fluctuations of the mean synaptic input. With short-term depression, synaptic efficacies saturate at a certain limiting value of the presynaptic frequency; this is turn provokes a saturation of the mean synaptic current to a neuron at the same limiting presynaptic frequency. This allows the persistent state solution to reach the region of the f-I curve which corresponds to high values of the CV.

We tested this idea both with numerical simulations and analytical techniques. For the analytical studies we used mean-field techniques, recently extended in presence of STD \cite{4}, that involves the use of the distribution of the interspikes intervals of an integrate-and-re neuron receiving a Gaussian current in input; this permits to obtain an accurate estimate of the statistic of the postsynaptic current in presence of STD and hence to find the stationary states in a self-consistent way. We also simulated both a fully connected excitatory network of leaky integrate-and-fire neurons endowed with STD, and a cortical network model composed of an inhibitory population and several stimulus selective excitatory populations. In both cases we find a large range of values of the synaptic efficacies for which the persistent activity is irregular, with values of the CV in agreement with the physiological findings.

Acknowledgments
We thank I.S.I foundation for support.

References
A Bayesian Perceptual Model Replicates Tactile Spatiotemporal Illusions

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When brief, punctate stimuli contact the skin in rapid succession at two or more locations, perception errs, strangely shrinking the intervening distance, and expanding the elapsed time, between consecutive events. Here I show that these effects, which I term perceptual length contraction and time dilation, are emergent properties of a Bayesian perceptual model that incorporates the prior expectation that tactile stimuli move slowly. Rapidly moving stimuli violate expectation, provoking perceptual length contraction and time dilation.

In its simplest form, admitting spatial but not temporal imprecision in the sensorineural signal, the Bayesian model gives rise to an elegant single-free-parameter formula that closely replicates a variety of length-contraction-based illusions, including the rabbit illusion, the tau effect, tactile temporal order judgment, and spatial attention effects. When the model admits realistic temporal as well as spatial imprecision, it additionally reproduces the kappa effect, a time dilation illusion.

The model makes several novel testable predictions. For example, it predicts more pronounced time dilation, and less pronounced length contraction, on body areas with finer tactile acuity (e.g., the fingertips), and it predicts a perceptual speed limit on the velocity evoked by punctate tactile stimulus sequences with fixed spacing.

The remarkable explanatory power of the model supports the hypothesis, suggested by Helmholtz, that the brain biases perception in favor of expectation. Specifically, the results suggest that the brain automatically incorporates prior expectation for speed to aid perceptual interpretation of an imprecise sensorineural signal. This powerful tactile model recalls a visual model, also with a low-speed prior, that reproduces many effects of contrast on visual motion perception [1].

Acknowledgments
I thank D. Gillespie for many helpful discussions. This work was supported by an individual Discovery Grant from the Natural Sciences and Engineering Research Council of Canada.

References
Phase-locking of mitral cell activity during gamma LFP oscillations: experiments and modeling

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In the mammal olfactory bulb, it is known that an odor presentation elicits oscillations in the local field potential (LFP) during episodes of the respiratory cycle. However, little is known about the relation between the activity of mitral and tufted cells (M/TCs), the bulbar principal relay cells, and these oscillations. In zebrafish, some phase-locking has been observed during the LFP oscillation [1]. In mammals, this question has been addressed here in anesthetized freely breathing rats, by performing simultaneous extracellular recordings of M/TC activity and LFP, looking specifically at the gamma frequency range (40-80 Hz) oscillation episode. During this episode, we found a clear change in the firing activity of the M/TC population and a large proportion of cells showing phase-locked firing. The spike trains were analyzed and classified according to patterns (p,q) of p spikes per q oscillation cycles when they were sufficiently close to one of them. We found a highly significant number of trains classified in patterns, the main patterns being (1,1), (1,2) and (2,1).

To understand these results, we have built a biophysical model to study the response of a single M/TC to realistic inputs. We have defined a reduced version of the conductance-based model of M/TC introduced in [2]. This cell receives noisy excitatory and inhibitory inputs like in vivo. As the inhibitory input to M/TCs has been found to oscillate relatively weakly during the gamma oscillation [3], M/TCs could be entrained by this oscillation, giving rise to phase-locking and a priori any (p,q) pattern. Considering that the mean input to the cell is constant during the oscillation episode, we calculated the entrainment properties of a cell for a large range of intrinsic frequencies (< 200 Hz) and oscillatory input levels. We could reproduce the main types of patterns seen experimentally and explain their prevalence. For a given pattern, the interval of intrinsic frequency where the cell is entrained gets wider with increasing oscillation amplitude, and could be very large (~ 50 Hz) for the (1,1) pattern. Interestingly, the widest intervals are found when the oscillation is in the gamma range. Even if the gamma episode is relatively short (~ 4-8 cycles), entrainment is found after only one cycle. We made a theoretical analysis of the model results to understand their origin and verify their robustness against parameter choices. In conclusion, the gamma oscillation of the inhibition is found to be able to entrain a significant proportion of cells. The subsequent correlations in the firing of these cells could be exploited by the system and the issue of odor encoding will be discussed.

References
Using rat chemotaxis to study the where problem of olfaction

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Animals use spatiotemporal patterns of odor concentration to locate what they smell¹,², a form of navigation known as chemotaxis. To understand how the brain uses olfaction to form a representation of “where”, we will study chemotaxis in rats. Many studies have demonstrated that rats excel at chemotaxis, although most of these studies use odor localization to study other problems such as learning³, odor discrimination⁴, or olfactory recognition of conspecifics⁵. It has also been shown that rats can use odor trails for navigation⁶, and that rats can smell in stereo⁷, which might be useful for navigation. Still, it is unclear what behavioral strategies and neural circuits rats use to locate odor sources. In species in which this problem has been studied in more detail, a common feature is that chemotaxis behavior seems to take two states: one for when olfactory signals suggest the animal is taking the correct trajectory, and one state for when the animal’s trajectory is incorrect. Thus, microorganisms such as E. coli and C. elegans navigate in straight runs in an increasing concentration gradient, and turn more frequently in a decreasing concentration gradient¹,⁸. Moths navigate in odor plumes dispersed by wind. Their chemotaxis behavior also seems to have two states: they fly upwind as they encounter filaments of an odor plume, and in the absence of filaments they fly perpendicular to the course of the wind².

To test whether rats use a similar two-state chemotaxis strategy, we wanted to build an olfactorium in which rats would have to experience both correct and incorrect trajectories as they navigate to odor sources. Our preliminary studies have shown that in our olfactorium, rats can correctly navigate to odor sources >90% of the time, but not without first initiating and correcting an incorrect trajectory on 50% of correct trials. Here we will describe our olfactorium, how rats behave when they experience correct and incorrect trajectories to an odor source, and how rats behave when we make the chemotaxis problem more difficult. With this system, we hope to understand what features of the spatiotemporal pattern of odor concentration can serve as the rat’s cue for chemotaxis, and, in the future, to understand the brain’s olfactory “where” pathway.

Acknowledgments
We thank Cori Bargmann and members of the Mainen lab for helpful discussions.

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Linear Modelling of Non-Linear Response Functions: Stimulus-Specific STRFs without Stimulus-Specific Adaptation

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Neurons in the central auditory system are often described by the spectrotemporal receptive field or response function (STRF), conventionally defined as the best linear fit between the spectrogram of a sound and the spike-rate it evokes. Unfortunately, the true stimulus-response relationships of auditory neurons are commonly non-linear, and this makes interpretation of the best linear fits difficult. An STRF is assumed to provide an estimate of the receptive field of a neuron, i.e. the spectral and temporal range of stimuli that affect the response and whether the effects are excitatory or inhibitory. However, when the true response function is non-linear, the STRF will be stimulus-dependent, and changes in the stimulus properties can alter estimates of the polarity and spectrotemporal extent of receptive field components. We demonstrate through simulations that these effects can be dramatic. Even when uncorrelated stimuli are used, simple and biologically plausible neuronal non-linearities can produce STRFs with spurious receptive field elements, indicating contributions from time-frequency combinations to which the neuron is actually insensitive. Only when the distributions of the stimulus values are statistically independent does the STRF reliably indicate features of the underlying receptive field, and even then it gives only a conservative estimate of the spectrotemporal extent. One consequence of these observations, which we illustrate below using natural stimuli, is that any stimulus-induced change in an STRF could arise, at least in part, from a consistent but non-linear neuronal response to stimulus ensembles with differing higher-order dependencies, rather than from stimulus-driven adaptation in response properties. In combination with related work [1], our simulations demonstrate that non-linearities can lead to apparent stimulus-specificity in the shape and extent of a receptive field, as well as stimulus-specificity of response properties within a receptive field. Thus, while auditory receptive fields may well adapt to the statistics of different stimulus ensembles, stimulus-dependence of STRFs alone is not sufficient proof of such adaptation.

Figure: Left, STRF estimate of a simple two-component multiplicative response function, derived from simulated responses to a database of environmental sounds [2]. Right, STRF estimate of the same multiplicative response function, derived from simulated responses to a selection of Bach violin partitas. Each stimulus ensemble was de-correlated for STRF estimation using standard techniques [3].

Acknowledgments
Supported by the Gatsby Charitable Foundation (GAT2579) and the Gatsby Unit.

References
Receptor neuron response dynamics drive odor-elicited spatio-temporal patterning in the antennal lobe

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Neural codes for odors in the antennal lobe (insects) and olfactory bulb (vertebrate) consist of spatiotemporal activity patterns across populations of principal neurons. Recordings in Drosophila (Hallem, and Carlson, Cell, 2006), locust (Ochieng and Hansson, Physiological Entomology, 1999), and zebra fish (Spors et al., Journal of Neuroscience, 2006) have shown that olfactory receptor neurons (ORNs) respond to odors with diverse and temporally dynamic spiking patterns. The contributions of this temporal heterogeneity to subsequent processing of olfactory information in the antennal lobe (AL)/olfactory bulb are not known. Using computational models of these olfactory circuits, we examined the relationship between ORN response dynamics and odor-elicited spatio-temporal patterning of projection neuron (PN) activity in the AL.

We propose a simplified parametric model of the receptor neurons: response of an ORN to an odorant is characterized by its rise (absorption), saturation (retention) and fall time constants (desorption), and its peak amplitude (affinity). ORNs converging onto the same glomerulus have similar response profiles. The model parameters were chosen such that odor responses of model ORNs qualitatively match results from locust and Drosophila, and the sum of the model’s diverse ORN responses match electroantennogram recordings from locust antenna. Trajectory analysis of the model ORN responses, using principal components, showed that, similar to PN ensemble activity recorded in vivo (Stopfer et al., Neuron, 2003; Ofer and Laurent, Neuron, 2005), ORN responses form fixed-point activity for long pulses (> 1s) as well as super-clusters for odor identity with sub-clusters for odor intensity.

We further examined subsequent processing of the ORN responses with a map-based model of the AL network. We observed a rich repertoire of spatio-temporal patterns across PNs comparable to those observed in recordings made in the locust. Our results suggest that information contained in the temporal dynamics of the ORN response is amplified into more temporally complex and distributed patterns across PNs through GABAergic inhibition from local neurons.

Our results further suggest that the AL serves to remap the receptor input to enhance odor discrimination beyond what is available at the receptor level, and to restructure the odor code into a format suitable for read-out and subsequent processing by its downstream neurons.

Acknowledgments
We thank members of Stopfer lab for helpful discussions and Maxim Bazhenov for providing us with an implementation of a map-based model for neurons. NIH-NIST postdoctoral fellowship award by National Research Council to B.R. Intramural support from NICHD to M.S and JT.

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Context Dependence and Response Predictability in the Auditory Cortex

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How do past events influence auditory cortical responses? Psychophysical studies have demonstrated that stimulus context strongly affects perception and auditory scene analysis in humans. Physiological studies on the effects of stimulus context (\textit{e.g.} forward masking) suggest that neural responses in the auditory cortex are highly dependent on stimulus history. However, even though the responses of auditory cortical neurons show high trial-to-trial reliability, they cannot be fully explained by linear encoding (spectro-temporal receptive field; STRF) models, and little is known about the underlying neuronal dynamics.

To study how neural dynamics depend on the stimulus context, we performed whole-cell recordings \textit{in vivo} in the anesthetized rat and examined the subthreshold responses to snippets of natural sounds (including animal vocalizations) and to synthesized sounds. We found that (1) the context dependence in the rat auditory cortex was more susceptible to the changes in overall intensities and frequencies than to the changes in the amplitude- and frequency-modulation rates; and (2) the context dependence sometimes lasted as long as four seconds in some neurons.

This context dependence on such longer time-scales explains in part why classical linear encoding models have failed. STRF models have a limited window length, typically several hundred milliseconds, and can capture only a quarter of the predictable response power. In fact, our data showed that even the best nonlinear model under additive noise assumption (\textit{i.e.} the mean response over trials) can capture only about three-quarters of the predictable power given the time-scale of hundreds of milliseconds. However, the performance of the linear models did not improve significantly by extending the window length and/or even with static nonlinearities, whereas that of the best nonlinear model did. These results suggest that stimulus-dependent (bottom-up) modulations of neural responses can be complex. It is a challenge for future works to address how neurons exploit stimulus features on longer time-scales, and how we can formulate a plausible nonlinear encoding model.
Contribution of inhibition to sensory processing in the accessory olfactory system

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A basic task of every sensory system is the transformation of its initial stimulus representation into a form that can be more effectively used to guide behavior. To best explore the mechanisms underlying this transformation, we chose to examine a system - the accessory olfactory system (AOS) - where examples of natural stimuli underlying specific behaviors are known, and where only two processing locations separate sensory input from behavioral output. Despite its relative brevity, the AOS resembles many other sensory systems in carrying out the basic tasks of sensory processing and pattern recognition in the context of layered inhibitory networks. Thus, this system provides an opportunity to explore the functional implications of these inhibitory networks in the context of known behavioral applications.

Significant work has been done characterizing the response patterns of the primary sensory neurons of the AOS to both natural stimuli and single compounds. Until recently, however, little has been known about how the representation of stimulus information is altered by the first stage of processing (located in the accessory olfactory bulb, or AOB). To explore this question, we have developed a preparation for recording extracellularly from the output layer of the AOB in an anesthetized mouse, while delivering natural stimuli directly to the primary sensory neurons. Single unit recordings show both spontaneous and stimulus-induced activity; stimulus-dependent responses have included examples of increases and decreases in firing rate, graded dependence on stimulus concentration, and selectivity for the sex of the mouse from which the stimulus (dilute mouse urine) was derived.

Using this preparation, we have explored the role of local inhibitory networks in processing natural stimuli in the AOS. By examining the additivity of responses to multiple stimuli, we have found evidence for the widespread presence of functional lateral inhibition. We have also used the GABA blocker bicuculline to probe the involvement of local GABAergic signaling in this process and to estimate the magnitude of inhibition at the level of single cells.

References


Adaptation and information transmission in fly motion detection

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Many sensory systems adapt to changes in stimulus statistics. In this work we investigate adaptation in H1, a motion-sensitive neuron in the fly visual system, to the variance of randomly fluctuating velocity stimuli. Previous work has shown that the well known velocity gain control of this neuron \cite{1,2,3} is an automatic consequence of the intrinsic nonlinearity of the H1 motion detection mechanism \cite{3}. Here we ask whether in addition to this effect, parameters of the underlying motion detector undergo genuine changes in response to the variance of the fluctuating signal. We model H1 as an array of Reichardt motion detectors, consisting of a high-pass filter (HPF), a low-pass filter (LPF), a multiplier and a subtraction stage, followed by a static nonlinearity. Model parameters are fit to spike trains recorded from H1 under a wide range of velocity variance conditions. We find that the HPF time constant and static nonlinearity adapt to the stimulus velocity variance ($\sigma^2$). We examine the influence of this adaptation on the effective gain and time course of the system's velocity response, and on its overall information rate. We show that adaptation in H1 does not yield a constant information rate. Rather, the information rate is a non-monotonic function of $\sigma$, decreasing at both low and high values of the stimulus velocity variance. This dependence is correctly predicted by the Reichardt model.

Acknowledgements
H.S. is partially supported by a U.S.-Israel Binational Science Foundation grant and funding from the Volkswagen Foundation. This work was partially supported by the Max Planck Foundation.

References
Possible role of convergent retinal inputs to LGN relay cells

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Historically, the most commonly proposed role of an LGN relay is to copy the retinal code to the cortex with little or no modification. In conformance with this view, it remains generally accepted that relay cells receive their primary retinal input from a single retinal ganglion cell (RGC). Whole cell recordings from relay cells in the anesthetized cat stimulated with natural movies, however, suggest that these cells may routinely receive weak (or silent) inputs from a collection of secondary RGCs. The possibility that relay cells receive convergent input from numerous RGC’s is at least consistent with the limited anatomical data currently available (Hamos & Sherman 1987). What might be the functional role of these secondary RGC inputs to an LGN relay cell? Our working hypothesis is that silent (NMDA-only) synaptic inputs from a ring of surrounding RGCs could function to “herald” the arrival of preferred stimuli into the relay cell’s receptive field center, leading to (1) an increase in the fraction of a relay cell’s output spikes that carry stimulus-locked signal rather than noise, and (2) an increase in the precision of relay cell spike timing in relation to stimulus timing. We are currently testing this hypothesis using a biophysically detailed relay cell model, and have found that the inclusion of inputs from a ring of secondary RGCs does indeed lead to selectivity for stimulus motion directed towards the RF center, arising from the advance activation of the peripheral (NMDA-only) inputs followed several milliseconds later by the primary (AMPA-rich) inputs. In continuing work we are exploring the possible role of dendritic inhibition via triadic synapses in sharpening the stimulus-locked timing effects.

Acknowledgments
This work was supported by NIH grant EY09593 and MH065918-3.

References
Dynamics and persistence of population responses in visual cortex

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A sequence of oriented stimuli evokes a sequence of population responses in primary visual cortex (V1). If the sequence is rapid, the responses to the individual orientations might interact with each other via summation, suppression, or other possible mechanisms. Knowledge of these interactions is key to predict the responses to arbitrary dynamical stimuli and to understand the functional connectivity of V1.

We measured population responses by imaging voltage-sensitive dye (VSD) signals in area V1 of anesthetized, paralyzed cats (dye RH-1692, [1]) with 5-10 ms resolution. Stimuli were 6 s sequences of 30-40 ms flashed gratings of random orientation [2]. We computed a preferred orientation for each pixel in the image to obtain population responses as a function of time and preferred orientation.

The population responses to successive orientations exhibited apparently complex dynamics. If two orientations in a sequence were separated by less than 30-45 deg, the population response seemed to shift seamlessly from one orientation to the other. A larger step in orientation seemed to elicit a suppressive interaction between population responses.

We asked whether these dynamics could be explained from the average response to a single orientation. This response had a center-surround organization in orientation, and increased rapidly 40-70 ms after stimulus onset and decayed after 150-200 ms. Convolving it with the stimulus, we computed a linear prediction of the responses.

This simple linear model provided a good description of the data (correlation r=0.997 ± 0.002). Whenever a stimulus was followed by another stimulus, the dynamics of model responses closely resembled those seen in the measured responses, thus explaining the apparent interactions between orientations.

However, we observed a discrepancy between the predicted and measured responses when a stimulus was followed by a blank screen. The linear model predicts a rapid decay of the response. The actual response, instead, persists for a few tens of ms after stimulus offset.

We conclude that population responses to rapidly changing stimuli are predicted by a simple linear model. These responses, however, are supplemented by persistent activity whenever the sensory drive is removed. This persistence might be supported by intracortical recurrent connections.

Acknowledgments
Supported by the National Eye Institute and by the McKnight Endowment Fund for Neuroscience.

References
Chromatic Statistics and Information in Natural Images

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To enable color vision, the human photoreceptor mosaic has three cone types sensitive to long (L), medium (M), and short (S) wavelength light. Two outstanding puzzles about this mosaic are that the S cones are rare (<10%), and that L/M ratio varies enormously between individuals. We measured how mosaics with differing proportions of cone types encode natural images and found that these two features of the human retina are consistent with a design that maximizes the encoded information.

We acquired a database of natural images with a calibrated camera. The image values at each pixel represented estimates of the L, M, and S cone quantal absorption rates. We measured 2- and 3-point spatial correlations, both within and across cone channels. The within-channel 2-point correlations were considerable (>0.25) up to separations of 100 pixels. The cross-channel 2-point correlations were also large, even for the L and S cones. We found that transforming the LMS cone images into a luminance channel and three cone-difference channels (cone absorption rate at each pixel minus the local mean luminance) led to a representation in which the four resulting channels were largely decorrelated from one another. In addition, while the luminance channel contained substantial 2-point spatial correlations at large separations, the 2-point correlations within the cone-difference channels dropped rapidly as separation increased. These latter correlations were close to zero for separations larger than 10 pixels.

If an image ensemble contains no structure beyond that captured by the 2-point correlations, then the 3-point correlations are derivable from the 2-point correlations. We found that 90% of the 3-point correlations were derivable from underlying 2-point correlations. We therefore estimated information in natural images on the assumption that the 2-point correlations adequately characterized image spatial structure. We asked what fraction of the cone mosaic should be L, M, and S to maximize information transfer from these images.

Because of long-range 2-point correlations, the information in the luminance channel grows slowly with the size of the cone mosaic (proportional to N^0.75 where N is the total number of cones.) Because of the more rapid falloff in their 2-point correlations, the information in the cone-difference channels grows nearly linearly with N. For this reason, the total information encoded by large arrays is dominated by the contribution from the cone-difference channels. Information encoded by single cone-difference response was estimated as \( I = \frac{1}{2} \log(1 + \text{SNR}) \), with SNR estimated for each cone type (L, M, or S) in terms of corresponding channel variance compared to photon and dark noise. If there were no spatial correlations, the optimal mosaic would contain only the cone type with the highest value of I, but consideration of spatial correlations favors a mixed mosaic. We incorporated within-channel spatial correlations into our calculations. The results showed that the optimal mosaic is dominated by L and M cones, but that the amount of information encoded is largely indifferent to the precise L/M cone ratio. This matches the observed sparseness of S cones and the large variation in L/M ratio within the human population.

Acknowledgments
We thank L. Seyfarth for collecting images and J. M. Klein for assistance with camera calibration. This work was supported by NSF IBN-0344678, NIH EY10016, & NIH EY08124.

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Visual Discrimination with and without Retinal Image Motion

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We are normally not aware of the continual occurrence of fixational eye movements, which, in the periods between saccades, keep the stimulus in constant motion on the retina. It is known that images tend to fade when retinal image motion is eliminated in the laboratory. However, it has long been questioned whether, during natural viewing, fixational eye movements have other functions in addition to prevent image fading. It was first speculated by Hering in 1899 that fixational eye movements might contribute to the perception of fine spatial detail, a proposal later refined into the dynamic theories of visual acuity. These theories were abandoned following the results of classical experiments, which found little or no effect of eliminating retinal image motion on visual acuity and contrast sensitivity [1]. These pioneering experiments, however, suffered from significant technological limitations. Subjects were required to maintain steady fixation for very long periods, an unnatural condition that unavoidably led to visual fatigue and fading. It was not possible to selectively stabilize the image during periods of visual fixation between saccades, as would have been desirable in order to study fixational eye movements in their natural context.

In this study, we reexamined the influence of fixational eye movements on the discrimination of patterns at various spatial frequencies. In a forced-choice discrimination task, subjects reported whether a noisy grating displayed for 1s was tilted by 45° clockwise or counterclockwise. We compared discrimination performances measured in two conditions: in the presence or absence of the retinal image motion produced by fixational eye movements. To overcome the limitations of previous experiments, we developed a new technique of retinal stabilization based on real-time processing of eye movements. This approach enabled rigorous comparison between the two conditions of normal retinal motion and retinal stabilization. It enabled us to (a) selectively stabilize the stimulus after a saccade, a condition that preserves the normal fixational motion of the eye, (b) randomly alternate trials with and without retinal image motion, and (c) assess the accuracy of retinal stabilization independently of the subject’s own judgment, a development that allowed inexperienced subjects to participate in our experiments. We show that fixational eye movements selectively improve discrimination of high spatial frequency patterns. Discrimination percentages were significantly higher in the presence of the normally moving retinal image than under retinal stabilization for high-frequency gratings, but not for low-frequency gratings. These results are consistent with the influence of fixational eye movements on the spatiotemporal power spectrum of the retinal stimulus. The temporal modulations of luminance introduced by fixational eye movements enhanced high spatial frequencies and attenuated low spatial frequencies in the visual input to the retina. The power spectra of natural visual environments are dominated by low spatial frequencies. The results of our experiments suggest that the acquisition of visual information by means of a jittering fixation is an effective strategy for analyzing natural scenes, as it facilitates the processing of spatial detail in the face of otherwise overwhelming low-frequency power.

Acknowledgments
This work was supported by NIH grant EY015732.

References
Neural computation of motion through depth is robust to binocular anticorrelation

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We have begun to investigate the neural computations underlying the human perception of motion through depth using binocularly anticorrelated random dot stereograms. In such anticorrelated displays, corresponding dots shown to each of the eyes have opposite contrast polarity (e.g., a black dot in the left eye is paired with a white dot in the right eye). These displays have been used extensively to probe the mechanisms of static disparity processing. This prior work has revealed that the introduction of binocular disparities between anticorrelated dots typically results in weak, inverted, or nonexistent percepts of depth.

In our psychophysical experiments, we presented displays in which the binocular disparities changed smoothly over time, consistent with motion through depth towards or away from the observer. In contrast to previous reports using static disparities, we find that observers report a strong and veridical percept of motion through depth when viewing anticorrelated stereograms. We also confirm that percepts of depth are degraded for a control condition in which anticorrelated dots with random disparities move laterally. This dissociation appears to hinge on a change of disparity over time, as both the “motion through depth” condition and the “motion within depth” control contain the same monocular motions and range of binocular disparities. Moreover, the dot motions were sinusoidal with randomized phases, to preclude confounds of gaze position and vergence posture.

This unexpected robustness of motion through depth processing suggests a novel neural computation. This computation allows the visual system to discount contrast polarity differences between the two eyes when inferring motion towards or away from the observer. It most likely occurs after or independently from the processing of static disparity and 2D motion, neither of which is similarly robust to anticorrelation. This robust extraction of 3D motions may be analogous to the chromatic insensitivity exhibited by neurons involved in the processing of 2D motions, such as those in area MT.

To search for the neural basis of this motion through depth computation, we performed fMRI measurements as observers viewed alternating blocks of motion through depth (towards/away from observer; each dot changes disparity over time) versus lateral motion within depth (left/right; each moving dot has constant but random disparity). Using both correlated and anticorrelated random dot stereograms, we have identified a candidate network of brain areas involved in the extraction of motion through depth. We attempt to link our psychophysical and neurophysiological data using energy models based on standard disparity processing, as well as those containing joint disparity/motion encoding and disparity/time inseparability.

Acknowledgments
We thank L. Cormack and P. Neri for helpful discussions. This work was supported by the UT-Austin Imaging Research Center and the Meadows Foundation.
Simple and complex cells as style and content variables in a bilinear model based on temporal stability

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A promising approach to the study of representation in the visual system is based on the idea that neuronal response properties reflect an internal model of the statistical structure of the environment, and can thus be derived or learnt from the structure and parameters of a statistical model of sensory observations, following the Helmholtzian notions of perception as an inferential process. The generative modelling framework is particularly appealing in this respect, because it defines the internal model by making explicit how the visual image is generated from external sources. Successful learning of the models parameters thus implies the identification of such causes, which are ultimately what is needed to control behaviour.

Here, we present a model of visual input where observations are generated from a set of binary “content” variables, each representing the presence of a particular visual feature. The appearance of each feature is modelled by a multidimensional manifold that represents its episodic pose, and is parametrised by a set of “style” variables. Contents are assumed to be independent of one another but individually persistent, with styles that vary smoothly over time. Content and style variables then combine bilinearly to form the image. The temporal priors on the latent variables allow us to overcome the degeneracies present in the bilinear model and to perform learning in a fully unsupervised way.

When this model is applied to natural image sequences, the resulting content manifolds are spanned by pairs of localised Gabor wavelets with similar position, orientation, and frequency, but with a 90 degree phase relationship. Consequently, the inferred activity of style variables in the learnt model resembles that of simple cells in the primary visual cortex. Content variables indicate the presence of a feature irrespective of its position on the underlying manifold, and are therefore insensitive to the phase of the corresponding wavelets. Their behaviour is thus similar to that of complex cells.

Thus, this generative model makes explicit an interpretation of complex and simple cells as elements in the segmentation of a visual scene into independent features along with a parametrisation of their episodic appearance. It also indicates their possible role in a hierarchical system that extracts progressively higher-level contents, starting from simpler, low-level features.

We are currently investigating the possibility that the segmentation in persistent contents underlies visual effects such as the tilt illusion: Due to the assumptions of the model, small changes in the input are explained away by the currently active contents while other content variables have to account for the residuals, which leads to a form of repulsion similar to that seen in temporal versions of the tilt illusion.

Acknowledgements
This work was supported by the Gatsby Charitable Foundation.
The Origin of Adaptive Temporal Integration in Visual Cortex

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Characterizing visual neurons in terms of spatio-temporal receptive fields (RFs) involves determining their profiles of spatial and temporal integration. In many V1 cells, however, these profiles are not fixed, but vary substantially with changes in the visual stimulus used to map the RF. For example, the temporal integration window for complex direction selective (CDS) cells in macaque V1 varies systematically with temporal frequency (TF), spatial frequency (SF), and contrast. In particular, integration is short-lived for rapidly moving stimuli and prolonged for slower stimuli. Currently, the mechanisms and loci of these apparently useful features of sensory processing remain unknown. If models of visual processing are to accurately predict responses to arbitrary stimuli, non-linearities such as this adaptive temporal integration (ATI) must be accounted for.

To determine where ATI arises, we assessed temporal integration in classes of cells that might lie upstream from V1 CDS cells, including simple DS, simple non-DS, and LGN cells. All data were recorded extracellularly from single units in anesthetized macaque monkeys. We used the same type of randomly moving sinusoidal grating stimulus that was used previously for CDS cells. We quantified temporal integration for DS simple cells using the width at half-height of the motion-domain spike-triggered average (STA). For non-DS simple cells and LGN cells, the motion-domain STAs were flat. These cells have a clear preference for the spatial phase of a sinusoidal grating; therefore, we transformed the stimulus sequence to a weighted toward-away representation in which each movement was coded as taking the stimulus toward or away from the preferred spatial phase. We computed toward-away STAs and deconvolved them to remove the influence of the stimulus autocorrelation in time.

For V1 simple DS cells, we found that temporal integration changes with the stimulus speed in a manner similar to that observed for CDS cells, spanning a range from about 60-70 ms for slow motion to about 20 ms for fast motion. This demonstrates that ATI is not exclusively a property of complex cells. Also, for the handful of simple non-DS cells that we have tested, we observed little change in temporal integration compared to that for DS cells. Preliminary data from the LGN suggest that some magnocellular cells increase their integration time consistent with ATI seen in the cortex.

It is still too early to make firm conclusions, but the results emerging so far are consistent with the idea that adaptive temporal integration may be a property of the motion pathway, including V1 DS cells (both simple and complex) and magnocellular cells in the LGN.

Acknowledgments

We thank Nicolas Heess for insightful discussion and assistance with data collection. This work was supported by a Wellcome Trust Senior Research Fellowship to WB.

References

Reading Out Visual Information from Populations of Neurons in Inferior Temporal and Prefrontal Cortex

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The ability of primates to recognize visual objects is believed to be based on a series of transformations of visual information that occur as signals travel down the ventral pathway from primary visual cortex (V1) through inferior temporal cortex (IT) and ultimately on to prefrontal cortex (PFC) where decision making circuitry is believed to reside. Thus, a key component to understanding how object recognition occurs is to determine how visual information is represented in these different cortical areas, as well as how these representations change with time in the course of recognizing an object.

To try to understand this process, we used population decoding methods [1] to analyze data that was recorded as macaque monkeys engaged in a delayed match to category task [2]. We trained a support vector machine on the firing rates of a pseudo-population of neurons to determine the time course and strength of stimulus category and identity information in IT and PFC.

Similar to the findings of the original studies [2] we see that IT contains more detailed visual information while the stimulus is still visible, and that PFC contains more category information during the delay period. Using these newer decoding methods, we are able to get a much finer temporal estimate of how information is transformed over time and across areas. In particular, we see that information in both IT and PFC is transformed from representing visual properties of the stimulus to ultimately being based on the semantic task-relevant category of the stimulus that is related to the monkey receiving a juice reward. The task-relevant transformation occurs earlier in PFC than in IT. Additionally, it appears that the same type of information about a stimulus (category/identity) is being represented by different patterns of firing rates at different time points relative to stimulus onset. Finally, we examine how findings based on population decoding methods relate to results obtained by analyzing individual neurons separately.

References
Natural movies evoke synaptic responses that produce dual modes of firing in the cat's thalamus.

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Thalamic relay cells transmit information from retina to cortex by firing either rapid bursts or tonic trains of spikes. Bursts occur when the membrane voltage is low, as during sleep, because they are mediated by specialized calcium channels that open only after prolonged hyperpolarization. Cells fire tonically when depolarized, as during waking. Thus, the two modes of spiking are usually associated with behavioral state. Growing evidence, however, suggests that both patterns contribute to sensation and that each plays a unique role in cortical processing. The possibility that bursts contribute to normal sensory function is important because the temporal pattern of spike trains determines the amount and type of information that can be encoded about the stimulus and also influences the probability of activating cortical neurons.

To ask if synaptic responses during vision induce both modes of firing we made whole-cell patch recordings from thalamic cells during the presentation of natural movies. First, we laid the foundation for our study by using simple stimuli to map the synaptic structure of the thalamic receptive field. In general, we found that if bright light excites a subregion of the receptive field (either the center or surround) then dark light evokes strong inhibition, a push-pull arrangement. The spatial pattern of responses we recorded were consistent with a simple retino-thalamic circuit in which excitation is supplied by input from ganglion cells of the same center sign (as the relay cell) and inhibition is routed through interneurons that receive input from ganglion cells of the opposite center sign. Because we labeled the cells we patched, it was often possible to use anatomy to distinguish relay cells from local interneurons. Both types of cell had center surround receptive fields with push-pull, consistent with the feed-forward circuit we describe.

We then asked if natural movies, because of their intrinsic temporal correlations, might evoke long stretches of inhibition that could prime bursts (previous extracellular studies had suggested that long periods of stimulation with the non-preferred stimulus enabled bursts). Hence we recorded from relay cells during the presentation of these stimuli and found that they routinely evoked long hyperpolarizations followed by bursts. The next step was to explore the relationship between receptive field structure and responses to movies to gain insight into how the underlying circuitry might mediate the physiological patterns we observed. Therefore we developed methods to separate excitation from inhibition in the intracellular signal and to reconstruct the receptive field for each from the responses to the movies. We found that the natural stimuli evoked strong push-pull responses from the center of the relay cell's receptive field, with only modest recruitment of the surround. This observation led to a simple conclusion, that retinogeniculate (feedforward) inhibition driven from the center of the receptive field is sufficient to prime bursts. Furthermore, we used cross-correlation analysis to show that most of these bursts were triggered by retinal input. Taken as a whole, our results suggest the relays cells use both tonic and burst modes of firing to encode the information they send downstream.

This work was supported by NIH grant EY09593 (JAH) and the Redwood Neuroscience Institute (KK and FTS).
Rapid Light Adaptation in the Retina

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The sensitivity of the visual system varies dramatically depending on the immediate history of light exposure. This light adaptation is essential for survival on a rotating planet with a single star, where intensities change over ~10 orders of magnitude in the course of a day. Much of the underlying gain modulation occurs in the retina, beginning with the biochemical transduction cascade in photoreceptors.

On a formal level, light adaptation is often regarded as a slow modulation of the fast dynamics of the visual response. In this picture, a visual neuron responds to the light input in the most immediate past, perhaps a tenth of a second. But the gain and the dynamics of that response are affected by the average light input over the more distant past, spanning perhaps seconds to minutes. Many visual studies seek to avoid the nonlinear gain changes from light adaptation, by using stimuli that vary rapidly and maintain a constant mean intensity. Here we report that there remains a large effect of light adaptation even under those conditions.

We recorded intracellularly from cone photoreceptors¹ of the tiger salamander under rapidly flickering illumination (Gaussian intensity distribution, random update every 30 ms, std dev = 0.35 · mean). We identified episodes during which the response gain appeared higher (lower) than average, and found that these correspond systematically to lower (higher) than average illumination in the preceding period. Overall, the photoreceptor gain was modulated by a factor of >2, and the dependence of gain on preceding intensity followed the typical Weber-Fechner relationship for light adaptation. The temporal weighting function for preceding intensity extended ~1s into the past, but with stronger weight for the most recent history. An increase in gain also entailed a slowing of the response kinetics.

To sample the consequences of such gain modulations on subsequent visual processing, we recorded from retinal ganglion cells under rapidly flickering stimuli. Again, there was a substantial modulation in sensitivity depending on illumination in the preceding 1s. The effect was particularly striking in Off-type cells: In these neurons, a transient dip in light intensity leads to rapid firing, and one might expect the response gain to decline during those times, because of spike adaptation or refractoriness. Instead, we found that the response gain was highest during those periods, presumably owing to light adaptation in cones.

We summarize the effects with two types of mathematical description. The first builds on the conventional Linear-Nonlinear model of the ganglion cell light response, in which the light stimulus is convolved with a linear filter followed by a nonlinear gain function to predict the neuron’s firing rate. Light adaptation can be introduced by making the filter function itself dependent on the preceding light stimulus. An alternative and potentially simpler formulation results from a dynamically nonlinear model of the photoreceptor, involving two variables with coupled dynamic equations and a single nonlinearity. Both the gain control (Weber-Fechner law) and the change in kinetics emerge naturally from this dynamical system. This model is successful with far fewer ad hoc parameters, and makes predictions for new kinds of adaptive phenomena.

Including the effects of rapid light adaptation will improve the quality of computational models for visual responses and help in parsing the contributions of different mechanisms to nonlinear gain control.
Fast visual responses: Is counting spikes enough?

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In visual processing, the cortex very quickly arrives at a hypothesis about the stimulus [1]. Thorpe et al. suggested, that this hypothesis is generated in a feed-forward network, where each feature-selective cell evaluates the order (rank) of incoming spikes [2]. However, to evaluate a rank code, every feature-selective neuron needs a local readout circuit. This is both biologically implausible and expensive to implement.

We propose, that post-synaptic neurons simply count the number of incoming spikes, and fire if the number of incoming spikes exceeds a threshold. This simple scheme for feature-selectivity uses spike-times only implicitly and does not require additional circuitry. We evaluate the quality of responses gained from a cascade of these labeled-line-encoders, given the tuning characteristics of primary receptors, and unreliable processing in the succeeding neurons.

To allow a quantitative analysis, we use a fully controlled visual environment, with parametric visual stimuli (colored blobs), and well-defined tuning of primary receptors. For the feature detectors, we apply a simple spike-counting neuron model with a binary output state (spike, no spike). The neuron signals an output spike with probability $p_1$, if the number of input spikes exceeds a threshold, and with probability $p_0$, otherwise. In cascades of labeled-line-encoders with $N$ steps and $L$ incoming lines per neuron, we evaluate the probability of correct responses to stimuli in the final step of the cascade, as a function of $(p_0, p_1, N, L)$. We present results from computer simulations and mathematical analysis.

This architecture is part of a functional model of the sensory cortex [3,4]. To incorporate high-level knowledge into processing at lower levels, it applies a form of cognitive bootstrapping, where an initial top-level hypothesis about the stimulus is used to steer processing in the lower areas. Unlike other approaches using similar architecture, spatial invariance and low error rates are not in the focus for hypothesis generation. Instead, top-level responses must be fast and reasonably correct, to be suited for cognitive bootstrapping in our cortex model.

References
Spike timing precision and the influence of cortical dynamics.

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The prevailing wisdom that visual cortex neurons are noisy and temporally imprecise is based largely on evidence from sequential single unit recordings in response to reduced visual stimuli such as drift gratings or spots of light. Moreover the benchmark for quantifying spike timing precision is the trial to trial variability in the post-stimulus time histogram (PSTH) of repeated presentations of the same stimulus, which explicitly ignores ongoing (or stimulus independent) cortical dynamics. We are exploring the limits of spike timing precision in local neuronal populations evoked by complex stimuli (natural scene movies), taking into account the ongoing activity as measured by the local field potential (LFP).

High-density silicon electrode arrays (polytrodes) were used to make simultaneous recordings of 100+ neurons spanning all cortical layers in anesthetized cat primary visual cortex [1]. Brief 5s natural scene movie segments [2] were presented 25-75 times (50Hz frame rate, 200Hz refresh). The complex analytic signal was used to obtain an instantaneous measure of LFP phase from 1-150Hz. LFP modulation of spike timing was quantified by fitting a von Mises distribution (circular Gaussian) to the histograms of spike phases relative to the LFP oscillation.

Evoked responses to natural scenes were characteristically sparse, punctuated with highly reliable events (Fano factors 0.1). Neurons showed varying degrees of phase locking to the LFP with predominant peaks in all the classically defined EEG bands. Individual neurons often had multiple peaks. The LFP itself also showed transient stimulus-dependent phase alignment across trials at several frequencies. Without considering the role of the LFP the full-width half-maximum of many spiking events was around 15ms. Dejittering the spike trains based on the phase of the LFP in the gamma band revealed ms-precise temporal patterns within the events.

Taken together we suggest that neurons in the primary visual cortex are capable of high spike timing precision comparable to that reported in the lateral geniculate and retina, but ongoing cortical dynamics introduces temporal jitter that may obscure this precision.

References
Predicting responses of V1 neurons to natural movies

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Response properties of visual cortical neurons have been extensively studied using a variety of stimuli, ranging from moving bars of light to images of complex natural scenes. One approach has been to characterize the conditional probability distribution that a neuron spikes given the presentation of a particular stimulus $X$, $P(\text{spike} | X = x)$. One functional class for this distribution is the linear-nonlinear Poisson (LNP) cascade receptive field (RF) model where $P(\text{spike} | x) = f(Kx)$ with kernel $K \in \mathbb{R}^{m \times n}$, stimulus $x \in \mathbb{R}^n$, and output nonlinearity $f : \mathbb{R} \to [0, 1]$. Here it is assumed $m \ll n$ with kernel $K$ projecting the stimulus space onto a much smaller ‘relevant’ subspace. This model was used to estimate simple and complex cell spatiotemporal RFs using artificial stimuli oriented in the preferred direction of the cell and spatial RFs using random frames taken from natural movies.

We studied to what extent these models account for the variance of responses of visual neurons to natural movies when fit using different training stimuli. First and second order spatiotemporal kernels $K^1$ (STA) and $K^2_i$ (STC) were computed from single cell recordings from the striate cortex of anaesthetized cats while they viewed full-field natural movies and msequence stimuli (see [5] for experimental methods). Natural movie kernels were corrected for the spatiotemporal correlations in the stimulus. An output nonlinearity of the form $r(t) = r_0 + \alpha (|K^1I + \theta|^p + \sum_i \beta_i (K^2_i I)^2)$ was fit to firing rates computed from a separate repeated natural movie segment.

Predictions based on first order kernels were far better for natural movies than for msequence stimuli. This was true whether or not the kernels displayed classic Gabor-like simple cell structure. Second order kernels computed from natural movies displayed additional structure where msequences did not. Furthermore, the improvement in the prediction using both first and second order kernels was significant when using natural movies but not so when using msequences. This demonstrates that fitting a spatiotemporal LNP model using full-field natural movie stimuli is feasible and that this model captures a far greater degree of response variability to natural movies than one fit with artificial stimuli.

Acknowledgments
This work was supported by NGA grant MCA 015894-UCB, NSF grant IIS-06-25223, and a Kopriva Fellowship to J.B.

References
A bottom up visual saliency map in the primary visual cortex, theory and its experimental tests

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Given the attentional bottleneck, the visual system must select a limited aspect of inputs for detailed processing. Much of the selection is by bottom up mechanisms to direct gaze to the selected or most salient visual locations for detailed processing. While saliency has been investigated extensively in behavioral studies, its physiological basis remains controversial. I will present the theoretical proposal that the primary visual cortex (V1) creates a saliency map of the visual space, such that the receptive field location of the most responsive V1 neuron to a scene is most likely selected for attentional processing. This proposal generates non-trivial predictions, and their experimental tests will also be presented. More details are available at www.gatsby.ucl.ac.uk/zhaoping
Equalization of ocular dominance columns induced by an activity dependent learning rule and the maturation of inhibition

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In cat primary visual cortex (V1), responses early in development are dominated by the contralateral eye [1]. Both physiologically and anatomically [1,2], inputs from the ipsilateral eye are restricted to patches within a continuous sea of contralateral-eye inputs. Then, beginning approximately at the onset of the critical period for plasticity in response to monocular deprivation, the inputs from the two eyes become roughly equalized and segregate into alternating ocular dominance columns [1]. This equalization and segregation does not occur if the eyes are not opened [1]. It was argued [1] that this equalization was unlikely to arise simply from Hebbian rules of synaptic plasticity. This was presumably based on the intuition that, in a Hebbian competition between two inputs with similar activities, the initially stronger input should win. In mouse V1, the onset of the critical period for monocular deprivation plasticity has been shown to coincide with, and depend upon, a sufficient maturation of intracortical inhibition [3,4]. The maturation of inhibition and the associated onset of the critical period does not occur if the eyes are not opened.

Here we show how these observations can be united: sufficiently strong inhibition forces equalization of the two eyes under a Hebbian rule. If intracortical connections are inhibition-dominated, then activation of some cortical cells by one eyes’ inputs evokes net inhibition that suppresses the activation of other cortical cells. This suppresses patterns in which a majority of cortex is driven by a single eye, leaving only those in which the two eyes equally share cortex. A periodically alternating ocular dominance pattern results if excitation and inhibition are organized in a “Mexican hat” pattern. In semi-linear models of plasticity, this solution is too inflexible: even after simulated monocular deprivation, the two eyes remain equal. We show that a nonlinear model that incorporates homeostatic as well as correlation-based plasticity can replicate the entire developmental sequence. If, on average, contralateral synapses are initially stronger, ipsilateral-eye dominant patches emerge in a continuous sea of contralateral-eye input. After maturation of inhibition, an equalized, periodically alternating ocular dominance pattern emerges, but monocular deprivation still causes an ocular dominance shift. Thus, if the onset of the critical period in cats coincides with a maturation of inhibition that depends on the eyes being open, as in mice, this suffices to explain the interocular equalization observed at the onset of the critical period in cats and its failure to occur under binocular deprivation [1].

Acknowledgments
This work was supported by the Japan Society for the Promotion on Science, a Grant-in-Aid No. 1806772 for JSPS fellows, and NIH grant R01 EY11001.

References
How thalamic circuits change visual signals en route from retina to cortex

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The lateral geniculate nucleus of the thalamus is in many ways the underdog of early visual pathway, taking a back seat to the retina and the cortex. Even the name of its principal neurons, “relay cells” seems to diminish its relevance by suggesting a passive role. Yet there is mounting evidence to suggest that the thalamus makes unique contributions to early visual processing. For example, past anatomical and cross-correlation analyses have shown that retinogeniculate wiring is complex and that some relay cells receive input from multiple ganglion cells. As well, nearly a third of neurons in the geniculate never leave the thalamus, but rather make inhibitory connections with local relay cells and with each other. Further, relay cells use dual modes of firing to transmit visual information downstream; they fire either rapid bursts or tonic trains of spikes depending on the level of membrane polarization.

Such findings compelled us to explore the physiology and anatomy of thalamic circuits directly by combing intracellular recording and staining in vivo with various computational approaches. We used many different types of visual stimulus, but focused on natural movies in order to evoke ecologically relevant patterns of activity. The talk will introduce three main projects that address how thalamic circuits operate. For the first project we map patterns of retinogeniculate convergence by analyzing the total pool of excitatory synaptic potentials that individual relay cells receive. In the second, we investigate local inhibitory circuitry by recording visually evoked inhibition in relay cells and by recording directly from interneurons. Last, we ask if patterns of synaptic excitation and inhibition evoked by naturalistic stimuli are able engage both burst and tonic modes of firing. A particular goal of this talk is to present empirical findings to theorists in order to foster discussion about thalamic function.
Retinal oscillations carry visual information to cortex

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Neuroimaging with PET and MRI have shown that ongoing activity in the resting brain accounts for more than 90% of energy consumption in the brain[1]. The function of ongoing activity, which is often oscillatory, is one of the big mysteries in Neuroscience. Here we report the discovery of an information channel that is mediated by ongoing oscillations and can be used to transmit information from the eye to the brain. Specifically, retinal oscillations provide a previously unknown independent second channel of information using a form of multiplexing similar to methods used in technical communication systems: The two different channels are assigned to separate frequency bands of the spike train of single relay cells in the thalamic lateral nucleus. We were able to unmask this novel channel by combing experiment, model and theory. First, we used whole cell recording in vivo to gain direct access to the precise timing of both retinal inputs (EPSPs) and thalamic spikes during the presentation of natural movies. Second, we developed new methods to detect intracellular events and to quantify the information carried in spike timings with respect to ongoing activity. Third, we devised a model of the thalamic relay cell that reproduced the experimental findings.

Previously, we showed that much of the variance in responses of thalamic relay cells to repeated stimuli could be explained by intrinsic retinal oscillations that are not time-locked to the stimulus. Specifically, we found that spike latencies with respect to the stimulus were far more variable than spike timing with respect to retinal EPSPs, which showed millisecond fidelity. Here we explored how the stimulus and the intrinsic oscillations influence spike timing by building a multiplicative model of the relay cell. The model described spiking by a point process where the density is given by the product of two functions. One is the usual stimulus transfer function, i.e., the low-passed convolution between visual input and the receptive field. The second function represented the impact of intrinsic retinal oscillations; its periodicity and phase were determined from recent synaptic input. The degree to which thalamic activity phase-locked to the retinal oscillations was described by a von Mises distribution whose two parameters were tailored for each cell. The model was able to reproduce experimentally measured spiking statistics and information rates and thus revealed a multiplicative scheme for thalamic spike trains to generate dual channels for visual information to reach cortex.

It is likely that the two channels transmit different types of information downstream. Stimulus-locked coding is suited to provide information about local patterns that fall on individual receptive fields. By contrast, oscillation-based coding, which is produced by spatially distributed retinal networks, could provide information about global context. Thus, beginning at the sensory periphery, the code formed by neural spike trains can be parsed into parallel streams that communicate complementary information about local detail and the big picture. Recent experiments in frog support the prediction that oscillations convey such contextual information[2].

Acknowledgments
This work was supported by NIH EY09593 (JAH) and the Redwood Neuroscience Institute (KK, FTS).

References
Coding 3D by 3V: How sensor motion constrains sensory coding

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Rats use their whiskers (vibrissae) to localize and identify objects in their vicinity. We studied neuronal variables used by vibrissal receptors to encode the coordinates of object location in three dimensions. We found that the most efficient neural code for each of the three spatial dimensions is different: spatial (labeled-line) for the vertical (along whisker arcs), temporal for the horizontal axis (along whisker rows), and rate for the radial axis (from the face out). One possible advantage of such a triple coding scheme is increasing channel efficiency by multiplexing; the same neurons can convey information on three dimensions at the same time without losing accuracy or reliability. The fact that a neuron fires conveys information about the vertical coordinate of an object; the time of its firing, in relation to other the radial coordinate. The output signal of such a neuron can be conveyed in parallel to different readout circuits, each decoding one specific variable. Another possible advantage of triple coding is reducing ambiguity, and by this simplifying decoding algorithms; a given neuronal variable encodes only one coordinate and is not affected by other coordinates (orthogonal coding). The vibrissal system partially utilizes both these advantages, and also monitors coding efficiency via a delicate control of whisker motion. Understanding how optimal motor-controlled coding is achieved will most likely advance our understanding of sensory perception.
**From spikes to space: reconstructing features of the environment from spikes alone**

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A common stimulus reconstruction paradigm involves first computing the receptive fields of recorded neurons (using both spike trains and the presented stimuli), and then using the receptive field information together with neuronal activity in order to “predict” the pattern of stimuli based on local stimulus features. Some brain regions (such as hippocampus) undergo remapping of receptive fields, depending on context. How do downstream neurons integrate the mosaic of individual neuronal responses, with potentially varying receptive fields, to extract global characteristics of presented stimuli?

In rodent dorsal hippocampus spatial information is encoded by place cells, i.e. pyramidal cells that fire in a restricted convex area of the spatial environment, and are mostly silent outside. The receptive fields of individual place cells (place fields) can be thus thought of as small convex domains in a two-dimensional environment. The place fields for the same neurons re-map from one spatial environment to another.

In this work we show how certain global features of a spatial environment can be computed from hippocampal spiking activity alone. In particular, we consider a variety of two-dimensional environments which differ in the number of obstacles (or holes) constraining the region accessible to a freely-foraging rat. Assuming only basic properties of hippocampal place fields, we construct an algorithm that distinguishes between these different environments by computing standard topological invariants (homology groups) from population spiking activity. These invariants precisely determine the numbers of obstacles/holes in the environment – and can be computed without ever using any position-tracking information, or any other feature of the rat’s trajectory through space. In particular, we never compute place fields or any other correlations between cell firing and external stimuli.

We tested the algorithm using simulated data, staying as close as possible to physiological parameters seen in real data. For each of five distinct environments, open field and \(N\)-obstacle environments for \(N = 1, \ldots, 4\), we simulated place cell spike trains corresponding to a random walk. (Place fields in different environments were completely unrelated.) The algorithm correctly identified each environment from the population spiking data. Furthermore, on shuffled data sets, the computed homology groups reflected high-dimensional, non-physical environments. We have thus shown that global features of the spatial environment can be reconstructed from hippocampal place cell spiking activity alone.

**Acknowledgments**

This work was supported by the Swartz Foundation.
On the agnosticism of spikes: attention, intention, and salience in the monkey lateral intraparietal area

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Attention is the process whereby the brain filters out sensory information unimportant for behavior. Clinical studies show that the parietal lobe is important for the attentional processes. Neurons in the lateral intraparietal area (LIP) filter out visual stimuli that are behaviorally unimportant, for example stable objects in the environment, although they do respond to those same stimuli when they appear abruptly in the environment.

Although LIP filters out behaviorally irrelevant visual stimuli, it does not filter out salient objects that are not the targets of a planned saccade. When a monkey plans a memory-guided saccade away from the receptive field of a neuron, the abrupt onset of a distractor in the receptive field evokes an enhanced response relative to the case when the monkey plans a saccade to the receptive field and the distractor subsequently appears in the receptive field. In these cases the distractor had no effect on the performance of the saccade.

Attention, as measured by an improvement in contrast sensitivity at the attentionally advantaged site, lies at the goal of a memory-guided saccade during the delay period, but it can be briefly captured by the abrupt onset of a distractor. The activity of neurons in LIP correlates with the monkey’s attention both when it lies at the saccade goal and when it lies at the distractor site, and the time at which attention returns from the distractor to the saccade goal is predicted by the activity of neurons in LIP.

Most studies of eye movements in awake, behaving monkeys demand that the animal make specific eye movements. We have developed a new paradigm in which the monkey performs a visual search for an upright or inverted T among 7, 11, or 15 cross distractors, and reports the orientation of the distractor with a hand movement. The search array is radially symmetric around a fixation point, but once the array appears the monkey is free to move its eyes. The monkey’s performance in this task resembles that of humans in similar tasks (Treisman and Gelade, 1980): manual reaction time shows a set size effect for difficult searches (the crosses resemble the T’s) but not for easy searches (the T pops out). Saccades are made almost exclusively to objects in the array, and not to intermediate positions, but fewer than half of the initial saccades are made to the T. We recorded from neurons in the lateral intraparietal area (LIP) while the monkey performed the search. LIP neurons distinguish the saccade goal at an average of 86 ms after the appearance of the array. The time at which neurons distinguish saccade direction correlates with the monkey’s saccadic reaction time, suggesting that most of the jitter in reaction time for free eye movements comes from the discrimination process reflected in LIP. However, they also distinguish the T from a distractor on an average of 111 ms after the appearance of the array even when the monkey makes a saccade away from the target, suggesting that LIP has access to cognitive information about the target independent of the saccade choice.

We suggest that LIP provides a salience map which can be used by multiple systems. The salience map is constructed from independent signals (visual, cognitive, saccadic) which are summed in a linear fashion. When a saccade is appropriate, the oculomotor system can use the peak of the salience map to drive a saccade. The visual system uses the same spikes to determine the locus of attention. The source of the spikes, whether from a saccade plan or the visual system reporting the abrupt onset of a visual stimulus, is irrelevant to the use to which the recipient area puts the signal.
Medial prefrontal cortex and the temporal control of action

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Neuroimaging studies in human beings and unit recording studies in primates suggest that medial areas of prefrontal cortex (mPFC) are involved in decision making and action selection\textsuperscript{1,2,3}. A major aspect of mPFC function that has not been widely studied is its role in controlling the timing of action, i.e., deciding \textit{when} to act. Our laboratory has addressed this issue in three recent studies. First, we used reversible inactivation methods to "knock out" mPFC activity during a simple delayed response task\textsuperscript{4}. This manipulation resulted in excessive premature responding and a lack of temporal control over response initiation. Second, we combined reversible inactivations in mPFC with ensemble recordings in motor cortex during a delayed response task\textsuperscript{5}. We found that inactivation of mPFC reduced delay activity in motor cortex. Third, we recorded in mPFC during a delayed response task\textsuperscript{5}. We found that about one-third of neurons fired persistently during the delay period. Most recently, we tested the hypothesis that activity in mPFC is sensitive to stimulus timing. In a baseline task with a 1s delay, the firing rates of 15\% of 170 neurons were modulated by the trigger stimulus. When animals learned to respond at an earlier delay (0.5 s), the percentage of stimulus-related neurons increased to 24\% (of 157). After learning, one-third of 368 neurons were active during the delay period and all of these neurons fired more at either the short or long delays. At the population level, strong temporal correlations between delay-related neurons were observed early, but not late, in the delay period. These effects were not observed in the motor cortex. Our results suggest that medial prefrontal cortex is critical for the temporal control of action because it accounts for the expected timing of trigger stimuli. We interpret our results in the context of previous anatomical studies of mPFC, especially its massive descending projections to limbic, autonomic, and monoaminergic centers\textsuperscript{6,7}. These studies suggest that mPFC might influence motivational and emotional brain systems to achieve temporal control over behavior.

\textbf{References}

Hemodynamic Correlates of a Perceptual Decision

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Does activity in primary visual cortex (V1) correlate with perceptual choices in a threshold orientation discrimination task? Single-unit physiology in monkeys has shown that the performance of neurons as measured by the so-called neurometric function matches well with the behavioral psychometric function \cite{Newsome1989}, and on individual trials, the response of single neurons weakly covaries with the monkeys’ choices. Given that perceptual choices are believed to be based on the population neural activity, we hypothesized that hemodynamic responses might more accurately predict perceptual choices.

Observers fixated a central fixation cross and viewed a circular low contrast (10\%), flickering square wave grating (20x20\degree, TF=8Hz, SF=2 cycles/deg) presented for 1 sec followed by an inter-trial interval of 5.4 to 10.2 secs. The orientation of the stimulus was near psychophysical threshold (\(\pm 2.5\), \(\pm 1.5\), \(\pm 0.5\), \(\pm 0.25\)\degree) and observers reported whether it was tilted left or right of vertical by pressing one of two keys. Concurrently, we measured BOLD fMRI using a 3T Siemens Allegra scanner (gradient-recalled EPI, TR = 0.8 seconds, TE = 30ms, 3x3x3mm voxels, 14 slices perpendicular to the calcarine sulcus).

To compare behavioral choices to the hemodynamic responses, we used a novel classification-based technique to estimate the neural activity for individual trials. Previous work has demonstrated that linear classifiers can decode the orientation of a stimulus from V1 activity in blocked fMRI experiments \cite{Kamitani2005}. We extended the applicability of this approach to an event-related protocol, by analyzing empirical hemodynamic response functions (HRF) in two steps. First, for each voxel, we projected the HRF for every trial onto the principal axis that best discriminated between different stimulus orientations and/or behavioral responses. By doing so we allowed for the possibility that responses to different stimuli might not simply vary in amplitude, but also in time course. Second, we trained linear classifiers using those projections to test how well the HRFs correlated with stimulus conditions and/or behavioral responses.

We quantified the degree to which hemodynamic responses in V1 can be used to discriminate stimulus orientations by a hemometric function and found it to be compatible with an observer’s psychometric function. Moreover, we found that the pattern of activation across voxels in V1 covaried with the observers’ choices on a trial-by-trial basis. Of particular interest are near threshold conditions in which for the same exact stimulus, observers’ choices varied across trials. In those cases, the output of the classifier predicted the observers’ perception even when they were incorrect. While pooling of responses implicit in fMRI measurements may not match the pooling scheme used by the brain, our results nonetheless provide evidence that observers’ choices arise from the correlated fluctuations of the neural activity in the sensory areas that support those choices.

Acknowledgments
Supported by NIH grant R01-EY11794. JLG was supported by an NRSA and a BWF career award.

References
Planning and decision-making in parieto-frontal circuits

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Although the posterior parietal cortex has historically been considered to be involved in sensation, attention, and cross-modal sensory integration, recent studies have also pointed to a role of this region in movement planning and decision making. Movement plans can be more readily decoded from posterior parietal cortex activity than the locus of spatial attention with the lateral intraparietal area (LIP) coding eye movement plans and the parietal reach region (PRR) coding reach plans. Detailed studies of PRR indicate a close connection with movement planning: 1) PRR integrates task context with sensory information to immediately code motor plans; 2) its activity reflects the choice of the animal when selecting reach targets; 3) PRR activity is related to expected value including expected type, probability and amount of reward; 4) during movements it codes both the instantaneous state of the hand as well as the movement goal; 5) there is greater bidirectional corticocortical communication between PRR and the dorsal premotor cortex when the animals are free to choose reach targets compared to instructed reaches. These data support the idea that the posterior parietal cortex is important for sensorimotor transformations and provides an interface between sensory and motor areas of the brain.
Neural Correlates of Tactile Detection: Combined MEG and Biophysically Based Computational Modeling Study

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Cortical correlates of sensory perception have typically been observed in higher order cortical areas, while there are conflicting reports as to their presence in primary sensory cortex. To investigate the cortical correlates of somatosensory perception in humans, we conducted studies of tactile detection using MEG. To this end, we developed an MEG compatible piezoelectric tactile stimulator with real time regulation of stimulus amplitude as a function of psychophysical response. We recorded 306-channel MEG signals (Elekta NeuroMag VectorView) and extracted somatosensory evoked dipoles by combining MEG with structural MR images.

A stimulus-level dependent equivalent current dipole (ECD) in the hand area of SI was observed in all subjects. Perception of the threshold level stimuli was predicted from ongoing ‘state’ properties and from post-stimulus evoked responses in SI. Perceived trials at threshold showed lower power in alpha (7-12Hz) and/or beta frequency bands (15-35Hz) in the signal immediately prior to stimulus onset (-500ms to onset; N = 6/7 Ss). In the evoked response, the magnitude and timing of peaks in the early SI ECD waveform predicted perception as early as 70ms post-stimulus (N = 7/7).

To make a direct and principled connection between the observed phenomena and the underlying neural dynamics, we developed a biophysically realistic computational neural model of a laminar SI cortex. The model incorporated the dendritic morphology and physiology of large pyramidal neurons known to be the primary generators of MEG ECDs. Results from the model led to the novel hypothesis that polarity and magnitude of peaks in the evoked SI ECD were induced by a sequence of feed-forward (from the periphery and thalamus) and feedback (from a “higher order” cortical area) input into the local SI network, characterized by the laminar location of their synaptic inputs. Further, specific manipulations of these inputs led to predictions on the neural dynamics underlying conscious perception. The observed signatures of perception in the SI ECD were reproduced in the model by simulating feedback and late thalamic inputs with earlier latencies and stronger magnitudes during perceived trials. An investigation with the model of ongoing state dynamics and their relation to evoked responses and perception is currently in progress.

Taken together, our results suggest that evidence of conscious perception exist in SI both in the ongoing state dynamics and in the evoked response, and that these effects can be investigated using biophysically realistic computational cortical modeling.

This work was supported by NIH: K25MH072941, 1RO1-NS045130-01, T32 GM007484. NSF: 0316933
Evidence for One Dimensional Dynamics of Attention and Decision Making in Macaque Parietal Cortex

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Where we allocate our visual spatial attention depends upon a continual competition between internally generated goals and externally generated distractions. Neurons in the macaque lateral intraparietal area (LIP) can predict the amount of time a distractor can shift the locus of spatial attention away from an internal goal imposed by a delayed saccade instruction.\textsuperscript{1,2} Individual neurons reflect this robust attentional switching time scale (350 or 425 ms in two different monkeys) in the time at which their decaying response to a distractor stimulus crosses their own level of sustained activity to a target of a delayed saccade task. Different neurons show this common crossing time despite substantial heterogeneity in their dynamics.

We propose that this remarkable correspondence between single neuron and attentional dynamics can be explained by a network model of LIP in which high dimensional, transient firing-rate vectors rapidly become one-dimensional. This single dimension is determined by a slowly decaying mode induced by recurrent connectivity within LIP. The model predicts that this slow mode will dominate the background activity during fixation as well as during the delay period, implying that delay period activity should correlate strongly on a cell-by-cell basis with background activity, but not with the visual transient, a prediction verified by the data. We also discover direct evidence for one-dimensional dynamics in the firing rates.

Furthermore we analyze data from a completely different experimental paradigm in which LIP mediates a decision making task via a ramp to threshold process driven by motion stimuli.\textsuperscript{3} We again find essentially one-dimensional dynamics: ramping activity at low motion coherences shows strong cell-by-cell correlation to background activity during fixation, albeit slightly weaker than in the delayed saccade task.

A functional advantage of having a single slow mode is that the temporal dynamics of this mode is relatively insensitive to stochasticity in single neuron biophysics. We propose that such a rapid reduction to low dimensional dynamics provides a common network organizational scheme whereby robust timing of behaviors, beyond attention and decision-making observed so far, can emerge naturally from the heterogeneous dynamics of single neurons.

Acknowledgments

Support Contributed By: R01 EY11001 R24 EY15634, R01 EY014978, HFSP, JS McDonnell, Swartz, and Whitehall Foundations.

References

Can attentional modulation of surround effects in V1 account for stimulus competition in V4?

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The effects of attentional modulation are often stronger under the condition of stimulus competition, which is obtained by simultaneously presenting two stimuli inside the classical receptive field (CRF) of a neuron in cortical area V4. One of the stimuli is preferred by the neuron, whereas the other is non-preferred, eliciting a much smaller response than the preferred stimulus. At the level of V1, each individual stimulus will activate a distinct ensemble of neurons, with neurons in different ensembles typically having non-overlapping CRFs. Hence, from the single V1 neuron’s point of view, stimulus competition corresponds to a surround effect and attentional modulation of stimulus competition may be identified with modulation of surround effects in V1. In order to determine whether and to what extent stimulus competition in V4 can be partially explained in terms of population responses at the level of V1, we study the response of a model network consisting of 56 by 56 columns (125000 neurons). The stimuli are combinations of two oriented bars placed at different positions in the visual field.

The column response was the firing rate averaged across all excitatory neurons in the column. We compared the response to two bars presented simultaneously (pair response) with the sum of the responses (sum response) to the individual bars presented alone. Columns were considered suppressed when their pair response was less than the sum response, and were facilitated otherwise. Stimulus competition was said to occur when the pair response was between the lowest and highest responses elicited by the component bars alone. The columns whose RF centers were close to either of the two stimulus locations exhibited stimulus competition or suppression, whereas those whose RF centers were in between these locations were often facilitated. Hence, at the single neuron level in V1 contextual modulation may manifest itself as a diverse set of changes in firing rate.

For each stimulus location, the population response function (PRF) was constructed as the level of activation as a function of the preferred orientation averaged across all neurons with their CRF centers within 0.5 degrees of the stimulus location. Downstream neurons in areas V2 and V4 receive inputs proportional to a weighted average of the PRF. For each location, the PRF for the pair stimulus was in between the PRF obtained to each component stimulus when it was presented alone. We explored the hypothesis that attention was mediated by a group of interneurons that project preferentially to other interneurons. Stimulus competition could then be biased by reducing the driving current to interneurons with CRF centers close to the location of the attended stimulus. The PRF in response to the pair increased to that obtained in response to the stimulus at the attended location when it was presented by itself, whereas the PRF at the other location decreased. This suggests that attentional biasing of stimulus competition observed in downstream areas such as V2 and V4 might be in part due to attentional modulation at the population level in V1, which has been hard to detect at the level of single neurons with current experimental protocols. We used model simulations to further explore how surround modulation at the population level depends on the range and feature-specificity of the intracortical connections.

Acknowledgments
This work was supported by start-up funds provided by the University of North Carolina and the Human Frontier and Science Program.
A unifying probabilistic computational framework for attention
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Attention plays a central role in many forms, and at many stages, of sensory processing. Dynamical neural models have successfully described ‘bottom-up’ attentional selection, and some features of the behaviour and physiology associated with ‘top-down’ attention [1]. However, an explanation of why attention is needed, as well as precisely what computational role it plays has proved elusive. One possible reason for this is that the various phenomena grouped under the rubric of attention may, in fact, be heterogenic. Indeed, although the concept of a ‘limited processing resource’ is often invoked to explain and unify these phenomena, attempts to give this concept a concrete definition in cognitive or anatomical terms have failed.

Here we propose a new framework for attention, which provides a unifying normative computational account of the nature of the limited resource, why it is limited, and how attention makes tractable the computationally inaccessible operations that result. Our view is grounded in the Helmholtzian notion that sensory systems infer the distribution of explanatory features \[ f_i(x) \] from sensory input \[ S \]. Noise and the ill-posed nature of the problem complicate this inference, but Bayesian probabilistic semantics provide a principled way to reason under the consequent uncertainty, yielding beliefs \[ P(\{f_i(x)\}|S) \]. The problem is that the resulting belief distributions may extend over many variables, and thus require representational resources that grow exponentially in the extent of the correlations. We suggest that each stage of processing finds an approximate belief \[ Q(\cdot) \sim P(\cdot|S) \], perhaps by neglecting some posterior correlations \[ Q(\{f_i\}) = \prod_i Q_i(f_i) \]. Attentional mechanisms then attempt to resolve the approximation by testing “hypotheses” \[ P_a(\{f_i\}) \] about the true distribution through feedback connections. The approximate code evolves to take into account this hypothesis \[ Q_a(\{f_i\}) \sim P(\{f_i\}|S)P_a(\{f_i\}) \], and the agreement between posterior and hypothesis can be measured by the size of the normalising constant \[ Z_a \] of this product. We suggest that the attentional hypothesis then evolves to find a local maximum in \[ Z_a \], thereby selecting a limited interpretation from the multitudinous possibilities allowed by the likelihood.

Some properties of this framework deserve emphasis. (1) In this view, attention changes the approximate distribution \[ Q(\cdot) \] rather than the neural code for the posterior; this avoids the difficulties involved in keeping downstream areas synchronised with changes in the code. (2) Redirection of attention due to cueing or priming can be incorporated as a bias of the attentional “hypothesis”, which might correspond to a saliency map effect in models of bottom-up attentional selection. (3) The attentional “hypothesis” is mathematically equivalent to an evolving, data-dependent, “prior”; this agrees with interpretations of attention as encoded prior information in priming experiments [2], as well as with computational implementations that have interpreted attention as a “prior” in semantically inappropriate contexts [3]. The framework is applied to a group of classic attentional effects including binding, task-driven bias, and precueing.

Acknowledgments
This work was supported by the Gatsby Charitable Foundation and the Wellcome Trust.

References
Attention in V4: A biophysical model

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When a monkey pays attention to a stimulus inside the receptive field (RF) of a V4 neuron, there is an increase in the firing rate \([1]\), an increase in the local field potential (LFP) power and spike-LFP coherence in the gamma frequency range \([2]\). Attention is transferred by top-down inputs, presumably coming from prefrontal areas including the frontal eye field (FEF) \([3]\). In this direction, recent experiments have shown the existence of precise links between FEF and V4 dynamics during attention \([4]\). These top-down inputs, produced by cortical feedback connections, are presumably excitatory and drive pyramidal neurons \([5]\). Using a computational modeling approach, our goal is to find by which mechanisms such top-down inputs can produce the observed attentional effects.

Our biophysical model of V4 consists of networks of pyramidal neurons and interneurons, interconnected with AMPA, NMDA and GABA\(_\text{A}\) synapses and receiving stimulus and attentional inputs. The gamma range oscillations of the LFP imply a certain level of firing synchrony in the V4 network, which is nevertheless relatively weak \([2]\). A network of inhibitory neurons interconnected by GABA\(_\text{A}\) synapses is known to show gamma frequency oscillation for a wide range of noise levels, provided recurrent inhibition is sufficiently strong \([6]\). Furthermore, a synchrony increase in the inhibitory inputs to a neuron has been shown to reproduce firing biases as in attention experiments \([7]\). We propose here that the V4 network is in a dynamical state where pyramidal neurons are close to asynchrony and where local interneurons -associated to the locus of attention in the RF- increase their level of synchrony in the gamma range with attention. The interneurons receive slow (NMDA) and fast (AMPA) synaptic currents from pyramidal neurons that combine into a slowly varying noisy input. We show that the changes in this input, induced by an attentional signal, can enhance the level of interneuron synchrony.

References


Center-surround filters emerge from optimizing predictivity in a free-viewing task

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In which way do the local image statistics at the center of gaze differ from those at randomly chosen image locations? In 1999, Reinagel and Zador [1] showed that RMS contrast is significantly increased around fixated locations in natural images. Since then, numerous additional hypotheses have been proposed, based on edge content, entropy, self-information, higher-order statistics, or sophisticated models such as that of Itti and Koch [2].

While these models are rather different in terms of the used image features, they hardly differ in terms of their predictive power. This complicates the question of which bottom-up mechanism actually drives human eye movements. To shed some light on this problem, we analyze the nonlinear receptive fields of an eye movement model which is purely data-driven. It consists of a nonparametric radial basis function network, fitted to human eye movement data. To avoid a bias towards specific image features such as edges or corners, we deliberately chose raw pixel values as the input to our model, not the outputs of some filter bank. The learned model is analyzed by computing its optimal stimuli. It turns our that there are two maximally excitatory stimuli, both of which have center-surround structure, and two maximally inhibitory stimuli which are basically flat. We argue that these can be seen as nonlinear receptive fields of the underlying system. In particular, we show that a small radial basis function network with the optimal stimuli as centers predicts unseen eye movements as precisely as the full model.

The fact that center-surround filters emerge from a simple optimality criterion—without any prior assumption that would make them more probable than e.g. edges, corners, or any other configuration of pixels values in a square patch—suggests a special role of these filters in free-viewing of natural images.

Figure 1: The two maximally excitatory stimuli

References

Modeling of perisomatic GABA-A mediated short-term synaptic plasticity on the hippocampal pyramidal neurons

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GABA mediated synaptic transmission is important for population oscillations and network plasticity. Perisomatic GABA-A synaptic transmission shares the dogma of short-term synaptic plasticity, but also has unique properties. Based on our patch clamp recordings from the pyramidal soma in CA1 region of mouse hippocampus, we expanded an existing synaptic phenomenological model. Our GABA-A data allows fitting of some of the model parameters during pair-pulse depression, post-tetanic depression and recovery of post-tetanic depression. We found our data did not support the hypothesis that there is an intermediate readily releasable pool inside the GABA presynaptic terminal. We also simulated data from CHL1 mutant mice, which had abnormal GABA-A synaptic transmission, and found the shift of TauR could significantly affect the short-term plasticity in the mutants. Our model could also explain how a change of intrinsic excitability of pyramidal neurons, through slow recovery of post-tetanic depression of GABA-A synapses, could facilitate CA1 long-term potentiation in the hippocampus. Thus, we conclude that disinhibition of pyramidal neurons by synaptic depression of GABA-A is an important factor in plasticity of neural network.

Acknowledgments
We are grateful to Dr. A. Dityatev and Dr. M. Schachner for letting us use the original data from their published paper to fit the model.

References
Asymmetric Nonlinear Interactions Influence Synaptic Integration in Pyramidal Neuron Basal Dendrites

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The precise nature of synaptic integration in thin basal and oblique dendrites of pyramidal neurons remains a question of great practical and theoretical interest. A recent in vitro study (Polsky, Mel & Schiller 2004) found that NMDA spikes contribute to nonlinear (i.e. sigmoidal) summation when two closely spaced synaptic inputs are activated on the same branch. In contrast, when two stimuli were distantly separated within a branch, summation was roughly linear, just as for inputs delivered to two different branches. To probe this spatial separation effect and to elucidate its underlying mechanisms, we carried out biophysically detailed compartmental modeling studies as well as experimental studies of synaptic summation in layer 5 pyramidal cells in brain slices. Using the compartmental model, we first tested, and then ruled out, the hypothesis that summation of proximal and distal inputs was necessarily linear due to the passive attenuation of voltage signals between the two sites. Thus, we could easily demonstrate nonlinear interactions mediated by voltage transferred between proximal and distal synapses, as long as the excitable membrane currents were of roughly equal potency at both locations. Second, we found using the compartmental model that linear summation of proximal and distal inputs as seen in Polsky et al (2004) could occur if proximal synapses contained a lower density of NMDA channels compared to more distal sites. However, new experiments addressing location-dependent nonlinear thresholding behavior in these cells appeared to rule out this possibility. Finally, we found using our model, and confirmed in experiments, that depending on the levels of excitatory input delivered to proximal and distal sites, summation could range from quasi-linear to highly nonlinear (still sigmoidal), depending on stimulus conditions. More interestingly, we found that the nonlinear interaction between proximal and distal sites was strikingly asymmetric, which is inconsistent with the view that basal dendrites act as monolithic, sigmoidally thresholded integrative subunits (Poirazi, Brannon & Mel, 2003; Polsky, Mel & Schiller, 2004). The functional implications of this type of asymmetric proximal-distal interaction will be explored in the context of classical and extraclassical receptive field organization.

Acknowledgments
This work was supported by NIH grant MH065918-03.

References
Modeling Neuron-Astrocyte Metabolic Interactions: From Hodgkin-Huxley to the BOLD Signal

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In recent years, accumulating evidences have shown that astrocytes play a critical role at synapses and in providing energy substrates for neurons [1]. Despite the ongoing revolution regarding their role in the nervous system, astrocytes have attracted only very little attention from the computational neuroscience community.

In order to study how neurons and astrocytes modulate imaging signals like the BOLD signal, we developed a mathematical model of the metabolic neuron-astrocyte interactions. Our model is based on recent work by Aubert and Costalat connecting the principal metabolic pathways to the cerebral blood flow [2]. The novelty is that our model is the first to bridge the gap between these approaches and the Hodgkin-Huxley model of neuronal membrane excitability. To constrain the model, it was fitted on experimental data assuming a specific steady-state. Parameters for which no precise measure is available were numerically optimized so that our model quantitatively reproduces recent results of NADH fluorescence dynamics [3].

Interestingly, the only acceptable parameter set resulting from this optimization procedure yields a model that strongly supports the astrocyte-neuron lactate shuttle hypothesis. Namely, the astrocyte continuously releases lactate that is consumed as an energy substrate by the neuron and thus even in the basal state. Moreover, the model successfully explains various experimentally observed behaviors like the biphasic dynamics of tissue lactate, the dynamics of tissue oxygen and the reduction of the oxygen-glucose index following stimulation. We propose that lactate could be used as an important vasoregulator signal potentially explaining why not all the consumed glucose is oxidized by the brain. Finally, the model allows us to decipher the contribution of the different cell types to the BOLD signal and supports the recent finding that an important part of energy demand and consequent metabolic response is linked to astrocytic activity [4].

Our results bring support for an active and central role of the astrocytes in brain energy metabolism. More important, our approach gives us the unique and novel opportunity to embrace the full range of observables and provides mechanistic insights into the existing coupling between astrocytes, pre and postsynaptic neuronal activities, cerebral blood flow and metabolism.

References


Suprathreshold response modes in a computational model of DCN cartwheel cells

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Unlike other neuronal populations in the dorsal cochlear nucleus (DCN), cartwheel cells (CWCs) have the ability to elicit complex spikes in response to various stimuli, including low-level depolarization just above AP threshold. However, CWCs can also respond to excitation with simple spikes, and it is not clear what parameters determine the response of CWCs to depolarizing stimuli. Although previous studies have shown Ca$^{2+}$ currents generate the slow suprathreshold depolarization that underlies complex spiking, current and voltage clamp recordings from identified CWCs in brainstem slices containing DCN have demonstrated that a persistent Na$^{+}$ conductance is required to generate a slow subthreshold depolarization that contributes to the suprathreshold activation of Ca$^{2+}$ channels during complex spiking. Furthermore, we hypothesize that the modulation of persistent Na$^{+}$, Ca$^{2+}$ and other conductances will determine whether CWCs respond to suprathreshold stimuli with either simple or complex spikes.

To investigate this hypothesis, we have constructed a single-compartment model of CWCs that incorporates biophysical models of various Na$^{+}$, Ca$^{2+}$ and K$^{+}$ conductances known to be present in CWCs. The responses of the model to brief subthreshold and suprathreshold current pulses were obtained and compared to the electrophysiological responses of CWCs to similar stimuli. The simple and complex spiking behavior of CWCs in vitro (upper traces) can be reproduced by the model when the magnitude of the persistent Na$^{+}$ conductance is changed from control levels (lower traces). To examine the role that various conductances play in generating the suprathreshold responses of CWCs, we have systematically varied maximal conductance levels and simulated the model responses to brief suprathreshold current pulses (3-D surface). Suprathreshold responses are characterized by the number of spikes elicited by brief stimuli; complex spiking is characterized by two or more spikes per stimulus. The default conductance levels are set to evoke a complex spike; simple spiking is observed with small decreases in the magnitude of a persistent Na$^{+}$ current, or with small increases in the magnitude of transient (A-type) and delayed rectifier K$^{+}$ currents. Suprathreshold responses were less affected by changes in the magnitudes of the hyperpolarization-activated cation current (Ih). Other conductances exhibited complex interactions: increases in the L-type Ca$^{2+}$ current magnitude promoted simple spiking due to an augmentation of Ca$^{2+}$-activated K$^{+}$ currents; and simple spiking produced by large decreases in the transient Na$^{+}$ current magnitude could be offset by small increases in the persistent Na$^{+}$ current magnitude. These results suggest that any ongoing modulation of specific voltage-gated channel subtypes by neurotransmitters and intracellular signaling pathways can have a profound effect upon the suprathreshold responses of these neurons.

Acknowledgments
This work was supported by the Deafness Research Foundation and NIH grant DC05325.
A Mathematical Derivative Performed by Convergence of GABA and Glutamate in the Vestibular Periphery

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Closed-loop neuromuscular control systems rely upon the nervous system to generate, in real time, motor outputs in response to sensory inputs. This typically requires the central nervous system to perform calculations analogous to the fundamental operations of mathematical calculus. A classic example of this is the vestibular ocular reflex (VOR), in which angular-velocity encoding afferent signals are input to the brainstem, mathematically integrated by the central nervous system in real time, and output by motor neurons to control the angular position of the eyes. Mathematical differentiation by the nervous system has received less attention than integration, but differentiation is just as fundamental and perhaps much more ubiquitous. For example, step stimuli often evoke in single neurons an initial increase in firing rate followed by a period of adaptation. The initial increase in discharge rate and subsequent adaptation can be approximated in some cases by a fractional mathematical derivative. For the most rapidly adapting neurons, the fractional exponent approaches one and the neural response approaches a Dirac delta function. A mathematical derivative similar to the fractional model is present in the vestibular periphery, and is evidenced by responses of first-order semicircular canal afferent neurons that respond with discharge rates proportional to the rate of change of sensory hair cell intracellular voltage [1]. Current injection into afferents does not reproduce the adaptation evoked by synaptic inputs and therefore mathematical differentiation is not an intrinsic property of signal processing by afferent neuron ion channels. The contrast between hair cell voltage modulation and afferent responses implicates synaptic transmission and/or convergence of multiple inputs as the underlying source of the mathematical derivative. To investigate the convergence hypothesis, we injected afferent neurons intracellularly and found that neurons expressing mathematical differentiation always contacted hair cells that labeled positively for the neurotransmitter glutamate and, at the same time, contacted other hair cells that labeled positively for GABA [2]. Intra-arterial administration of CGP55845, a GABA_B antagonist, eliminated the mathematical derivative thus showing the critical role of two-transmitter convergence in mathematical differentiation in this system. Furthermore, mathematical differentiation was shown not to be present in afferent responses when stimulating using sinusoids at frequencies above the GABA_B G-protein delay time constant. A simple model incorporating the G-protein time delay and the convergence of excitatory and inhibitory inputs is sufficient to account for the data. Results demonstrate a simple mechanism utilized by the nervous system to perform low-frequency mathematical differentiation.

Acknowledgments
This work was supported by NIH grant DC0006677.

References

Observed pre-motor firing patterns constrain a network model for vocal learning

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Electrophysiological recordings in adult zebra finch indicate that firing patterns in the robust nucleus of aracopallium (RA), an area activating vocal motor neurons during singing, are (i) only weakly correlated across neurons and (ii) only weakly correlated with the acoustic signal of song. Furthermore, these recordings suggest that (iii) firing in RA neurons tends to be bimodal; at any given time a neuron is either silent or firing at high rate (Leonardo et al., 2005).

Motivated by these experimental results, we pose two broad questions. First, what can we infer from these experimentally observed properties about the architecture of the underlying song generation system in the adult zebra finch? Second, what can we infer about the learning process by which the bird arrives at a mature song driven by neural activity with these properties?

In the current study we use neural network models to address these questions. We show that RA firing patterns that satisfy (i) and (ii) occur quite generally in network models of the song generation system in conjunction with stochastic learning rules. Because of the vast convergence from thousands of RA neurons to a small number of muscles, multiple different firing patterns in RA neurons can sum to produce the same motor output. Stochasticity in the learning rule or in initial conditions insure that the system sample broadly from among all possible firing patterns. The resulting RA firing patterns are weakly correlated across neurons and weakly correlated with acoustic output, experimentally observed properties (i) and (ii). In generic network models, however, bimodal firing patterns, property (iii), make up only a small subset of the possible driving patterns for a given output. As a result, we conclude that either something additional and special about network architecture itself constrains firing patterns to be bimodal or else, something about the learning process selects only bimodal firing patterns. We show that stochastic learning rules on saturating input synapses to RA result in bimodal firing patterns, similar to those observed experimentally. We propose several different, potentially experimentally distinguishable, stochastic learning mechanisms. We also propose and investigate other possible learning mechanisms to see whether they too can generate firing patterns that are consistent with experiment. Finally, other motor systems do not exhibit firing patterns with similar properties. Why not? We discuss possible implications about the nature of memorized vocalization, and more generally, about practiced, stereotyped actions, in contrast to other sorts of motor output.

Acknowledgments
We thank members of the Fee Lab and H. Sompolinsky for helpful discussions.

References
Storing branching sequences in a recurrent neural network model with bias and common external input

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Retrieval of memory sequence is one of the important functions in the brain. There has been much of study about neural networks that process the memory sequence. Songbirds have attracted interest as a model animal for sequence learning and sequence generation. Songbirds learn own song from adult bird and generate it through complex motor pattern. Among the songbirds, the Bengalese finch sings a song that is described by a finite state automaton, i.e., branching sequence [1]. The branching memory sequence also is a necessary requirement for human language. Most of existing sequential memory models, however, can store fixed sequences but not branching sequences.

Kawamura and Okada reported that common external input enable sequential retrieval of memory patterns in an associative memory model [2]. In this study, we propose a recurrent neural network model with common external input, which stores branching memory sequences. Our model stores each memory pattern as a quasi-attractor. State transition among quasi-attractors is caused by the common external input. The directions of state transition are determined by weak-sequential connection and weak bias input. To analyze the behavior of the model, we derive the macroscopic description as a probability density function. The results obtained by the theory agree with those obtained by computer simulations.

The state transition mechanism in our model is consistent with the experiment in songbirds that suggest common external input is injected to the song control nucleus HVC from other nucleus at beginning of each song notes [3]. A pervading view of sequence generation mechanism in HVC is owing to propagation of synchronous pulse packets, i.e., the synfire chain. We provide a different view of the mechanism in HVC: state transition among quasi-attractors induced by common external input (Fig.1a). It differs from of the synfire chain in which trajectory in state space is described as a limit cycle attractor (Fig.1b). We discuss the relationship between some physiological experiments of songbirds and our model.

![Figure 1](image1.png)

Figure1: a schematic illustration of state transition mechanisms in the state space (a) of our model and (b) of synfire chain hypothesis in HVC. ξᵢ ( ⊳ remenory patterns) represent memory patterns, i.e., particular firing pattern.

References
Ideal Bayesian learning in human scene perception

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Humans are confronted with massive amounts of visual information that must be collapsed into meaningful chunks, describing which elements of a visual scene belong together, for efficient recognition of faces or objects. This entails the classic model-selection trade-off: choosing the right inventory of chunks that accurately captures the structure of scenes already observed but is not too specific to their details so that it also generalizes well to new scenes. Here we address this problem by asking two questions: what are the optimal learning strategies for the formation of visual chunks, and do humans employ these strategies during unsupervised learning? We implement an ideal learner that uses Bayesian model comparison, a principled statistical solution for the model-selection problem, to extract and store only those chunks that are minimally sufficient to encode the scenes. We then contrast this model with previous pair-wise associative and iterative accounts of learning in a psychophysical experiment. We show that human performance is well above chance when pair-wise statistics in the scenes contain no relevant information. In contrast to previous accounts of human learning, our ideal Bayesian learner can reproduce the result of the experiment, as well as a large set of previous empirical findings. These results suggest that humans learn new complex information from visual scenes by generating economical representations based on previous experience and not by encoding the full correlational structure of the input.

Acknowledgments
FJ was supported by the Volen Center, GO was supported by a Sloan Schwartz postdoctoral fellowship grant and the IST-FET-1940 program, and ML was supported by the Gatsby Charitable Foundation.
A recipe for optimizing a time-histogram with variable bin sizes

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Peristimulus time histograms (PSTHs) are popular tool to estimate the instantaneous rate of neuronal spike discharges. The problem to choose the histogram bin size, on which the shape of the histogram significantly depends, was solved by the authors elsewhere [1, 2]. It was proved that the goodness of the fit of a histogram to the unknown underlying rate can be estimated from the data by using the formula \((2k - v)/\Delta^2\), where \(k\) and \(v\) are the mean and variance of the number of spikes in the bins. The bin size that minimizes this formula is optimal. In this contribution, we extend this method developed for the regular histogram to a method for constructing a histogram whose bin sizes vary over time because the goodness of the fit of a variable-bin-size histogram to the underlying rate can be superior to that of the regular histogram.

In many PSTHs of neurophysiological experiments, a significantly fluctuating rate are followed or preceded by a period of relative stasis. An example is tonic spontaneous neuronal firing, followed by phasic discharges of a neuron responding to a stimulus. The optimal bin sizes of regular histograms for the underlying rate processes with different characteristics are different: The optimal bin size is small if the underlying rate significantly fluctuates, and large if the underlying rate modestly fluctuates. Therefore if the underlying rates are composed of the processes with different characteristics, a PSTH whose bin sizes vary over time may better represent the unknown underlying rate.

To construct a time-histogram with variable bin sizes, we iteratively applied the method for the regular histogram. If the optimal bin size was smaller than the observation period, we divided the period into two parts, and then applied the method of optimal bin size selection to each portion of the data. We repeated this procedure until the optimal bin size equates with the divided period because it indicates further division of the period is not suitable. We compared the goodness of the fit of the variable-bin-size time-histogram to the underlying rate with that of the regular time-histogram.

Acknowledgments
This work was supported in part by Grants-in-Aid for Scientific Research to SS from the Ministry of Education, Culture, Sports, Science and Technology of Japan (16300068, 18020015). HS is supported by the Research Fellowship of the Japan Society for the Promotion of Science for Young Scientists.

References

A model for structural plasticity in neocortical associative networks trained by the hippocampus

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The hippocampal formation plays a crucial role in organizing cortical long-term memory. It is believed that the hippocampus is able of fast (one-shot) learning of new episodic information followed by extensive time periods where corresponding neocortical representations are trained and “compressed” [1]. Here “compression” usually refers to processes such as chunking spatially and temporally distributed activity patterns. We take the complementary approach and optimize the synaptic network by structural plasticity, e.g., replacing unused synapses, thereby making full use of the potential connectivity [2].

We apply the frameworks of structural plasticity and hippocampus-induced learning to the training of neocortical associative networks [3]. Associative networks such as the Hopfield or Willshaw model are at the heart of many cortex theories and have been analyzed for a long time with respect to information storage capacity and plausible retrieval strategies [3, 4]. For example, it is well known that a completely connected network can store about 0.7 bits per synapse. However, for incompletely connected networks the capacity per synapse can be massively reduced or even vanish, depending on the retrieval algorithm [4].

In this work we analyze how structural processes combined with hippocampal training and synaptic consolidation [5] can restore high capacity for neocortical associative networks by emulating full (or increased) synaptic connectivity. We assume that a set of activity patterns can be stored in the hippocampus by one-shot learning. Then the hippocampus trains the neocortex by repeatedly replaying the patterns in a sequence. Synapses of the neocortical network are consolidated depending on Hebbian learning. In each time step a fraction of the unconsolidated synapses are removed and replaced by the same number of new synapses at random locations thereby maintaining total connectivity. We show that this procedure can improve the synaptic capacity of a cortical macrocolumn massively (factor 10-20 or even up to factor 200 for pattern capacity). In a second step we analyze the model with respect to the time (or number of repetitions) necessary to increase effective connectivity from base level to a desired level. The analysis shows that acceptable training time requires a certain fraction of unconsolidated synapses to keep the network plastic.

References
Bayesian image recovery for low-SNR dendritic structures

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In neuroscience, what we see often limits what we know. Experimental research seeking to resolve neuronal structures constantly contends with restrictions set by imaging. For example, quantitative analysis of dendritic spine morphology has potential to teach us a great deal about transmission [1] and long-term synaptic plasticity [2] at synapses.

We present methods for making better use of currently obtainable data, focusing upon algorithms for two-photon laser scanning microscopy (TPLSM) image recovery. In the low signal to noise regime (SNR), imaging can be modeled as a Poisson process which introduces a blur per pixel (PSF) and additive noise by: $\text{Image}_{\text{out}} = \text{Poiss} \{ \text{Image}_{\text{in}} \ast \text{psf} + \text{noise} \}$. Many groups have contributed to the general problem of restoring noisy blurred images. With various refinements, maximum likelihood (ML) techniques have been particularly successful for image restoration [3].

We build upon previous literature by incorporating important prior information about the dendrite (namely, the dendrite’s simply connected geometrical structure). By combining the statistical model for image degradation with our priors, we can apply powerful likelihood-based tools from Bayesian statistics to the problem of optimally recovering dendritic shape (including spine size, etc.). Neuronal fluorescence may be modeled as a step-function in space, with different constant values inside and outside the dendrite; in turn, we model possible neuronal shapes as step-functions. The strength of our approach becomes especially apparent with low-SNR, a consequence of restricting imaging time scales and intensities to avoid photobleaching or damage to the preparation.

We first examined a naïve ML algorithm under the constraint that neurons remain simply connected. With just this prior, a naïve maximum likelihood algorithm fails to reproduce the original image; the ML estimate is too “greedy,” incorporating any pixels where photons have been detected. Imposing additional prior constraints on the neuron, by penalizing the jaggedness and length of the edge, helps reproduce the original image. This corresponds to a maximum a posteriori estimate given a prior on smooth edges. Two techniques show promise for automatically fitting hyperparameters on dendritic smoothness. One method withholds data and compares validity of images produced by different values of the parameters using cross-validation. This necessitates an Expectation-Maximization approach to maximize the likelihood of the image over both the observed (“training”) and hidden (“test”) pixels. Another potential method for automatic fitting involves computing marginal likelihoods of the hyperparameters via Metropolis-Hastings sampling. Besides fitting model hyperparameters, this Bayesian approach can establish confidence intervals, in a sense, for the image—e.g., quantifying uncertainty about the size and number of spines, given a single noisy image.

References
Jitter methods for investigating spike train dependencies

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Many important questions in neural data analysis revolve around the time scale of statistical dependencies in spike trains. For example, changes in background firing rate across trials introduce broad time scale correlations into spike trains that can be confounded with other dependencies. This is in our terms related to the general issue of how to analyze neural data in cases where standard assumptions of statistical repeatability across trials are not reasonable, or when there is no clear notion of a trial at all.

Standard descriptive methods, such as the cross-correlogram (CCG) and the joint peri-stimulus time histogram (JPSTH) \cite{1} can be adapted to distinguish event-locked from non-event-locked correlations, as in the shuffle-predictor. However, these modifications do not easily disambiguate interactions on multiple time scales, and are confounded by non-repeating trials.

We have been developing a class of statistical techniques, called jitter methods \cite{2}, designed to investigate the time scale of arbitrary spatio-temporal dependencies in spike trains. Jitter methods work by comparing the original data set to surrogate data sets generated by randomly perturbing (jittering) spike times over (typically, small) time windows. Varying the width of the jitter window permits some exploration of dependencies on differing time scales, even in situations where the notion of a repeated trial is nonexistent or artificial.

Jitter methods provide a simple method for modifying CCGs and JPSTHs that allows for some disambiguation of time scales. The figure contrasts the jitter and shuffle correctors for a simulated data set containing both broad and narrow correlations, neither of which are aligned with the trial. The two corrections are confounded under the shuffle-predictor, whereas the narrow correlation is isolated by the jitter method.

We will present several variations on this idea, and illustrate their application.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{jitter_methods.png}
\caption{Comparison of shuffle and jitter correctors for simulated data set.}
\end{figure}

Acknowledgments

This work was supported in part by the National Science Foundation under Grants DMS-0240019 and IIS-0423031 and a Postdoctoral Fellowship in Biological Informatics to AA, by the Army Research Office under Contract DAAD19-02-1-0337, and by the Office of Naval Research under Contract ONR N000140610749.

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Spatial Symmetry and Stability of V1 Receptive Fields Analyzed by Two-Dimensional Hermite Functions

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The concept of a receptive field is central to understanding sensory systems. It succinctly describes neural feature selectivity and quantitatively predicts responses to synthetic and natural stimuli. Simple receptive field models are typically inadequate: though they may account for responses to one class of stimuli, their components appear to be modulated by input statistics (i.e., context). Characterizing these modulatory effects remains a challenge. We address this problem in primary visual cortex of cat and macaque, where such modulatory effects are considered to have substantial functional significance. We do this by analyzing responses of neurons to two stimulus sets: two-dimensional Hermite functions (TDH’s) that are matched in spatial extent, contrast, and power, but differ in their two-dimensional organization [1]. We find that coarse spatial features of receptive fields are less modulated by context than fine details. More surprisingly, independent of spatial scale, receptive field components that are invariant under 180-degree spatial rotation are less susceptible to modulation by context than components that do not have this invariance (Figure). This was observed in receptive fields computed via reverse-correlation [1] or maximally-informative-dimension [2] methods. Our results may have implications for not only adaptive properties of neural circuits, but also learning rules that guide their development.

Figure. Relationship – best rotation matrix – between a set of computed receptive fields (n=51) for Cartesian and polar stimuli. Receptive fields under both conditions are specified by their 36 projections onto polar two-dimensional Hermite functions. Stimulus dimensions are grouped by their rank, from 0 to 7, with patterns of lower rank describing more coarse and central features, and high rank patterns more extended in space with finer spatial organization. All patterns of even rank are invariant under 180-degree spatial rotation, and all patterns of odd rank change into their negative with 180-rotation. Changes in apparent receptive field shape are manifest by departures of the illustrated matrix from the identity. These departures are more prominent for odd-rank components than even-rank components.

Acknowledgments
We thank F. Mechler, M.A. Repucci, K.P. Purpura for help with experiments. This work was supported by the Swartz Foundation, and NIH grants 5K25MH068904 to TOS and 2RO1EY009314 to JDV.

References
A Numerically Efficient Approach for Constructing Reach-Trajectories Conditioned on Target

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The problem of decoding the neural signal to predict a behavioral variable of interest has received much attention from the neuroscience community. The accuracy of state-estimation methods for decoding trajectories can be improved by appropriately restricting the space of possible states. In this work we focus on constructing trajectories, for reaching movements, conditioned on known target states. We show how previous approaches [1, 2] can be extended and improved, by deriving results for computing the priors in a numerically efficient manner, enabling real-time implementation.

In our framework, we model the free-reach equation of the arm by a linear state equation with gaussian noise, \(\mathbf{d}\bar{x} = R\mathbf{x}dt + WdB_t\), with \(B_t\) standard Brownian motion. We observe \(\bar{y} = K\bar{x}_T + \epsilon\), where \(\epsilon \sim \mathcal{N}(0, M)\), with \(\epsilon\) independent of \(\{\bar{x}(T)\}\). To construct the smoothed trajectory conditioned on the entire data we follow the approach proposed in [3]. The smoothed state at a point in time is obtained by optimally melding the output of two filters running forward and backwards in time, with the backwards filter propagating the inverse of the error-covariance matrix. This approach has the advantage that it requires fewer inverses. We can solve for the relevant quantities analytically, using a matrix exponential approach, instead of the slower recursive formulation adopted by [1]. Fig. 1 shows a sample simulation of the single-terminal-state-conditioned-trajectory along with the standard deviation. The terminal state \(x(T) = [1 \ 1]'\) with the reach motion starting from the origin. \(R = \begin{bmatrix} -1 & 1 \\ 0 & -1 \end{bmatrix}\), \(W = [0 \ 1]'\), and \(K\) is taken to be the identity matrix.

Figure 1: Sample Simulation for Reach Trajectory Conditioned on Terminal State

Acknowledgments

J.E.K. would like to acknowledge the Swartz Foundation for a post-doctoral fellowship which supported this research.

References


Seizure Induction by Glia-Mediated Synaptic Scaling
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Hebbian synaptic plasticity refines connectivity in an activity-dependent manner, but it also tends to destabilize network dynamics, making it more prone to runaway excitation or quiescence. Consequently, additional homeostatic mechanisms that adjust intrinsic neuronal excitability or synaptic strengths are necessary for normalizing network activity. One biological mechanism for synaptic scaling involves glia and the pro-inflammatory cytokine TNF-α [1]. Specifically, it was shown that acute application [2] or long-term production (by chronic activity blockade) of TNF-α increases AMPAR surface expression in hippocampal neurons.

As homeostatic synaptic plasticity can, in special conditions, drive the network into a hyperexcitable state [3], we investigate the effects of synaptic scaling in the context of biological reports relating TNF-α to seizures. We model a layer of glial tissue interacting with a network of spiking neurons. We use regular spiking excitatory neurons and fast spiking interneurons [4], locally connected in a lattice structure through AMPA/GABA synapses, with propagation delays. External input is provided by a set of independent Poisson processes. Glia cells monitor excitatory drive to neighbouring neurons via glutamate spillover. They release soluble TNF-α as a function of current activity, which diffuses to the neurons and triggers the adaptation of excitatory synapses by multiplicative scaling.

We find that the network can be driven into a state of seizure-like activity by external TNF-α application or by forcing the glia cells to overproduce the protein, as illustrated in the figure. Seizures are triggered by transient increases in input and occur robustly for various synapse types, inhibition strengths, or network sizes, with some variation in burst frequency and duration.

In conclusion, modeling the interaction of neurons and glia cells may help to better understand regulation of neural activity and its deregulation under pathological conditions. Our model is a first step in this direction.

Being the first approach of this type, our work suggests that explicit modeling of neuron-glia interactions can help to better understand the processes involved in neural activity regulation and the pathological conditions triggered by their dysfunction.

Acknowledgments
FIAS is supported by the ALTANA AG, the Hertie Foundation, EC MEXT-project PLICON, and EC NEST-project MAMOCELL.

References
Causal inference in Cue Combination
Konrad Paul Kording, Ulrik Beierholm, Wei Ji Ma, Steven Quartz, Josh Tenenbaum & Ladan Shams

When we see a friend talk we perceive the voice as coming from the mouth, but this percept can be fooled: a good puppeteer makes us perceive his voice as coming out of a puppet's mouth. In both cases, we infer a common cause to explain the correlation between the movement of the mouth and the sound of the voice. Numerous psychophysical studies have investigated how two cues are integrated into a common estimate of the position of the source. These position estimates are often consistent with an optimal Bayesian strategy. However, the brain must solve a harder problem than these models do: we are often surrounded by several sources of sensory stimulation. For example a car alarm may go off while someone is speaking. Given any two signals from different modalities, such as vision and audition, how does the brain decide whether they have a common cause or two independent causes -- and hence whether they should be integrated or processed separately?

Here we formalize these problems in terms of an optimal observer model that infers the causal structure that is associated with the observed stimuli. This model considers the information we have about the cues and combines it with prior information about causal structures. The estimates obtained by this model lead to precise predictions of human behavior, much better than those of previous Bayesian models. The model explains counterintuitive finding from several laboratories. It explains nonlinear interactions between cues as well as the way people infer whether there is a common cause or independent causes.

In the study of higher-level cognition, many experiments have shown that people, starting from infancy, interpret events in terms of the actions of hidden causes. If we see a window shatter, something or someone must have broken it; if a ball flies up into the air, something launched it. These causal inferences in higher-level cognition may seem quite different than the causal inferences in sensory integration we have studied here: more deliberate, consciously accessible, and knowledge-dependent, rather than automatic, instantaneous, and universal. Our finding that very similar optimal statistical principles can explain causal inference in sensory integration suggests similarities in the processing of low level sensory and high level cognitive stimuli. Problems of inferring common causes from observed conjunctions arise everywhere across perception and cognition and the brain may have evolved similar or even common mechanisms for performing these inferences accurately, in order to build veridical models of the world's underlying structure. Moreover, low level cue combination can be readily studied in electrophysiological experiments. Such experiments can unveil how the nervous system implements the interesting nonlinear interactions between cues that are prominent in behavior. It may thus make it possible to ask in electrophysiological experiments how and where the nervous system makes inferences about the structure of the world.
Controlling synfire chain by inhibitory synaptic input

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The synfire chain, a stable propagation of highly synchronous population firings, was proposed to be one of the possible ways employed in the brain to transmit signals. The synfire chain is expected to explain accurately timed firings of multiple neurons observed in various brain preparations, which are otherwise difficult to explain. Simulation and analytical studies demonstrated that there actually are multiple modes of propagation of a pulse packet, synchronous population firings, on a simple feedforward circuit consisting of excitatory neurons. However, the multiple propagation modes would have a limited value if a convenient mechanism to switch between different propagation modes is lacking. The present study shows that the feedforward network is naturally equipped with a flexible bidirectional switching mechanism if each neuron is modeled in a biologically realistic manner.

Our simulations using the feedforward circuit consisting of the Hodgkin-Huxley (HH) neurons reveal that an inhibitory input to a layer in the circuit can either enhance or suppress a propagating pulse packet depending on the timing of the modulatory input relative to the pulse packet arrival to the layer (Figure 1). In contrast, an excitatory input is an inappropriate modulator because it works mostly unidirectionally and also overrides and erases the timing information carried by the propagating pulse packet.

The bidirectional nature of an inhibitory modulation stems from repolarization current into each single neuron [3,4] existing not only in the HH model but also in virtually any biologically realistic neuron model so that the switching mechanism itself is also considered common. This flexible modulatory mechanism would be useful in switching between different modes in a feedforward circuit and switching between different feedforward circuits embedded in the network [5] as well.

References

\textbf{Figure 1:} a) Feedforward circuit used for the simulations. White circles represent a HH neuron. b) Bidirectional modulation of a propagating pulse packet. Triangles show the timing of modulatory input. c) A bidirectional change in the total area of a pulse packet depending on the timing of an inhibitory input. Different colors correspond to different inhibitory conductance values in mS.
Analysis of functional connectivity in large-scale network models

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Numerous methods exist in the literature for assessing the functional connectivity of small networks of neurons. Among others, there are methods based on Granger causality [1], maximum-likelihood estimates over stochastic spiking processes [2], and nonlinear optimization of deterministic spiking models [3]. However, these methods have generally been validated by applying them to very small networks where the activity of all the neurons is observed. This scenario is drastically different from that seen in cortical recordings where population of observed neurons is embedded in a much larger network of unobservable units. To investigate the ability of several functional connectivity algorithms [1-3] to capture the network dynamics in a scenario much more similar to that observed in recordings from awake, behaving animals, we have created a model network of O(10,000) neurons. The parameters of the model network have been taken from the physiological literature. In this simulation environment, we treat a small, O(10) network as the observable units and the remainder of the network is unobserved.

We compare the efficacy of functional connectivity algorithms. The dynamical equivalence of the “functional” and “real” networks is demonstrated. Another potential difficulty in measuring functional connectivity in real cortical networks is that the properties of the real network may be nonstationary. Properties like the mean firing rate, amount of correlation in the network, and the patterns of connectivity are systematically examined, and the utility of the various algorithms under changes in these properties is quantified.

References


Folding forces: How brains get into shape

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The idea of mechanical factors shaping the cortical features goes back as far as the end of the 19\textsuperscript{th} century \cite{1} and has been recently revived \cite{2, 3} and investigated with computational models \cite{4}. Our current model deals with the impact of various mechanical factors on the formation of cortical convolutions, by simulating gyral collisions.

Our finite element model implements a collision detection and repulsion mechanism for intersections of the growing cortex with both the skull and with other portions of the cortex. For a fixed skull size, we observed that if the growing cortex impacts the skull prior to folding onset, no folds form after the impact, and the growth of the cortical region only occurs radially [F1]. If the cortex is already folded at impact, growing gyri may overlap despite repelling mechanisms [F2]. For a variable skull size with similar growth parameters as the cortex [F3], there was no influence on convolution pattern. The presence of a skull had a limiting effect on growth, leading to a deepening of sulci, without much influence on the shape of gyri. We also investigated the potential role of radial fibers in cortical folding, as proposed by Toro and Burnod \cite{4}. Our simulations show similar folding onsets in the presence [F4] or in the absence of radial fibers [F5]. However, the overall smaller brain size rendered by the presence of radial connections and/or skull appears to facilitate the collisions of gyri. [F2-4]. We consider these collisions of growing gyri as an important stage in the folding process, since they allow for a mechanical self-organization of the cortex, leading to the formation of deep sulci with parallel cortical surfaces.

Our model offers a promising strategy for explaining characteristic features of brain convolutions, such as the relative thickness of sulci and gyri \cite{4} and the parallel walls of sulci, as a result of collision events in the folding process. The model can be further developed to study the impact of other forces on brain shape development, such as those produced by corticocortical fibers \cite{2, 3}.

References

Synchronization of excitatory neurons
with strongly heterogeneous phase response

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Synchronous firing of cortical neurons is considered to play an active role in cognitive functions of the brain. Synchronizing dynamics depends not only on the neuronal network structures but also on the cellular intrinsic properties. Phase response is an intrinsic property of neuronal oscillators, and it describes how a timing shift in the next output spike depends on the timing of the input stimulus and has crucial information about synchronization [1,2]. Phase responses of cortical neurons have been categorized into two types: with negative value (Type II) or not (Type I), and the neurons with Type-II phase response tend to synchronize each other easily rather than the neurons with Type-I phase response in the case that the phase responses of these neurons are homogeneous and they are coupled through the excitatory interaction [3].

According to our in vitro study in which we analyzed the phase response of these pyramidal neurons in layers 2/3 vs. 5 from the intracellular and whole-cell patch-clamp recordings [4], the phase-response types of pyramidal neurons depend on the cortical layers in which they exist. Furthermore, even though neurons are categorized into the same type, the shapes of those phase response are not exactly the same; namely heterogeneous. Little is known about the dynamics of the neurons with heterogeneous phase responses. To address this issue, we investigated the dynamics of such a population through the globally coupling with the excitatory synaptic interaction.

We analyzed the dynamics of excitatory neuronal oscillators with heterogeneous phase responses and numerically examined the simple model which has only the two lowest Fourier modes. We found that in the Type-II-like neurons, small heterogeneity of phase response curves can destroy the frequency synchronization, while in the Type-I-like neurons, heterogeneity drives the perfectly synchronizing state into the perfectly non-synchronizing state via the partially synchronizing state.

Acknowledgments
We thank Y. Kuramoto, T. Mizuguchi, H. Nakao and H. Cateau for fruitful discussions and valuable comments on this study.

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V1 activity as optimal Bayesian inference

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Previous theoretical approaches relating neural activity in the primary visual cortex to formal computational goals that V1 might be optimized for focused mostly on the filter-like properties of cells [1,2] or on related features such as contrast invariance [3]. The key insights gained from these studies were that V1 neurons (simple cells, in particular) can be seen as implementing an efficient code for statistical estimates of natural scene stimuli and that this code can be learned from a set of natural image patches. However, this approach only accounts for the mean responses of cells averaged across multiple presentations of the same (set of) stimuli, and therefore completely neglects the rich within-trial dynamical interactions between cells. For the same reason, it is also incapable of accounting for the richly structured spontaneous activity in V1 [4].

In order to better understand the relation of the intrinsic dynamics of V1 to its computational role, we explored the idea that activity in V1 reflects sampling of the ‘recognition distribution’, the probability distribution of possible hypotheses that are congruent with both the present and past inputs to the system [5]. We also used this sampled approximation to the true recognition distribution in a variant of the expectation-maximization algorithm to adapt the synaptic weights between cells so that they form the efficient code hypothesized in earlier work [1]. Beyond reproducing the linear filter properties of simple cells, our results also account for temporal and spatial correlations between cells as seen in multi-electrode recordings, and give a normative account of the experimentally observed close correspondence between spontaneous and stimulus-driven network activity in V1 [4].

Acknowledgments

GO was supported by a Sloan Schwartz postdoctoral fellowship grant, FJ was supported by the Volan Center, and ML was supported by the Gatsby Charitable Foundation.

References

An Efficient Algorithm for Sequential Optimal Design of Neuro-physiology Experiments

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http://www.prism.gatech.edu/~gtg120z/rtmodel

We present an efficient algorithm for selecting optimal stimuli for estimating the conditional response function of a neuron. Stimuli are selected by optimizing an objective function which quantifies the expected reduction in uncertainty about the unknown response function. Our objective function is based on mutual information and leads to an optimality criterion known as D-optimality \cite{Fedorov}. Our implementation overcomes the computational hurdles of sequential optimal experimental design in this setting. Simulations show that using optimally chosen stimuli can reduce the number of trials needed to estimate the conditional response function by more than an order of magnitude.

Our algorithm has three main components. 1) We model the conditional response parametrically using General Linear Models (GLMs). This is a very flexible nonlinear model which can capture many firing rate statistics of a neuron. Furthermore, it is possible to incorporate effects such as adaptation, refractory periods, and burstiness. We consider a restricted class of nonlinearities for the GLM which ensures the log-likelihood is concave \cite{Paninski}. Concavity of the likelihood improves the tractability of many of the necessary computations. 2) We approximate the posterior distribution on the parameters of the conditional response function as a Gaussian distribution. Asymptotically this approximation is accurate \cite{Paninski}. The normal approximation makes it easier to update the estimated parameters and to compute the mutual information. 3) We show that choosing the stimulus to maximize the mutual information requires at worst one 2-d optimization per trial.

We present a number of simulations to demonstrate the potential utility and applicability of our algorithm to neurophysiology experiments. A theoretical and empirical analysis shows that the running time of our algorithm grows on average as the square of the dimensionality. We compared the estimated parameters using stimuli drawn according to our algorithm to the estimated parameters using I.I.D stimuli drawn from a uniform distribution. These simulations looked at the performance when: 1) the parameters are very high dimensional 2) spike history effects are included and 3) the parameters are non-stationary. The validity of our Gaussian approximation is tested using Monte-Carlo methods to measure the Kullback-Leibler distance to the true posterior. Finally we show that asymptotically our uncertainty about the unknown parameters decreases at a rate near that predicted by a theoretical analysis of the information maximizing approach.

Acknowledgments JL is supported by the DOE and by the NSF. LP is supported by the NEI and the Gatsby Foundation. We thank P. Latham for helpful conversations.

References


Two Unsupervised Learning Principles to Learn Place Cells from Grid Cells

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The study of spatial cognition in mammals has revealed the existence of neurons with spatially localized activity. Firstly, the place cells of the hippocampal formation are activated when the animal’s position correlates with unique regions in an environment, the so-called place fields [1]. Secondly, the grid cells of the medial entorhinal cortex (MEC) show higher firing frequency at multiple regions in space, or subfields, that are arranged in regular triangular tessellations [2]. The entorhinal cortex is found one synapse upstream of the hippocampus, which suggests that place cells could be learned from the activity of grid cells.

Here, we investigate this hypothesis by using a model of place cells that was shown to extract invariant features from a continuous input video stream leading to the formation of place fields as observed in the hippocampus [3]. We simulate the activity of 10×10 entorhinal grid cells based on the physiological distributions of the grid parameters (i.e. grid spacing, orientation and phase) and driven by the position of a virtual rat exploring randomly a one square meter arena. The unique position information of 4×4 place cells is extracted from the grid cell activity by a gradient ascent on two objective functions, i.e. stability and decorrelation. The stability objective allows extracting unique spatial representations, with a smooth increase of the cell firing rate as the rat approaches the center of a place field. The decorrelation objective prevents the formation of place fields at identical locations. Our results show that the resulting activity of the output layer of the model is consistent in good detail with experimental characteristics observed in physiological recordings of place cells. Additionally, we quantify the difficulty of the learning problem by varying different environmental and model parameters and show in particular that the two computational principles of stability and decorrelation are complementary in the learning process. Our results further suggest that grid cells may provide a fundamental substrate of spatial cognition, by showing firstly that they can support the formation of place fields and secondly that this process can be learned by itself.

Figure 1: a. Mean activity maps of four representative simulated grid cells (network input). Odd columns: normalized mean activity as a function of the position of the virtual rat. Red and blue regions correspond to a high and low cell activity. Even columns: normalized mean activity as a function of the rat’s orientation. Black contours and gray regions represent normalized mean cell activity ± standard deviation. b. Representative output of 4 place cells.

References
On the origin of the cortical architecture

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In tangential penetrations across primary visual cortex, one often observes systematic changes in the receptive field properties of neurons (such as their preferences for orientation and ocular dominance), while vertical electrode penetrations encounter cells sharing similar response properties. The full two-dimensional structure of these ‘functional maps’ has been best visualized using intrinsic optical imaging. Despite years of research onto the columnar architecture of the cortex there are many important questions that remain unanswered, including the actual origin of the maps, their shapes and mutual relationships and, above all, their functional significance in normal visual processing.

Theoretical approaches to cortical map formation based on self-organization and symmetry-breaking normally assume initially random, or disordered, maps. However, we now know that salient features of the adult cortical organization, including the subregion segregation of simple cells, orientation, and ocular dominance maps, and cytochrome oxidase blobs, manifest themselves at the earliest stages of cortical development, before the onset of the critical period. Thus, to fully understand cortical map formation we need to answer the following two separate questions. Initial map establishment: What are the factors that determine the structure of maps at the earliest stages of development? Map maintenance and plasticity: To what extent do activity-dependent developmental processes maintain, modify, or refine, this initial state? The relative contributions of these two stages of development can be properly assessed only after clear descriptions of both processes are obtained.

Here I address the first of these two questions. How exactly are the initial cortical maps established? Two main hypotheses have been considered so far: (a) Correlation-based mechanisms relying on the pattern of spontaneous activity in the retina and the LGN, and (b) molecular guidance directing the developing thalamocortical projections into forming the desired maps. This study elaborates on an alternative hypothesis: the blueprint for the formation of simple-cells receptive fields in layer 4, the feature maps in the cortex, and many of their inter-relationships, may reside in the layout of the retinal ganglion cell mosaics along with a simple statistical connectivity scheme between the thalamus and the cortex.

I show that this simple ‘statistical connectivity’ model accounts for a large number of experimental findings, including the relationship between retinotopy, orientation maps, spatial frequency maps and cytochrome oxidase patches. The theory’s simplicity, explanatory and predictive power makes it a serious candidate for the origin of the cortical architecture.

Acknowledgments

This work was supported by NIH grant EY12816 and DARPA FA8659-06-1-7633
Enhanced neural threshold detection using a point process state-space model analysis

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Developing a consensus on how to quantify important properties of neural systems is a challenging signal processing problem because different methods often yield widely different estimates of the same property. The neural threshold, which conceptually, is the lowest stimulus level that reliably elicits a neural response, is a property for which numerous estimation methods have been proposed. Most of these methods do not consider the point process nature of the spiking activity, the relation between neural responses at different current levels, and do not correct for the multiple hypothesis tests required to determine the detection threshold. We introduce a point process state-space generalized linear model (SS-GLM) of auditory responses to electrical stimulation that considers both dependence of neural activity on spiking history and the dynamics of the responses across all stimulation levels. We fit the model to neural responses to current stimulation by maximum likelihood using an EM algorithm, and establish that model goodness-of-fit is highly adequate using several metrics for point process models prior to determining the detection threshold. Following a concept recently introduced in behavioral data analyses [1], we define the detection threshold as the lowest current stimulation level at which there is reasonable certainty (> 0.95) that the electrically-induced spiking responses for that level are statistically different than spontaneous activity, and remain so for higher current levels. We applied our method to the activity of 31 multi-units recorded in primary auditory cortex (A1) in response to electrical stimulation of the inferior colliculus (IC) across 19 current levels between 0 to 56.2 µA in logarithmic steps [2]. We compared our results to firing-rate based signal detection theory (SDT) analysis, an objective and mathematically grounded threshold estimation procedure, and found that the SS-GLM analysis gave median detection threshold estimates 8 dB lower than the SDT estimates. This improvement arises because our approach models the joint relationship in the experimental data across all current levels and as a consequence, yields narrower and potentially more accurate confidence intervals than those from the SDT analysis. These findings have important implications for developing theoretically-sound and practical definition of the neural threshold and the signal-to-noise ratio for neural systems as well as for understanding information transmission between the IC and A1 and possibly for the design of auditory implants.

Acknowledgments
Support contributed by NIH grant T32DC000038, R01 DA015644, P41 EB2030 and F31 DC007009.

References

Simple low-dimensional models for complex data

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During short-term memory maintenance, different neurons in prefrontal cortex (PFC), recorded under identical conditions, show a wide variety of temporal dynamics and response properties [1]. These data are a specific example of the more general finding that neural recordings from frontal cortices often reveal that different neurons have very different response characteristics. Modeling this complexity of responses has been difficult. Most commonly, some features of the responses are focused on, and models that fit those reduced features are built (e.g., [2]). But can the full complexity of responses be easily captured?

We have previously reported that the complex responses in PFC during short-term memory can be summarized in 5 dimensions (i.e., 5 parameters suffice to capture most of the variance in the data across neurons; Machens et al., COSYNE ’06). Olasagasti, Goldman, and colleagues have described a method to fit experimentally-obtained steady-state firing rates (that is, no dynamics) in a network model of persistent activity (Olasagasti et al., COSYNE ’05, COSYNE ’06). We now combine and extend these two approaches, and show how a simple linear fitting procedure leads to a model that describes the data in few dimensions yet captures most of the complexity and dynamics of the neural responses.

Let us assume we have observed, experimentally, \( M \) timepoints in the firing rates of \( N \) neurons— a total of \( M \cdot N \) data points. Let us model this data in a recurrent network of \( N \) neurons, with full connectivity. Such a network will have \( N^2 \) weights (i.e., as yet undetermined connection strengths). If \( N > M \) we have more unknowns than data points, and we could in principle solve the system exactly, reproducing all of the measured neural firing rates. The fitting procedure we use to achieve this requires the inversion of a matrix \( D \) representing all the data. The fitting procedure we use to achieve this requires the inversion of a matrix \( D \) representing all the data. To avoid overfitting the data, we use the singular value decomposition to represent, and then easily invert, the data matrix \( D \): setting small singular values to zero corresponds to reducing the dimensionality of the model, which avoids overfitting. For the PFC data during short-term memory that we have previously analyzed, we find, in accordance with our previous results, that five dimensions suffice to describe the data (Machens et al., COSYNE ’06). The current approach now maps these data directly onto a neural network model, reproducing the dynamics of the data with most of their experimentally-observed richness and variety.

Acknowledgments
We thank Mark Goldman for helpful discussions. This work was supported by a Swartz Fellowship and an Emmy-Noether-Grant of the DFG to CKM and by NIH grant R01-MH067991 to CDB.

References

Game Theory Explains the Emergence of the Size Principle

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We apply a new Game Theoretical approach to analyze the competition between motoneurons (MNs) innervating a common muscle. At birth, each muscle-fiber is innervated by several MNs, of which the connection of only one becomes permanent. Each MN innervates initially many muscle-fibers and therefore engages in many competitions simultaneously, winning at some muscle-fibers and losing at others. The group of muscle-fibers that are eventually innervated by the same MN is called a “muscle unit”. In the adult system, MNs with successively higher activation-thresholds have successively larger muscle units. This is called “the size principle”, which is believed to be one of the most fundamental principles in the organization of motor-unit behavior - Therefore it is important to understand how it evolves. In viewing the elimination period as a game in which MNs are competing to innervate a maximal number of muscle-fibers, the translation of the size principle is that less-active MNs (i.e., MNs with higher activation thresholds) win in more competitions than more-active MNs. But surprisingly, the majority of the experiments that have selectively manipulated the activity of MNs during the competition period - seem to point to the opposite conclusion – that it is the more-active MNs that are advantageous in this process. This has been termed a paradox by several authors.

In addition, although there is no doubt that activity plays a role in this process, researches disagree on its importance or centrality in determining the outcome of the competitions. Using strategic considerations we prove that either way, unless the competitions are extremely biased in favor of more-active MN, less-active MNs indeed win in more competitions. This explains the emergence of the size principle. Using the same considerations, we resolve the paradox of contradictory experimental data described above.

The main idea is as follows: On the basis of the experimental data, we conclude that more-active MNs are more likely to win in early competitions and less-active MNs are more likely to win in later competitions. We prove that as the resources of MNs are limited, restricting the number of connections it can maintain, it is better to win in later competitions in order to win in more competitions. Thus the less-active MNs, which start winning only in later stages of the game, win in more competitions, and so the size principle emerges.

We believe that this work shows the importance of using a game theoretical approach - when analyzing a competitive process in the nervous system. First, it provides an appropriate framework for thinking about competition: Our game theoretical result - that the time of winning is not a neutral factor but rather it has a competitive value, enabled us to explain the emergence of the size principle and to resolve the paradox of contradictory experimental data. Secondly, using this new approach led to conclusions about a competitive process, even though the mechanisms underlying the competition is not fully understood and is under debate.

The evolutionary advantage of properties as the size principle, emerging as a consequence of competition rather than being genetically hardwired, is that it endows the system with plasticity, such that the outcome may be fine-tuned to fit the environment. In accordance with this idea, the model provides new testable predictions regarding the magnitude of the size principle in different muscles. All the results in this work are proven mathematically, and are additionally illustrated by simulations using Matlab.

Acknowledgments
This work was supported by the NIH and HFSP to IS, by the Iris Berben Foundation for Brain Research, and by the Richter Foundation.
An expectation-maximization Fokker-Planck algorithm for the noisy integrate-and-fire model

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We develop an expectation-maximization (EM) algorithm for a class of noisy integrate-and-fire models, in which the voltage evolves according to the linear stochastic differential equation $dV(t) = (-g(t)V(t) + I(t))dt + \sigma dB_t$, with $B_t$ standard Brownian motion, and $V(t)$ is reset after each spike (Paninski et al., 2004; Pillow et al., 2005). The functions $I(t)$ and $g(t)$ (the input current and membrane conductance, respectively) are given by $I(t) = \sum a_i I_i(t)$ and $g(t) = \sum b_j g_j(t)$, where the functions $I_i(t)$ and $g_j(t)$ are assumed known; thus the unknown parameters that we want to estimate are $\theta = \{\vec{a}, \vec{b}, \sigma\}$. (The reset and threshold voltage parameters may be assumed known, by the usual change of variables.)

We fit the parameters $\theta$ via maximum likelihood, given only the functions $\{I_i(t)\}, \{g_j(t)\}$, and the observed spike times; no intracellular currents or voltages are observed. We previously (Paninski et al., 2004) described methods for computing the likelihood and directly ascending the likelihood by a hill-climbing procedure. In (Paninski et al., 2005) we proposed an alternate method to compute the likelihood, which facilitates the computation of gradient information. However, the computational complexity of this gradient method scales as $O(d^3)$, where $d$ is the number of time points a given inter-spike interval is divided into (the larger $d$ is, the higher the numerical precision of the calculation). By casting the model as a hidden Markov model in continuous time and space (Paninski, 2006), we may adapt standard EM approaches to derive a method for computing likelihood gradients that only requires $O(d^2)$ time (Salakhutdinov et al., 2003). In addition, the EM algorithm provides a good “warm start” for optimization via conjugate gradient ascent. The E-step of the algorithm requires the solution of a forward and backward Fokker-Planck equation with time-dependent coefficients; we derive an efficient and unconditionally stable algorithm for solving this partial differential equation.

References


Avoiding the Bias due to Nonzero Mean Input in Volterra Series Analysis

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The experimental identification of a nonlinear system is often studied within the framework of functional expansions, i.e. Volterra or Wiener Series [1]. This framework allows the representation of a wide class of systems, e.g. sensory systems that encode stimuli in neuronal activity. Typically the cross-correlation method [2] is used to estimate the Wiener kernels. This method assumes the average of the stimulus to equal zero, in order to faithfully estimate the kernels. In some stimulus domains a zero average is physically impossible, e.g. in the auditory domain the spectrogram of the stimulus is commonly considered as the input domain rather than the time-varying sound-pressure. The spectrogram represents the level of the stimulus, hence only assumes positive values and consequently exhibits a positive mean. If in this case the cross-correlation method is used for identification of the coefficients of the Wiener Series, each kernel-estimate will be systematically influenced by the presence of other kernels in the system. Hence, for any nonlinear system the distinction and interpretation of the different kernels is complicated.

This study approaches the problem from a theoretical and a practical perspective. On the one hand we derive the exact form of this influence for arbitrary input distributions, explicitly for gaussian, white noise with nonzero mean. On the other hand we explore different methods that perform empirical correction, either directly by linear regression and by empirical orthogonalization of basis functionals (via Korenbergs exact orthogonal algorithm [3]). In this context, simulations and experiments of amplitude modulated stimuli from the early auditory system are presented to illustrate the improvements in kernel estimation and consequences for response prediction. The analysis presented here can be beneficial to a range of fields in neuroscience, especially when at least a second order nonlinearity is present in the system.

Acknowledgments
We thank N. Bertschinger, E. Olbrich and T. Lochmann for interesting discussions. This work was supported by Graduiertenkolleg Interneuro of the DFG.

References
Dynamical analysis of Bayesian inference models for the Eriksen task

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We analyze Bayesian compatibility bias and spatial uncertainly models for the two-alternative forced choice Eriksen task [1, 2], in which subjects must correctly identify a central stimulus and disregard flankers that may or may not be compatible with it. We simplify the models, deriving linear, uncoupled, discrete dynamical systems and their continuum limits: stochastic differential equations. Analytical solutions of these allow us to describe how posterior probabilities and psychometric functions depend upon parameters. We compare our results with numerical simulations of original inference models and show that agreement is good enough for them to be useful in parameterizing such models. Our analysis also reveals that Bayesian updating is closely related to a simple drift diffusion process that can be derived from neural network models. We believe that this work makes an important contribution in establishing a useful bridge between neurally-based and probabilistic decision models.

Acknowledgments
This work was supported by PHS grants MH58480 and MH62196 (Cognitive and Neural Mechanisms of Conflict and Control, Silvio M. Conte Center).

References
The role of the superior colliculus in goal-directed movements in rats

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The superior colliculus (SC) is known to integrate sensory information across multiple modalities and to play an important role in motor output. In primates, the SC has been shown to be critical for the selection and production of saccadic eye movements to visual targets. In rats, stimulation of the SC causes head and body movements in a direction determined by the specific site of stimulation. However, whether such motor output is relevant to the movements undertaken during goal-directed behavior remains unknown, because the activity of rat SC neurons during behaviors requiring movement toward a goal has not been assessed.

In order to address this issue, we simultaneously recorded from multiple SC neurons in rats performing a two-alternative choice odor discrimination. The rat was required to sample an odor at a central port, and, depending on which odor was presented, to move to the left or the right goal port, where it would receive a water reward. This task is well-suited to the study of goal-directed movement because each trial required the rat to plan and execute a movement in one of two discrete directions (left or right) in order to receive reward. In addition, odor-related responses and movement-related responses could be readily distinguished because more than one odor was associated with each side, and because on a significant minority of trials the rats chose the incorrect side for a particular odor. Rats typically performed several hundred trials within each recording session.

We analyzed neuronal activity while the rat sampled the odor and presumably planned its movement, and while it executed its movement from the center to a side port. We found that the firing rates of many SC neurons were modulated during these periods. Moreover, the activity of a subpopulation of these neurons was selective for the direction of movement, either prospectively (during odor sampling) or contemporaneously (during the movement itself). Thus, the SC appears to play a role in the planning and execution of goal-directed movements in rats. Future studies will attempt to identify the sources of olfactory input to the SC, and to determine whether the observed SC activity is causally related to the chosen movement, with the ultimate goal of elucidating the role played by the SC in goal-directed decision-making.
A Robot Based Model of the Pre-Frontal Cortex: The Mechanisms of Rule Learning and Rule Switching

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Humans and animals are able to make near optimal use of their knowledge to achieve their goals. This ability is seen as a hallmark of intelligent behavior [1]. Rule learning describes a main subset of intelligent behavior. On a neuronal level rule learning has been shown to critically depend on the pre-frontal cortex (PFC) [2]. Two main properties of the PFC critical for the expression of rules are sustained activity and activity modulation [2]. How this organization facilitates rule learning and switching in real time is however not yet known.

In our work we investigate how rule learning can be modeled using sustained activity and activity modulation following a conceptual approach using realistic robot simulations. Our model is based on the Distributed Adaptive Control (DAC) [3] architecture for behavioral control. DAC comprises of three tightly coupled layers of behavioral control; reactive, adaptive and contextual. The reactive and adaptive layers provide the robot with basic behavior supporting simple tasks. The contextual layer coordinates ongoing behavior in the context of behavioral plans. Here we develop a new contextual control layer able to express and learn rules. The contextual layer is based on a group of laterally connected model neurons. The sustained activity of these neurons is driven by perceptual inputs and modulated by lateral connectivity and rewards. A competition mechanism selects the neurons with the highest activity which subsequently trigger one the possible actions. The model is validated in a T-maze rule learning task analog to delayed conditional discrimination [4]. The robot has to choose one arm of the T-Maze according to a cue color patch situated at the start of the maze. After the completion of a predefined number of successful trials the reward contingency changes. This paradigm allows to validate the rule learning and rule switching capabilities of the model.

Our experiments show that sustained activity and activity modulation are enough to learn and express sequential rules in real time. A reliable performance could be achieved by including a mechanism to ensure the stability of the reward function. This stability is explicitly needed in real world environments where the model has to cope with high noise levels. In addition we showed that our model can efficiently adapt to changing reward contingencies which means that rule switching is significantly faster than learning the rules initially. A detailed analysis of the reward function shows that fast forgetting is essential for fast rule switching. The behavioral results show that the DAC framework is applicable for changing environments and forms a promising basis to accomplish complex real world tasks.

References
Neural Activity Related to Temporally Discounted Values in the Prefrontal Cortex of Macaques

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Decision making often involves a tradeoff between magnitude of a reward and its delay. For example, people and other animals sometimes prefer a small but more immediate reward to a large but more delayed reward. This indicates that the subjective value of a reward is depreciated as a function of its delay, a process known as temporal discounting. To understand the neural basis of temporal discounting, we trained two rhesus monkeys in an oculomotor inter-temporal choice task. Each trial began when the animal fixated a small white square presented at the center of a computer screen. After a 1-s fore-period, two peripheral targets were present along the horizontal meridian. The animal was required to shift its gaze towards one of these two targets when the central square was extinguished after a 1-s delay period. One of the targets was a green disk and delivered a small reward, whereas the other target was a red disk and delivered a large reward. The time between target fixation and reward delivery was indicated by a clock consisting of yellow and cyan dots that disappeared at the rate of 1s/dot and 4s/dot, respectively. The delay for each target varied pseudo-randomly across trials.

The animal’s behavioral data were analyzed using a logistic regression model that included the difference between the temporally discounted values for the two targets. Discounted values were calculated using an exponential or hyperbolic discount function, and the model parameters were estimated using a maximum likelihood procedure. In 85% of the sessions, a hyperbolic discount function provided a better fit to the data. We also recorded the activity of 160 neurons in the dorsal lateral prefrontal cortex (DLPFC) of the same animals. The activity during the 1-s delay period was analyzed using a linear regression model that included a set of variables related to the stimulus display, such as the position of the large-reward target and the number of dots for each target, as well as the animal’s choice and the discounted value for each target. When corrected for multiple comparisons, 32.5% of DLPFC neurons showed significant modulations in their activity related to the discounted utility of a particular target. To examine the time course of neural signals related to the discounted values and other stimulus parameters, we also carried out the same regression analysis using a sliding window. During the first 300 ms after target onset, the percentages of neurons that significantly modulated their activity according to the number of dots, discounted values and choice were 19.9%, 14.7% and 7.1 %. During the 300-ms interval in the middle of the delay period, the corresponding percentages were 18.6%, 34.6%, and 12.2%, and they became 10.9%, 28.8% and 19.9% during the last 300-ms interval in the delay period. Therefore, the fraction of neurons signaling the number of dots decreased during the delay period, whereas the fraction of neurons encoding discounted values and the animal’s choice increased. Similarly, during the first half of the delay period, the regression model that included variables related to reward magnitude and delay tended to perform better than the model that included discounted values, whereas the reverse was true during the second half of the delay period. Thus, signals directly extracted from the stimulus display might be gradually converted to discounted values and choices in the DLPFC.
Temporal anticipation affects decision-making in an olfactory discrimination task.

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Time is an important variable in decision-making. Human reaction time (RT) studies have emphasized the concept of “speed-accuracy tradeoff”, whereby performance accuracy tends to covary with the speed of response, sometimes for several seconds. But for most simple perceptual decisions, performance saturates much more quickly¹. Indeed, studies of olfactory processing in rodents reported RTs of 200-300ms²,³, suggesting a rapidly-developing olfactory code and short integration times. However, in a recent report using an auditory ‘go’ signal to instruct mice when to respond odor discrimination performance improved for up to 1.0s⁴, challenging these results and suggesting that rats simply trade accuracy for speed in RT studies. Here, we sought to address this controversy by replicating their results.

Performance is affected not only by the amount of time available for a decision but by the ability to anticipate when the decision must be made. The effects of temporal anticipation can be seen as a kind of "attention in time", modulating both the speed and the accuracy of decisions⁶. The ‘go’ signal paradigm presents subjects with a random response deadline. Performance may vary depending on how subjects allocate their attention to the time interval during which the signal occurs. Mathematically, how an ideal observer would allocate attention in time is given by the hazard rate, which, for a probability distribution of an event in time, quantifies the probability of that event to occur, given that it has not already occurred.

Could increased readiness with elapsed time masquerade as temporal integration? For events distributed exponentially in time, the hazard rate is flat. However, for a flat probability distribution (0.1 – 1s), as used in the previous ‘go’ signal study⁴, the hazard rate is monotonically rising. In order to test whether this could account for the previous results, we directly compared performance on a ‘go’ signal instructed odor mixture discrimination task using an exponential and a flat probability distribution of ‘go’ signal delays. As predicted by the hazard rate manipulation of temporal attention (as well as a temporal integration model), performance accuracy increased over >0.7 s when ‘go’ signals were distributed to achieve a rising hazard rate. In contrast, performance asymptoted in <0.3 s in a flat hazard rate condition. When the same rats were trained on the RT paradigm, accuracy was equivalent to that obtained with the highest readiness in the ‘go’ signal paradigms. Further testing with 1.0 s fixed ‘go’ signal (on difficult mixture ratios, resulting in <75% peak accuracy) failed to result in improved performance.

These results confirm the notion that temporal manipulations exert a strong influence on olfactory discrimination performance, but point to the readiness of the subject to respond as a predominant factor for odor sampling time longer than 0.2-0.3 s. The results confirm the idea that rats’ RTs are well-matched to the temporal requirements of their olfactory systems⁵. Although it remains a possibility that longer temporal integration and temporally evolving olfactory code could improve performance on a different class of olfactory problems, these results support the previous contention that fine odor mixture discrimination can be performed optimally in 200-300 ms or 1-2-sniffs by well-trained subjects.

Acknowledgments: Supported by the NIDCD.

References
Representation of Choice and Reward Action Values in Decision-Making Neural Circuits

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We studied the effects of past choices and rewards in decision-making. Reinforcement learning paradigm estimates action value that represents the amount of expected reward associated with a particular action and this value determines the choice of future action in a probabilistic manner. Hence, the estimation of action value is critical for understanding animal’s behavior and its relationship to neural activity. Previous studies estimated action value based on past rewards (1, 2). However, it is unclear whether past rewards are sufficient or other factors should be considered for accurate estimation of action value. A recent study has shown that behavioral choices of animal are well predicted by a dynamic model that takes into account not only past rewards but also past choices (3), suggesting that the effect of past choices must be included in the estimation of action values.

In this work, we divided action value into two parts - choice and reward action values that quantify the effects of past choices and rewards, respectively. Past choices are represented as the length of the same choices (run-length). The choice action value for a given run-length can be estimated based on behavioral data during steady state, in which mean reward contingency associated with each choice stays constant, using a generalized linear model, because the reward action value term becomes constant in this condition (3). Assuming animal’s behavior depends on the latest run-length, the coefficient for the latest run-length becomes the inverse temperature (i.e., the degree of noise) in action selection. To estimate the reward action value, we introduce a state-space model (softmax action selection rule) including the estimated choice action value (4, 5). This model defines the reward action value with confidence intervals so as to valuate animal’s discrimination ability in a statistical manner. This analysis reveals independent effects of past choices and rewards, and explains which factor determines a particular behavioral choice and whether the choice is exploitation (choosing larger action value) or exploration caused by noise. The reward action value stabilizes as the animal discovers reward contingencies associated with each choice and the choice action value varies according to past choices (run-lengths). Simulation results show that a model including both effects estimates action values more accurately than a model neglecting past choices. These results suggest that we must estimate two effects separately for accurate estimation of action value regardless of the degree of learning. Choice and reward action values estimated in this work can be used in classifying neurons for their roles in a reinforcement learning task and in modeling a neural circuit related to decision making.

References
Relative reward encoding in parietal area LIP

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Reward information is a critical element of optimal choice behavior. Recent evidence suggests that many of the neural systems underlying decision-making encode the reward contingencies of available actions. In the monkey lateral intraparietal area (LIP), visuomotor neurons are strongly modulated by reward-related variables such as the expected gain and prior probability of reinforcement, which control the value of the associated saccades, suggesting that a neural representation of value is an integral part of the decision mechanism. More recently it has become clear that this neural representation takes the form of subjective encoding; firing rates are linear functions of subjective, rather than objective, measures of value.

While it is now clear that the subjective value of actions is represented in decision-making circuits, the exact form of that representation remains uncertain. Each LIP neuron may encode the subjective value of its associated saccade, independent of other available rewards and actions. Alternatively, the subjective value of a given saccade may be represented in a relative form, for example normalized against all other available rewards (as in a gain ratio):

$$V_i = \frac{V_i}{\sum V_i}$$

One advantage of such a relative representation is that it can achieve dynamic range compression and optimal efficient coding, both properties that have been well studied in visuo-cortical circuits.

To determine if LIP neurons encode subjective value in an absolute or relative manner, we examined the activity of single LIP neurons while varying the reward for movements that lay outside the response field of the LIP neuron under study. For each neuron, two targets were presented during central fixation, one inside the response field (IN target) and one well outside the response field (OUT target), typically in the opposite hemifield. Monkeys subsequently were instructed on different trials to choose the IN target or the OUT target, or were free to choose either target. In contrast to previous studies, we manipulated the magnitude of the OUT target reward, holding the reward associated with a saccade to the IN target constant, as well as manipulating the IN target reward while holding the OUT target reward constant. We found that LIP neurons are strongly and negatively correlated with the magnitude of reward associated with the OUT target and positively correlated with the reward associated with the IN target. Furthermore, we show that this negative relationship between LIP activity and OUT target reward is entirely consistent with the positive correlation between LIP activity and IN target reward, if subjective values are expressed in terms of a gain ratio.

Acknowledgments

This work was supported by the NEI (EY010536) and the NINDS (NS051914-01A1).
Optimal learning: a route to depression?
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Despite their epidemiological importance, psychiatric diseases are only poorly understood. Nevertheless, judging by the efficacy of pharmacological treatments, most appear to involve characteristic dysfunctions of the dopaminergic (DA), serotonergic (5HT) and/or noradrenergic neuromodulatory systems that are the foci of intense computational neuroscience studies. We seek to use this tie to provide a link from normative neuromodulatory models to psychiatric dysfunction, here in particular in the context of extensively validated animal models of depression.

The main clinical characteristic of depression is anhedonia – a disability to perceive or act upon rewards. This would seem to fit well into a reinforcement learning (RL) framework, providing a possible functional tie to DA and 5HT. However, key animal models observed to lead to anhedonia are learned helplessness (LH) and chronic mild stress, and LH in particular is taken to argue for the importance of the perception (and systematic generalizability) of controllability – a concept alien to standard RL treatments.

We study three facets of RL models of depression. First, we show that it is possible to capture key aspects of the LH data in a habit-based (average-reinforcement learning) model, independent of any explicit notion of controllability. This works by generalizing to other contexts any irrelevance found for action choice in one context. Human behavioral data support this idea, which also has wider application to such things as understanding the emotional regulation of pain.

Second, we construct an explicit, hierarchical Bayesian account of control. We consider as readily controllable, environments in which single actions have low-entropy consequences, and for which each possible goal can be achieved by at least one action. We consider parameters describing these characteristics to be what generalize from one domain to the next. High-control priors lead to higher average reward predictions, as sometime rewarding actions are assumed to be anytime exploitable. Generalizations as to likely controllability determine optimal exploratory behavior. Only under high-control priors do actions differ substantially in terms of predicted outcome; low-control priors can give rise to the behavioral insensitivity to rewards mentioned above, which is measured in terms of action choice. We also consider the fraction of controllable reinforcement and find that this can account for the occurrence of anhedonia after both acute severe and chronic mild stress.

Finally, these formulations of controllability can be seen as placing simple priors on the decision trees of MDPs. Making inferences in large trees is computationally challenging, and standard practice is to prune branches that are either proveably or just likely to be inferior. We show that this pruning can explain some of the confusing effects of 5HT, which has been postulated to report negative values and inhibit actions that lead to negative outcomes; but decreases of which produce powerful relapses of depression. We appeal to a combination of Pavlovian and instrumental effects to account for the fact that high 5HT seems to produce high average reward predictions, and that lowering 5HT decreases the average reward and potentially induces or maintains a depressed state.

In sum, we show that learning about the relevance of reinforcers to environments and about levels of control accounts for major kinds of depressed animal and human behaviors; and that some of 5HT’s contradictory functions are explained by a mapping onto RL. This provides a normative characterisation of putatively non-normative psychiatric effects.
Calcium-based models for spike-timing-dependent plasticity

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It has been considered that an amount of calcium elevation determines the synaptic plasticity. However, it has been pointed out that simple application of this principle cannot reproduce the timing dependence of spike-timing-dependent plasticity (STDP) [1, 2]. A few mechanisms were previously proposed to solve the problem [3, 4]. These are possible mechanisms, but it still remains unclear what mechanism is true for actual STDP. Here, we present two other mechanisms to solve the problem. One is a fixed threshold model with a finite time window for the calcium elevation, and the other one is a mechanism using dynamically sliding threshold determined as the linear summation of calcium elevations induced by single pre-synaptic and post-synaptic spikes.

Assuming an integrate-and-fire neuron and a delta-function-type effect of an action potential, we derived the analytical results and found that both models reproduce the timing-dependence of STDP. In addition, we found that the dynamically sliding threshold model (the latter one) can also reproduce the initial strength dependence of STDP, which was found to be asymmetric for synaptic potentiation and depression [5], whereas no explicit initial-strength dependence are incorporated into the model.

\[
\frac{\Delta w}{w(0)} \quad t_{\text{post}} - t_{\text{pre}} \quad [\text{ms}]
\]

\[
\log(w(0))
\]

Acknowledgments
This work was partially supported by the Grant in Aid for Priority Researches, no.18019034 and a Tamagawa University 21st Century Center of Excellence grant from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

References
Orientation selectivity in goggle-reared kittens: An overcomplete unsupervised learning model

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Unsupervised learning models applied to natural scene statistics almost ubiquitously generate V1-like receptive fields. To assess further how well these models describe the functional goals of its neural representation, we applied such a model to the V1 responses of animals raised in environments with unnatural statistics, namely the recent sustained goggle-rearing experiments of Tanaka [2]. We show that an over-complete product-of-experts model (POE) [1] captures well many characteristics of V1 simple cells observed under both normal and goggle-reared input.

Tanaka [2] used optical imaging and electrophysiological methods to show that severely restrictive striped goggle rearing for many months post-eye opening has extreme effects on neural development. The percentage of neurons in goggle-reared kittens preferring the orientation permitted by the goggles was over five times that of neurons in normal kittens along with other more subtle changes.

We simulated the effects of goggle-rearing by training POE, an over-complete extension of independent components analysis, with inputs consisting of unadulterated natural scenes and/or natural scenes that had been filtered with (software-defined) goggles. Different proportions of the two inputs were used in order to model innate mechanisms favoring the statistics of natural scene-like input or incomplete striped rearing. We applied POE models with differing degrees of over-completeness, the other variable that is known to exert significant influence over the nature of receptive fields in functional models.

Our results show that there is a significant regime in which model filters at the goggle-filtered orientation (GO) are over-represented, together with a relatively even distribution of filters for other orientations, as is seen in the experimental data. The degree of orientations selectivity can be quantified by an over-representation index, ORI=(n oriented at GO)/(n oriented elsewhere) where n is the number of neurons. In experiment, ORI values ranged from 3.74-12.7 [2] and the results of our modeling spanned a similar range, with ORI values that scaled with the percentage of GO stimuli present in the input. Also like goggle-reared neurons, our model neurons exhibit; a lower proportion of oriented-localized neural RFs relative to normally-reared kittens; narrower tuning widths for RFs at GO (characterized by the full width half max (FWHM) of the tuning curve; and larger and more elongated shape of RFs at GO ([2]; and Tanaka personal communication).

Figure: Sample of model (a) and experiment (b; reprinted from [2]) results showing an orientation histogram and average FWHM values (white lines) as a function of preferred orientation. Experimental FWHM is overlaid on a 2D plot of all imaged pixels, color-coded for preferred orientation.


Homeostatic plasticity and ocular dominance diversity can account for the differential expansion of the left- and right-eye receptive fields of V1 neurons after monocular retinal lesions.

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When V1 neurons are subjected to a loss of subcortically-mediated feedforward input they respond by expanding their receptive fields, apparently due to an increase in the efficacy of the input arriving via their intracortical connections. This is likely to reflect a generalised strategy that allows neurons to recover from deficiencies in synaptic drive by uniformly potentiating subthreshold input connections to suprathreshold levels at which these connections can engage in activity-dependent Hebbian competition [1]. It is plausible that this sub- to supra-threshold transformation is achieved by some kind of homeostatic modulation of gain [2], where the efficacies of all synapses are scaled such that excitatory neurons become more responsive and inhibitory neurons become less responsive to input (effectively producing disinhibition) [3]. However, after being partially deafferented by a monocular retinal lesion, binocular neurons in V1 appear to show receptive field expansion of their lesioned eye receptive fields only [4]. Such a bias appears to be inconsistent with the hypothesis that a non synapse-specific form of homeostatic plasticity underlies this receptive field expansion. In this study we examined experimental results from monocular lesion experiments and compared them to the behaviour of a network model of V1. The feedforward and horizontal connectivity of each modeled neuron population (or ‘column’) had a specific ocular bias, and the distribution of ocular dominance within the network was based on in vivo data. We found that if the modeled columns underwent homeostatic plasticity at an intensity proportional to their input loss the distribution of the ratios of lesioned eye to non-lesioned eye receptive field expansion matched the distributions observed in vivo. Our results support the hypothesis that neurons are able to undergo homeostatic plasticity that is proportional to changes in their total synaptic input. In addition, the results indicate that the spatial specificity of this plasticity is at least below that of the scale of ocular dominance columns.

Acknowledgments
Support contributed by: BMBF 10025304 (Germany), ARC (Australia).

References
The role of cortical interaction for spatial discrimination, localization and its learning-induced changes

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We provide a general computational framework to understand spatial discrimination and localization abilities and their alterations during learning. Cortical population activity is modeled using a mean field approach with a Mexican hat interaction of short-range excitation and longer-range inhibition. Single site stimulation evokes single peaks of activation, while simultaneous stimulation at two sites evokes 2 peaks. We assume that the former codes for the subjective experience of a single point, while bimodal distributions are read out for perceiving two. It has been shown experimentally that for large distances two peaks of activation interact only weakly, while lateral inhibition leads to substantial suppression for shorter separations [1].

Localization refers to the ability to precisely read out the location of monomodal distributions of population activation. Several approaches have been formalized how single parameters may be estimated from population distributions of activation (f. e. [4]). Psychophysically both long term [5] as well as short term plasticity [2] improve discrimination abilities on the cost of localization indicating a trade-off. Here we show that spatial discrimination and localization are affected oppositely by lateral interaction: While lateral inhibition leads to deterioration of discrimination it improves localization. This effect is due to a reduction of coexisting activation leading to smaller influences of noise and a subsequent reduction in the variance of the read out peak position.

Learning on a cortical level is assumed to be mediated through a decrease of inhibitory interaction. As a result, decreasing the strength of lateral inhibition in the model increases the size of the cortical representation as observed in fMRI studies [3]. For discrimination the decrease in inhibitory interaction leads to bimodal activation profiles for distances that before learning evoked single peaks explaining learning-induced improvement of discrimination ([2], [3]). In contrast, for localization weakening winner-takes-all mechanisms allows coexisting activation leading to stronger influence of noise thus deteriorating localization abilities. Combined, modeling lateral cortical interaction in population representations provides a unifying framework that explains task-specific requirements in tactile perception and their alterations evoked by perceptual learning.

References

Long-term retention of motor adaptation explained by a model of short-term learning.
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An extensive amount of theoretical and neurobiological work has focused on the mechanisms by which short-term memories are transformed to a stable, enduring state. Several previous studies have shown that short term motor adaptations have the potential to develop into long term motor memories with practice, but the mechanisms governing this consolidation are not yet well understood. We recently showed that interactions between two distinct processes underlie short-term motor adaptation and provide a unified explanation for a variety of learning phenomena not previously linked – including interference, savings, and rapid unlearning [1]. One of these learning processes rapidly responds to error but has poor retention, while the other responds slowly to error but retains information well.

Here we investigated whether these two processes differentially contribute to the formation long-term motor memories. The simulations plotted in figure 1 show that the fast learning process accounts for most early learning but the slow learning process dominates the late learning period. We hypothesized that the slow learning process might contribute to long term retention much more strongly than the fast system. This hypothesis predicts that as learning progresses, relative improvements in the amount of learning are surpassed by relative improvements in the amount of retention – a little extra learning leads to a lot of extra retention. Furthermore, this hypothesis predicts that the amount long term retention will eventually asymptote with increasing training and it predicts the break-point at which this asymptote will occur.

We used a force-field adaptation paradigm to study formation of the capacity for long term retention. 40 healthy volunteers divided into 4 groups were trained to make quick reaching movements to targets while grasping a robot manipulandum that could apply force to the hand. Subjects performed 150 baseline reach trials in each target direction, followed by a variable number trials in a clockwise viscous curl force-field that induced motor adaptation. They were then tested for retention of learning either immediately or 24 hours later.

Figures 2 & 3 show the main results of this series of experiments. Figure 2 shows that learning proceeds rapidly during the first 10 trials and then more gradually over the next 100 trials before reaching asymptote and that after 45 learning trials 85% of the final performance level is attained. In contrast, Figure 3 shows that only 50% of the final 24 hour retention is achieved after 45 learning trials – essentially the same as predicted if long-term retention were solely dependent on the slow learning process (blue line) but not predicted if long-term retention depended on net adaptation levels (red line). Furthermore, this figure shows that 24 hour retention asymptotes after 130 learning trials as predicted by a model of slow process learning. These results show that 24 hour retention is strongly related to the amount of slow process learning but not the overall amount of learning. This suggests that two learning processes underlying short-term motor adaptation contribute differentially to the long term retention of motor memories – the fast process contributes weakly and the slow process contributes strongly.

Hebbian Inspecificity in Unsupervised Learning

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Long-term potentiation, the biological realization of the Hebb Rule, is not completely synapse-specific, probably because the underlying spine head calcium signals can spread to other synapses, which are more densely spaced than the space constant for dendritic calcium diffusion. Since complete chemical isolation also implies total electrical isolation, the complete specificity assumed in neural network models is unrealistic. We have investigated the effects of Hebbian inspecificity in two standard unsupervised learning models, PCA and ICA.

We assumed that, averaged over patterns, the strengthening (or weakening) of one connection is equally likely to contribute, at a low level, to the strengthening (weakening) of all other connections, both because connections are made up of multiple, randomly scattered, synapses, and because of anatomical turnover. Therefore inspecificity is modeled as an error matrix $T$ whose offdiagonal elements are all equal, representing the erroneous contribution of changes in one connection to another. If the number $n$ of inputs increases, synapses will become more crowded (due to geometric constraints), so this “error” element remains rather constant as $n$ increases, while the diagonal “quality” element decreases with $n$. In the standard Oja PCA model we find that the stable fixed point of the erroneous learning dynamics is the leading eigenvector of $TC$ ($C$ is the input covariance matrix), and we derive stability conditions on the learning rate. The angle between the correct and erroneous stable weight vectors increases smoothly with the intrinsic error rate (which reflects the leak of calcium from a spine head), but more steeply at higher $n$. This means that even tiny leakage can seriously degrade, but not completely prevent, learning in very large networks.

In the Oja model the input-output relation is linear, and only pairwise statistics are learned. To learn higher-order statistics, a nonlinearity is required. Our simulations show that in the nonlinear ICA model, rather than smoothly degrading, learning suddenly fails at a low value of error. This means that realistic synapses cannot do unsupervised learning of high-order statistics if $n$ exceeds a critical value. Since the neocortex must learn high order statistics, it must have solved the inspecificity problem, possibly explaining its unique circuitry and physiology.
Experience-dependent Dynamics of Spatio-temporal Precision and Synchrony in Place Cells

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The hippocampus is crucial for the formation of episodic memories, the What, When and Where of events. The fine time scale temporal precision of hippocampal neural activity is thought to be essential for binding these memories together across time. Hippocampal activity occurs during two main states, an active state where the 8 Hz theta rhythm strongly modulates hippocampal firing and a quiescent state where short (~100 ms) high frequency (100-200 Hz) bursts of activity known as ripples are prominent. In the active state, place cells show phase precession where the phase of theta at which spikes occur becomes progressively earlier as the animal moves through the place field. As a consequence, cells with overlapping place fields fire together within short windows (< 60 ms). Similar patterns are seen during ripples, where neurons that were active together during active exploration fire together within each ripple. The presence of these forms of temporal organization is well established, but little is known about whether and how this organization changes to reflect the encoding of new memories.

We developed a new adaptive algorithm that makes it possible to accurately describe the dynamics of phase precession during learning, and applied this to recordings of CA1 neurons from rats performing a spatial alternation task in both an entirely familiar environment and in an environment which contained one novel arm. The new model fits the data well: for approximately 70% of the neurons, the model prediction was statistically indistinguishable from the actual spike train at a 99% confidence level, as compared to less than 50% for previous adaptive models. These models can therefore be used both to analyze spatio-temporal dynamics in place cells and to simulate highly realistic place cell spike trains.

When we examined the dynamics of phase precession, we found clear dynamics as a function of experience in the novel arm. Some cells showed clear phase precession on the first exposure to the novel arm, but on average the precision of phase precession was significantly lower than in the familiar environment. Phase precession in the novel arm evolved with experience, becoming more precise over 2–3 days until it was indistinguishable from that in familiar environment. The difference in theta phase precession seen on day 1 was not a result of differences in the theta rhythm or the modulation of spiking activity by theta, but rather reflected disorganization of the spatio-temporal structure of the spike train. The dynamics of phase precession were accompanied by an evolution in the synchrony of activity during ripples. On day 1, cell pairs with overlapping place fields on the novel arm fired more synchronous spikes during ripple events than did pairs with overlapping place fields in the familiar arm or pairs with non-overlapping place fields on the novel arm. Furthermore, synchronous firing diminished within 2–3 days, similar to the dynamics of phase precession. These results provide the first direct link between the dynamics of place cell activity during exploration and the dynamics of activity during the quiescent state, and suggest that synchronous activity during ripples may be important for establishing spatio-temporal organization during active exploration.

Acknowledgments
This work was supported by the Swartz and Sloan Foundations, the John Merck Scholars Program, the McKnight Foundation for Neuroscience and NIH RO1 MH59733.
Are lateral inhibition and Hebbian learning responsible for visual perceptual priming?

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Perceiving and identifying an object is improved by prior exposure to the object. There is experimental evidence that behavioral priming is accompanied by reduced neural activity, but it is still unclear how suppression of neuronal activity with repetition correlates with improvement in psychophysical measurements of behavior. In contrast, in the field of perceptual decision making better performance is thought to be associated with higher neural activity in appropriate cortical areas. In the present work we suggest a model that can address the contradiction. Key assumptions of the model are 1) sharpening representations in lower visual areas, such as V1, is due to Hebbian learning, 2) sharpening in lower areas leads to sparser representations in higher areas, such as IT, and 3) sparser representations in higher areas facilitates the competition among many competing representations, therefore shortening the response time.

The model predicts that blockade of long-term plasticity in lower visual areas should produce a stronger deficit in priming compared to blockade of plasticity in higher areas.
Dissociating Rule-based Categorization and Set-shifting from Action Selection in Monkeys

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Dynamic, rule-based categorization is usually tested by requiring subjects to choose between actions based on current category membership. This confounds categorization and action selection. Such confounding makes it difficult to investigate neural correlates of cognitive functions such as rule-based categorization if the brain areas under investigation are also considered important for dynamic selection between actions (the prefrontal cortex being a typical example). Here, we show how categorization and attentional set-shifting can be tested in monkeys with a task that does not require action selection. We find that eliminating the need for action selection substantially reduces the training time for acquiring the task when compared to conventional approaches. Thus the cognitive and the action-selection requirements are two separate steps.

In our task, there is a single instrumental response, identical for all trials. To obtain a reward, the monkey has to release a bar when a red target changes to green. Error trials have to be repeated until performed correctly. At the beginning of each trial, we also present a visual cue that, although not relevant for performing the instrumental task, indicates whether the reward after a correct response will be delivered immediately ("pleasant") or delayed ("unpleasant") – based on the current category assignment of the cue. The cues were created by producing morphs between two shapes and two colors, which allows us to use either the color or the shape dimension for dividing the stimulus set into two subsets. Assigning immediate and delayed rewards to the two subsets results in four different categorization rules.

For all four monkeys tested, both the error rates and the reaction times differed significantly between the immediate and the delayed conditions. Thus, even though the identities of the cues are irrelevant for carrying out the task, the monkeys learn their meanings. By switching the categorization rule without announcement within sessions, we found that monkeys follow both extra-dimensional (color to shape, or vice versa) and intra-dimensional (reversal within color or shape) set-shifting in this task.

Our results show that monkeys can form rule-based categories and switch between them in a task that requires no choice between actions. This offers the opportunity to probe the contribution of different brain areas, e.g., individual parts of prefrontal cortex, to rule-based categorization and set-shifting when there is no requirement for action selection.

Acknowledgments
Support Contributed By: IRP/NIMH, JSPS/Japan
Efficient supervised learning in networks with binary synapses

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Recent experimental studies indicate that synaptic changes induced by neuronal activity are discrete jumps between a small number of stable states. Learning in systems with discrete synapses is known to be a computationally hard problem. Here, we study a neurobiologically plausible on-line learning algorithm that is derived from Belief Propagation algorithms. We show that this algorithm performs remarkably well in a model neuron with \(N\) binary synapses, and a discrete number of 'hidden' states per synapse, that has to learn a random classification problem. Such a system is able to learn a number of associations which is close to the information theoretic limit, in a time which is sub-linear in system size, corresponding to very few presentations of each pattern. Furthermore, we show that performance is optimal for a finite number of hidden states, that scales as \(\sqrt{N}\) for dense coding, but is much lower (\(\approx 10\)) for sparse coding. This is to our knowledge the first on-line algorithm that is able to achieve efficiently a finite capacity (number of patterns learned per synapse) with binary synapses.

The algorithm is similar to the standard 'perceptron' learning algorithm, but with an additional rule for synaptic transitions which occur only if a currently presented pattern is 'barely correct' (that is, a single synaptic flip would have caused an error). In this case, the synaptic changes are meta-plastic only (change in hidden states and not in actual synaptic state), and go towards stabilizing the synapse in its current state. We suggest this rule is sufficiently simple to be easily implemented by neurobiological systems, and discuss several experimental predictions.

Acknowledgments
We thank A. Colleague for helpful discussions. This work was supported by NIH grant DC999999.

References
Hippocampal contributions to control: a normative perspective

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The mammalian brain possesses multiple memory systems, including the striatum, the locus of procedural memories underlying habits, the neocortex, the main site for long-term general perceptual and semantic knowledge, and the hippocampus, the area largely responsible for storing and processing specific autobiographical memories [1,2]. These three systems and their interactions have been extensively studied, both empirically [3] and theoretically [4], but their collective roles in guiding optimal behavior have only rarely been addressed [5]. The contribution of episodic memory is particularly mysterious. Here, we develop a normative framework of control in the face of uncertainty, in which each plays a precisely delineated part.

Uncertainty arises in control from inherent stochasticity of the underlying tasks, and ignorance of the controller about the tasks, even if they are otherwise deterministic. Following others [6], we see the neocortex as a learning system making efficient use of available information in such conditions. A key aspect of such a system is that it represents not only single values of relevant variables, but also the uncertainty surrounding those values, thereby at least approximately performing optimal statistical inference [7]. However, we also observe that while it may be ideal – if at all possible – to keep account of uncertainty for learning, ironically, it is precisely the same careful bookkeeping of uncertainty that renders impractical planning sequences of actions using such a model. The more uncertainty there is to represent, the less feasible it is to model all the consequences of taking an action by enumerating recursively all possibilities that it entails in the future. This problem becomes exponentially harder as the time horizon of the task broadens, making direct approximations, such as pruning or sampling, suffer from serious biases.

The striatal habit-based system has been suggested to offer a solution to this problem, but is only effective in the limit of substantial samples [5].

We suggest that a different class of approximations, namely recalling episodic memories of specific behavioral sequences that proved successful in the past, can be a powerful alternative to the other two systems. The eventual reduction of ignorance-related subjective uncertainty and the steady accumulation of sufficient information to license reliable habits, imply that the hippocampus should be particularly important in the early stages of training on a task or exploring an environment.

Our results suggest normative accounts of the widely observed time-limited role of the hippocampus in processing memories [2], and the apparently more semantic characteristics of distant memories [8]. This offers a different perspective from the popular, but computationally challenging hypothesis that memories are consolidated out of the hippocampus and into the neocortex, or elsewhere [4].

Acknowledgments

The authors thank many useful discussions with Nathaniel Daw and Quentin Huys. ML and PD were supported by the Gatsby Charitable Foundation, ML was also funded by the ECAGENTS project.

References

Localized Activity in Inhibition Dominated Network – Fluctuation Driven Bump States –

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The spike patterns of neurons in vitro in response to current injection is typically very regular, however in vivo, from the sensory to prefrontal cortex, the degree of spiking irregularity is known to be high [1, 2]. In the prefrontal cortex, neurons seem to switch from a background state to an active firing state during delayed response tasks and their spikes trains are highly irregular in both types of states.

One robust mechanism to obtain high spike irregularity is to balance the excitation and inhibition in recurrent connections [3]. Although it is easy to obtain self-sustained states with a connectivity dominated by excitation dominant network, CV of spike trains typically decreases when the firing rate increases. In inhibition dominated networks, firing patterns can be irregular depending on the parameters of the network, however it is usually difficult to obtain bistability because the mean input to the neuron is inhibitory.

Here it remains unclear how to achieve simultaneously high firing rate and high spike train irregularity. Here we focus on the possible firing states in a spatial working memory model. More specifically, we investigate the dynamics of sparsely interconnected spiking neurons embedded in a ring structure. We construct a self-consistent theory of the macroscopic variables of the system, and calculated the stable states of the system. The activity of recurrent network of spiking neurons have been studied by mean-field approach [4]. We found the network shows various patterns of activity, e.g., traveling wave, oscillating wave, standing wave, uniform activity states, and quiescent state.

In this meeting, we report that spatially localized activity (bump) states can exist in inhibition dominated regions with sub-threshold external input. In these region, bistability can be achieved thanks to fluctuations of the recurrent input which provides localized positive feedback. Similar fluctuation driven bistability might be relevant to the spontaneous activity in the primary visual cortex.

Acknowledgments
K.H. is supported by JSPS Research Fellowship.

References

EXAMINING THE PERCEPTION OF TEMPORAL INTERVALS SEQUENCES USING DIFFERENT STIMULUS AND RESPONSE MODALITIES

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Interacting with a dynamic world requires the capacity to perceive and represent temporal intervals and patterns. Often, as in speech or music perception, patterns composed of multiple temporal intervals are of importance. Using the auditory input modality, and following Penel, Hollweg and Brody \cite{Penel2005}, we have presented sequences of three brief tone pips (i.e., sequences of two temporal intervals) to human subjects. Participants had to reproduce the presented sequences via either tapping, or vocal responses, or placing two vertical lines on a screen at a position that represented the timing of the second and third pips. In contrast to Penel et al’s previous study, here the total time between the first and last pip was not fixed, but varied from trial to trial within the range 700 to 1300ms. The timing of the middle pip was drawn, for each trial, from a uniform distribution between the first and the last pip.

Successfully carrying out the tasks requires the subjects on each trial to sense the stimuli, store a mental representation of them in short-term memory, and then report the sequence via motor activity. In order to separate effects due to the reporting method from effects of other processing stages, we examined three different output modalities (spatial, vocal and tapping). Similarly, to distinguish effects pertinent to sensation, we had two different input modalities (auditory and visual) in our experiment.

The main effect that we observed was that the accuracy of reproduction depends on the ratio of two intervals of a stimulus, with greatest accuracy when the ratio is 1:1, and high accuracy for one or two pairs of ratios, each pair of the form (m:n and n:m). The effect was the same for different input and output modalities.

We used the distribution of reported reproductions as surrogates for the distribution of mental representations that the subjects formed of the temporal sequences. Using these distributions, we could predict performance in a classical two interval, two-alternative forced-choice (2AFC) experiment. Here subjects hear a first three-pip sequence, then a second three-pip sequence, and must compare the two sequences, producing a binary response as a result of the comparison. Predicted performance matched the experimentally-obtained performance with the same dependence of the ratio of two intervals as in the reproduction task. This result further indicates that the observed ratio effect is not due to the motor component of the reproduction task.

References

Wireless Recording from Rat Hippocampus

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Present-day multi-channel recording is physically constrained by the wires that connect electrodes to a recording device. In studies of awake behaving animals, this restricts the subject’s movements to a small and enclosed two-dimensional arena. To overcome these constraints, we have developed a 64-channel wireless recording device. Here we describe pilot recordings from the hippocampus of a freely-moving rat.

The system consists of:
• (A) a 28-tetrode microdrive, to be mounted on the skull;
• (B) an integrated 64-channel amplifier/filter/multiplexer [1], connected to the microdrive;
• (C) a battery pack, mounted on the animal’s back with a harness;
• (D) a miniature 2.4 GHz FM transmitter;
• a remote FM receiver;
• a fast data acquisition card.

The head-mounted components weigh ~27 g, and the backpack ~50 g. Battery power is sufficient for 10 hours of recording. The transmitter operates with a range of >60 m at a signal-to-noise ratio of >200. Over the band of 10-2000 Hz, the noise introduced by the entire recording system is <5 µV rms, as referred to the electrode input. We compare the wireless recordings to conventional wired recording of the same signal, and discuss the quality of spike sorting from tetrode data. In addition to action potentials, the system can resolve low-frequency signals in the theta range.

The present instrument is suitable for recording from a variety of animal and human subjects. With modifications to the integrated circuit, smaller and lighter models are possible.

Representation of movement direction in the human entorhinal cortex

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Our work examines the neuronal correlates of human route navigation. We recorded single-neuron activity from epilepsy patients while they played Yellow Cab, a spatial-navigation video game [1]. In this variant of Yellow Cab, subjects used a joystick to drive between randomly selected stores arranged on the outside of a square track (Figure 1A). The center of this track was closed, limiting movement to either clockwise or counterclockwise directions. We compared the activity of each neuron with the subject’s spatial location and direction of movement in the virtual environment. This analysis identified a set of neurons in the entorhinal cortex (EC) that were preferentially active during either clockwise or counterclockwise movement. For example, Figure 1B shows the activity of a “counterclockwise cell” that had a greater firing rate when the subject was driving in a counterclockwise direction than when they were driving in a clockwise direction. This direction-dependence was present during both turning and straight movement. These findings indicate that the EC is part of the neural representation of movement direction, and support the idea that the EC plays a general role in cognition by representing contextual feature information [2].

Acknowledgments
This work was sponsored by the National Institutes of Health research grants MH61975 and MH062196, NSF grant SBE0354378, and the Swartz Foundation.

References
The influence of external dynamics on motor planning

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Optimal control strategies have been implemented to overcome the ill-posed nature of motor planning by minimizing cost functions to identify potential motor planning criteria. Different theories posit that humans aim to optimize kinematic, dynamic or variance costs in the planning of supported reaching movements in the horizontal plane. While each theory explains some facet of movement trajectories in the horizontal plane, none can fully explain real human behavior. A more complete exploration of human motor behaviors across a variety of tasks is needed to understand the degree to which each of these theories explains normal human behavior. Here, we discuss the influence of inertial, viscous and gravitational dynamics on motor planning. We conclude that changes in external movement dynamics can highlight key differences between the performances of leading motor planning strategies.

We simulated the human arm interacting with either a mass in the hand or a viscous force field. We found that the mass did not change the trajectories predicted by the minimum torque change (MTC) or minimum end point variance (MEPV) hypotheses. In contrast, viscous forces clearly differentiated MTC and MEPV predictions from both minimum jerk (MJ) predictions and from human behavior. We conclude that learned behavior in the viscous environment could arise from minimizing kinematic costs, but could not arise from a minimization of either torque change or end point variance.

We also considered the role of naturally occurring dynamics on human behavior and optimal control strategies. Human subjects performed 10 cm, center-out movements in a vertical plane intersecting the shoulder and produced hand paths that were slightly curved. The change in direction-dependent gravity torques was significantly (p slope=0.0008) correlated (r²=0.868) with curvature; an increase in gravity torques throughout the movement resulted in counterclockwise curvatures, and a decrease in gravity torques resulted in clockwise curvatures. We then simulated a two degree of freedom dynamic arm model. We found that MTC replicated human hand paths in five out of eight movement directions. In the other directions, MTC predicted the direction, but underestimated the magnitude of human path curvature. MEPV hand paths drastically overestimated the curvature seen in subjects. Our results indicate that even a simple, steady state, dynamic environment, like gravity, can cause systematic, behavioral differences over its horizontal analog.

We show that movements made interacting with an inertial load, a viscous force field or a gravitational force elucidate key differences in motor planning strategies. Our results indicate that changes in external dynamics influences the predictions of current models of optimal control. People did not consistently favor a particular cost in their movement selection: external viscous forces elicited straight hand paths that violated dynamic optimality, and gravitational forces elicited curved paths that correlated with direction-specific torques and violated kinematic optimality. We therefore reject the notion that a single optimality principle can explain normal human behavior; rather people consider a variety of movement features and plan movements dependent on task specific context and dynamics. A much richer set of psychophysical and computational studies are necessary to determine what quantitatively constitutes normal motor control.

Acknowledgments
This work was supported by McDonnell Center for Higher Brain Research and the Whitaker Foundation.
Event-related fMRI of goal-directed behavior in alert monkeys and humans: spatially-specific and nonspecific signals during delayed response tasks

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Delayed (memory) response paradigms have been used extensively in monkey electrophysiology and more recently in human fMRI studies, to dissociate visual and motor responses and to investigate intervening mechanisms of working memory, movement planning and decision-making. However, the exact relationship between these studies is not clear due to differences in methods and time-scales. In particular, most human imaging experiments utilize much longer delay periods (10-15 s) as compared to 0.5-2 s typically used in monkey electrophysiology. This may result in dissimilar mnemonic and preparatory strategies employed by the two species and thus in a difference in the dynamics of underlying neural signals. Hence, alert monkey MRI studies are necessary to establish a link between large bodies of data accumulated with the two methods, and to interpret BOLD activity in terms of neuronal response.

Here we provide a direct comparison between monkeys and humans with the same tasks and techniques, using a high-field 4.7T vertical scanner for monkeys. We recorded BOLD activity and behavior while subjects made visually- and memory-guided saccades following long variable delays. Extending previous monkey fMRI studies that utilized a block design, we developed event-related analysis of BOLD time-courses, delineating responses from different epochs in the trial – fixation, cue, delay period, saccade execution and reward. In particular, we compared activation patterns preceding visually- and memory-guided saccades to extract persistent “cognitive” signals related to spatial working memory and motor preparation. In monkeys, frontal and parietal areas, including discrete bilateral regions in arcuate (AS), principal (PS), intraparietal (IPS), and superior temporal (STS) sulci, exhibited spatially-specific, contralateral cue and memory/preparation activity (Fig.1A). Event-related time-courses revealed differential activation seen as a separate peak or elevated activation in the middle and late memory period, distinguishable from the early cue response (Fig.1B). In the “no-memory” (visually-guided) condition we observed spatially-nonspecific preparatory signals exhibited as activity ramp-up towards the end of the delay. Consistent patterns were found in functional human homologs, although exact time-course and contribution of these signals varied between subjects and species. Our results demonstrate that dynamics of mnemonic and preparatory signals can be detected in monkeys using event-related fMRI, making it a powerful link between human imaging and monkey electrophysiology.

Acknowledgments: Supported by Moore Foundation, National Eye Institute, Boswell Foundation.

Figure 1. (A) Activation maps for memory delay in slices showing IPS (LIP), STS, and AS (FEF). (B) Event-related average time-courses from the ROI in FEF. Note contralateral delay activation (light blue trace).
The subcortical vestibular system mediates visual context-dependent processing of gravitational motion during interception in humans

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Summary. Human visual sensitivity to acceleration is known to be poor, implying that the brain cannot rely only upon online stimulus trajectory analysis for accurate estimation of ballistic target arrival time. We demonstrate that human subjects can utilize contextual information in a naturalistic visual scene to enhance interception performance for gravitationally accelerating objects. This visual context-driven effect on gravitational motion processing was localized to the midline cerebellum and vestibular nuclei using functional magnetic resonance imaging (fMRI).

Methods. Human subjects (n=33) intercepted virtual accelerating targets overlayed upon either a naturalistic (pictorial) static scene or a blank (non-pictorial) static scene, while undergoing fMRI. In both visual conditions, target spheres ascended vertically from and returned to a central container, moving with randomized initial velocity, and constant acceleration of either gravitational (g, 9.81 m/s²) or non-gravitational (-g), scaled to the size of the objects and apparent viewing distance of the pictorial scene. Interception responses were made with a button press, while subjects maintained fixation on a point on the launch container. The background images of the two visual conditions were matched for color hue and luminance, and target motion was identical.

Results. In both visual context conditions, subjects responded significantly differently to g and –g motion. However, in the pictorial condition, group mean response errors to g targets were close to zero and –g response errors were substantially early, while this g bias was absent in the non-pictorial condition. The visual context effects were maintained across the range of target flight durations. Pooling of mean [g – (-g)] BOLD responses across visual context conditions revealed a pattern of g-sensitive activation in vestibular cortical areas similar to that identified in our earlier fMRI study and proposed as a possible substrate for an internal model of gravity [1]. However, we did not detect significant context-driven modulation of vestibular cortical areas. Instead, an interaction between type of visual context and direction of acceleration (i.e., enhanced g-sensitivity in the pictorial visual context) was localized to subcortical areas comprising the left vestibular nuclei and cerebellar vermis (activation peaks in Lobules VII-X), both known to integrate visual and vestibular information.

Computational implications. The present results show that visual context can influence motion processing in humans, and specifically, available naturalistic visual surround cues positively influence interception performance for gravitational targets. Furthermore, our results are consistent with the hypothesis that subcortical vestibular areas integrate high-level visual analysis with an internal model of gravity [1, 2], this neural ensemble possibly representing the substrate for perceptual constancy of gravitational motion.

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This research was supported by the Italian Ministry of Health, the Italian Ministry of University and Research, and the Italian Space Agency.
Multi-digit movement synergies in an unconstrained haptic exploration task.

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The human hand is extremely dexterous. It is composed of 27 bones that are controlled by 39 muscles with multiple joints that are inter-connected with tendons and ligaments. Although the hand has in excess of 20 degrees of freedom, movements at various joints are not independent, but tightly coupled during object manipulation and recognition. Previous studies of hand motion have analyzed the movements during simple activities such as reaching and grasping [1] or skilled activities such as typing [2]. These studies have revealed that for such simple tasks a very small dimensional space accounts for a large fraction of the observed postural changes. Even individuated finger movements, which are the hallmark of any skilled activity, occur with synergistic couplings between adjacent digits [3].

In the present study we expand on previous findings, and estimate synergistic patterns of hand motion from an unconstrained set of hand postures. Specifically, hand postures were measured, using 23 infrared sensors attached to the hand (Optotrak) while blindfolded subjects explored and identified the curvature, roughness, and sharpness of fifty everyday objects. The objects were chosen to span a large range of size and shapes, and subjects were allowed to explore the objects in any way that they wished. Since the explorations were unconstrained we believe that the evoked postures are a good representative sample of naturalistic postures used during general object manipulation and recognition. Principal component analysis (PCA) on this set revealed that the first seven principal components capture in excess of 90\% of the observed variance. Further, we identified nine vectors (or synergies) that were remarkably similar across multiple subjects. These vectors perform well (capture more than 90\% of the variance) in reconstructing hand postures during novel and skilled task such as D1-D2 pinch grip, D1-D3 pinch grip and D1-D5 pinch grip, but perform poorly in explaining the postures evoked during D1-D4 pinch grip.

Acknowledgments
This work was supported by NIH grants NS34086.

References
Stability of recurrent neural networks with activity-dependent homeostatic scaling of excitability

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Neuronal and synaptic properties show significant plasticity. At the same time, neurons have a limited dynamic range over which they are sensitive to changes in the synaptic input. Consequently, in order for neurons to remain functional, neural excitability needs to be continuously matched to the mean synaptic input level. Experiments have shown that neurons indeed regulate membrane conductances in response to altered input activity levels, thereby changing their excitability on the time scale of many hours up to days¹. This homeostatic scaling of excitability (HSE) can also occur on time scales down to tens of minutes, suggesting that this process has a prominent role in neural functioning on different time scales².

As neurons are embedded in networks, adaptation of the excitability at the single neuron level will affect the dynamics at the network level. This is especially relevant in highly recurrent networks of excitatory and inhibitory neurons, which are ubiquitous in the neocortex. Experimental and theoretical work has illustrated that such networks show a delicate balance between excitation and inhibition for maintaining network stability. Disturbance of this balance can lead either to quiescence or to runaway excitation.

Here we investigated the consequences of HSE for dynamics of recurrent networks, in particular its capacity to compensate for ongoing plasticity and maintain the network in a functional state where all cells function within their dynamic range. We addressed this issue using both mathematical analysis and numerical simulations. First, we analyzed the requirements for stability of adapting recurrent networks using a mean-field approach, describing the activity levels of interacting excitatory and inhibitory neurons at the population level. Based on experimental results, HSE is implemented as activity-dependent shifts of the input-output function². The results show that stability of the adapting network depends critically on the relationship between the adaptation time scales of the two neuron populations combined with their respective input-output gains. We subsequently modeled recurrent networks consisting of excitatory and inhibitory leaky integrate-and-fire neurons showing HSE. The results confirm that stability of such networks requires a specific relationship between the time scales of adaptation: inhibitory neurons need to adapt sufficiently slow compared to the excitatory neurons. We find that in stable, adapting networks, HSE can maintain all neurons in the network in a functional state, rendering network activity robustly stable for varying levels of input. HSE can also, up to a certain limit, compensate for changes in network connectivity, e.g. resulting from synaptic plasticity or degenerative loss of neurons. However, while HSE can keep neurons in their dynamic range under such conditions, it will affect the risk of network instabilities. This suggests that the interplay of HSE (single cell intrinsic properties) and network level processes (connectivity changes) may play a significant role in pathological conditions, such as epilepsy.


Theories of Pattern Adaptation in the Retina

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Pattern adaptation, namely the adaptation of neural sensitivity to spatial correlations in the visual input, is well documented in the visual cortex. For example, the response to a grating stimulus of a given orientation wanes under prolonged stimulation, without suppression of the response to the orthogonal orientation. Such pattern-specific adaptation is almost universally explained as resulting from the depression or fatigue of neurons selective for the orientation present in the sustained stimulus. This view ascribes pattern adaptation to the cortex and discounts the possibility of similar sophisticated adaptation at earlier stages in the visual pathway, because these are devoid of pattern-tuned cells.

Recent experiments demonstrate that pattern adaptation occurs as early as in the retina [1]. For example, under stimulation by a flickering vertical grating, ganglion cells partially lose their sensitivity to inputs with vertical spatial correlations while retaining sensitivity to inputs with horizontal correlations. This adaptation phenomenon and the ensuing recovery occur on a time scale of a few seconds. How do ganglion cells achieve pattern-specific adaptation in the absence of pattern-tuned presynaptic cells? To detect spatial correlations, ganglion cells must compare inputs originating from distant points on the retina. Thus the explanation must involve a presynaptic network, rather than purely local adaptive mechanisms. Here, we discuss two competing models that may explain pattern adaptation in ganglion cells. They combine known properties of synaptic dynamics with identified aspects of retinal circuitry.

Model 1 was sketched in previous work [1], and relies upon correlation-based strengthening of amacrine-to-ganglion cell synapses. These synapses pick up correlations in the visual input and deliver a proportionate amount of inhibition to postsynaptic ganglion cells, thus counter-acting excitation in a pattern-specific manner. The principle amounts to a form of anti-Hebbian learning that serves to reject prominent patterns in the input. Model 2 is introduced in the present work. It relies on the activity-dependent depression of bipolar-to-ganglion cell synapses. Many bipolar terminals receive afferents from an amacrine cell; the so-formed diad synapses are excitatory, but their strength is modulated by inhibition. If the inhibitory input is anisotropic in space, for example if only one or a few amacrine cells contribute to it, then the diad synapse can act as a ‘mini pattern-detector’, which adapts due to synaptic depression.

Both models are formulated in terms of simple nonlinear differential equations involving few parameters: a gain and a time scale. From these equations, one can derive the adaptive evolution of the ganglion cell’s receptive field as a function of the visual input. This treatment recommends new experiments that could distinguish the two synaptic mechanisms based on ganglion cell recordings alone. We illustrate this point with an example experiment.

The models discussed here may be relevant to other instances of correlation adaptation, beyond retinal processing, and they extend the repertoire of neural mechanisms that can perform this important computation.

Ising models for networks of real neurons

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Ising models with pairwise interactions are the least structured, or maximum-entropy, probability distributions that exactly reproduce measured pairwise correlations between spins. Schneidman et al [1] have used such models to describe the correlated spiking activity of populations of neurons in the salamander retina subjected to naturalistic stimuli; they show that for groups of N≈10 neurons (which can be fully sampled during a typical experiment) these models with O(N²) tunable parameters provide a good description of the full distribution over 2ᴺ possible states.

Here we analyze the same recordings and use Monte-Carlo-based methods to construct the appropriate Ising model for the complete 40-neuron dataset [2]. We show that pairwise interactions still account for the observed higher-order correlations and argue why the effects of three-body interactions should be suppressed. We furthermore examine the thermodynamic properties of Ising models of various sizes derived from the data. This allows us to suggest a statistical ensemble from which the observed networks could have been drawn and, consequently, to create synthetic networks of 120 neurons. We find that with increasing size the networks operate closer to a critical point and start exhibiting collective behaviors reminiscent of spin glasses; among these, we examine more closely the appearance of multiple single-spin-flip stable states.

Acknowledgments
This work was supported in part by NIH Grants R01 EY14196 and P50 GM071508, by the E. Matilda Zeigler Foundation, by NSF Grant IIS–0613435 and by the Burroughs Wellcome Fund Program in Biological Dynamics.

References

Symmetry and Periodic Solutions in Canal-Neck Network

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The vestibular system in almost all vertebrates, and in particular in humans, controls balance by employing a set of six semicircular canals, three in each inner ear, to detect angular accelerations of the head in three mutually orthogonal coordinate planes. Signals from the canals are transmitted to eight groups of neck motoneurons, which activate the eight corresponding muscle groups. These signals may be either excitatory or inhibitory, depending on the direction of acceleration. McCollum and Boyle [1] have observed that in the cat the network of neurons concerned possesses octahedral symmetry, a structure that they deduce from the known innervation connections from canals to muscles.

We re-derive the symmetry from mathematical features of the probable network architecture, and model the movement of the head in response to the activation patterns of the muscles concerned. We assume that connections between neck muscles can be modeled by a system of coupled ODEs whose variables correspond to the eight muscles. The network and its symmetries imply that these ODEs must be equivariant under a suitable action of the octahedral group.

We show that with the appropriate group actions, there are six possible spatiotemporal patterns of time-periodic states that can arise by Hopf bifurcation from an equilibrium representing an immobile head. Counting conjugate states, whose physiological interpretations can have significantly different features, there are 15 patterns of periodic oscillation, not counting left-right reflections or time-reversals as being different. We interpret these patterns as motions of the head and note that all six types of pattern appear to correspond to natural head motions.

Acknowledgments
This work was supported in part by NSF Grant DMS-0244529. The work of IS was supported in part by a grant from EPSRC.

References
Separate image durations activate distinct neuronal populations in the human medial temporal lobe.

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Previous experiments have demonstrated that neurons in the human medial temporal lobe (MTL) may respond differentially to visual categories when human observers performed a face/non-face discrimination task in images presented for 1000 ms [1]. This presentation duration, however, is much longer than needed to perceive an object and perform a simple discrimination task [2]. Thus, it is unclear whether category-specific neurons, as well as image-specific neurons, would be observed for durations shorter than 1000 ms.

To examine the effect of duration on category selective visual responses in the MTL, we varied presentation duration from 800, 500, to 300 ms. 15-20 pictures, selected from 5-6 image categories (animal, building, famous people, indoor scene, outdoor scene, and tools) were shown. Subjects were pharmacologically-resistant epilepsy patients who had undergone intracranial electrode implantation. Primary recording sites were in the medial temporal lobe (including the hippocampus, amygdala, and entorhinal cortex) and occasionally in the frontal lobe, as determined by clinical criteria. The patients performed a face/non-face discrimination for each of the images.

We identified 42 well isolated neurons recorded from three patients. Neural responses were first tested for a category selective visual response at each of the 3 durations (response during 0-1000 ms from the onset of stimulus, 1-way ANOVA, p<0.05). Table 1 shows the number of neurons with category selective responses during each of the 3 durations and their combinations. The vast majority of neurons respond to only a single duration. A 2-way ANOVA (p<0.05) of the responses as a function of image duration and image category showed that 20 of 42 neurons had a primary effect of image duration.

These findings suggest that separate populations of neurons within the human medial temporal lobe are activated by different durations of presentation and may have separate cognitive functions in memory or learning.

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Table 1. Number of neurons responded at specific durations or at a number of durations.

Acknowledgments
This work was supported by the Whitaker Foundation (RG-01-0422) and the James S. McDonnell Foundation (20002058).

References

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Two-Color, Bi-Directional Optical Voltage Control of Genetically-Targeted Neurons

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Much effort in neuroscience is devoted to determining the contribution of neural activity in specific brain regions or neuron classes towards specific behaviors, neural computations, and pathological states. This quest would be greatly aided by a technology that enables rapidly inducible and reversible neural activation and inactivation at the millisecond timescale, while having no side effects on cell physiology or survival, and requiring no exogenous chemicals to be delivered. Having found a powerful method for activating neurons with blue light in the protein Channelrhodopsin-2 (ChR2) \cite{1}, we sought to augment the toolbox by finding a single-component system capable of mediating light-elicited neuronal inhibition. We identified a powerful tool, the mammalian codon-optimized version of the light-driven chloride pump halorhodopsin, from the archaebacterium \textit{Natronobacterium pharaonis} (here abbreviated Halo) \cite{2}.

We report that cultured hippocampal pyramidal neurons expressing Halo-GFP under the CaMKII promoter experienced strong hyperpolarizations (> -20 mV) upon exposure to brief pulses of moderate-intensity yellow light (~565 nm). In the absence of light, Halo-expressing neurons were physiologically indistinguishable from wild-type neurons. Halo could mediate 100\% optical blockade of neuronal spiking induced by somatically injected intracellular current pulses (~300 pA), with millisecond-timescale onset and offset of the blockade (\textit{right}). In addition, Halo could mediate naturalistic trains of inhibitory voltage deflections at physiologically relevant frequencies, with almost no attenuation of voltage amplitude from pulse to pulse. We also demonstrated that in individual neurons expressing both yellow-light driven Halo and the blue-light driven cation channel ChR2, neural inhibition and excitation could be efficiently driven and independently controlled at the millisecond timescale, by interleaving brief pulses of yellow and blue light (\textit{left}). Thus, Halo powerfully extends our ability to analyze and engineer neural circuits, and will facilitate determination of the time-resolved causal roles of specific neurons and neural activity patterns in behavior, computation, and disease.

\textbf{Acknowledgments}

Thanks to R. Needleman, J. Tittor, J. Lanyi, S. Erdman, and members of the MIT Center for Bits and Atoms and the MIT Media Lab for sharing reagents, advice, and equipment. This work was funded by an anonymous donor and the MIT Media Lab (E.S.B.), and the Helen Hay Whitney Foundation (X.H.).

\textbf{References}

Emotional and Behavioral Responses to the Devaluation of Stimuli by Satiation: a Computational Model

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A neural network model is proposed that addresses how motivation influences the learning and valuation of Pavlovian stimuli. The model takes a neural systems approach, representing neurons with membrane equations and brain areas as regions distinguished by specific afferent and efferent connections. Model outputs are directly comparable with experimental recordings. Brain regions in the model fall into four functional classes: \textit{Perceptual}—registering visual or gustatory inputs (inferotemporal and rhinal); \textit{Drive}—calculating the value of anticipated outcomes (amygdala and hypothalamus); \textit{Incentive}—resolving the value of competing stimuli (orbitofrontal); and \textit{Adaptive Timing}—detecting the omission or delivery of rewards (basal ganglia and SNc/VTA). Sensory, drive, and incentive regions are linked to form a circuit that mediates incentive-based control of attention.

Free reward, Pavlovian conditioning and simultaneous visual discrimination tasks are simulated. The model replicates behavioral, autonomic, and electrophysiological data observed during the learning and performance of these tasks both before and after associated food reinforcers are devalued by food-specific satiety. Simulated lesions replicate previous data and make novel predictions regarding amygdala and orbitofrontal cortex. The model replicates data showing conditioned but not unconditioned stimulus processing is impaired with respect to blood pressure and reinforcer devaluation following amygdala lesions [1][2]. The model predicts that amygdala lesions impair dopamine bursting responses to conditioned but not unconditioned stimuli. The model replicates data showing orbitofrontal lesions impair conditioned but not unconditioned responses following reinforcer devaluation [3]. The model predicts orbitofrontal lesions do not strongly impair blood pressure or dopamine bursting responses. In the visual discrimination task reinforcer devaluation by food specific satiety leads to changes in cue preference which are disrupted by lesions of the amygdala and orbitofrontal cortex [4]. The model replicates these data and predicts that differences in reaction time are also disrupted following amygdala lesions.

Acknowledgments
Partially supported by NSF grant SBE-0354378 for CELEST, hosted at Boston University.

References
Population dynamics during timing behavior in the rat prefrontal cortex

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Survival depends on being in the right place at the right time. Animals are able to keep track of elapsed time from the occurrence of behaviorally relevant events, and to act at the appropriate moment in order to, e.g., obtain a reward, or avoid a punishment (see e.g., [1]). As with any timing device, the neuronal signals used by the brain to read out elapsed time must change during the relevant interval, and must be reliable, so that whenever the amount of elapsed time since a relevant event is the same, their state should also be approximately the same. In this way time could be inferred from the current activity of the appropriate neuronal population. This scheme, however, poses a challenge for such a signal to be instantiated in the spiking activity of cortical neurons, since neurons are usually quite unreliable. When examining the responses of cortical neurons during a behavioral task across repeated trials, it is usually found that the variance in the spike-count is approximately proportional, or even higher, than the mean (see e.g., [2]).

In order to investigate this issue we recorded the simultaneous activity of neuronal ensembles from the medial prefrontal cortex of rats performing a timing task that requires them to make a single, temporally precise response, a few seconds after a sensory cue. We found that a substantial fraction of the cells we recorded are unusually reliable, with variance-to-mean spike count ratios as low as 0.3 in time windows of a few hundred milliseconds. This reliability is present despite relatively low firing rates on the order of 10 Hz. The reliability we observe is not the product of precise spike timing across trials, but rather of rhythmic, or regular, spiking. These cells show wide troughs in their auto-correlograms and different measures of inter-spike interval (ISI) variability (designed to take into account slow modulations in firing rate) reveal coefficients of variation significantly smaller than one.

A majority of cells in our current data-set are more faithfully locked to the animal’s motor response (the time of which varies from trial to trial) than to time per se, so that time discrimination from this neuronal population is not possible throughout the trial. Discrimination is, however, possible on the few seconds before the motor response, with an accuracy on the order of one second. By generating artificial Poisson data, we directly assess the relevance of the spiking statistics of the recorded cells regarding time discrimination.

This research might contribute to the establishing of a quantitative framework for the understanding of the neurophysiological basis of self-timed behavior.

Acknowledgments
This work was supported by NIH grant R01MH073245.

References

Exact Neural Inference Over Graphical Models

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There is increasing neurophysical evidence that the brain performs Bayesian inference in a number of experimental paradigms including cue integration, visual scene processing, and decision making. However, as the probability distributions become more complex, it becomes more difficult to integrate out irrelevant variables to find the marginal posterior probabilities of specific variables. So, computationally, it is common to use graphical data structures to represent the dependencies between variables. We present a neural model that performs exact inference over abstract variables in graphical models. In our model, the posterior estimates of variables are proportional to the mean firing rates of idealized biologically plausible two-level neurons \cite{1}. The relations among the variables are stored as the gain of synaptic regions and are represented as conditional probability distributions. The gains are updated incrementally using a generalized Hebbian learning rule corresponding to Bayesian updating. In this way, the neural circuit uses each evidence both to update posterior estimates of the variables quickly and to learn about the relationships between the variables over a longer time scale.

We illustrate the ability of our neural model to estimate conditional probabilities on-line and then apply the learned conditional probabilities using the cue-integration task. Humans combine location estimates formed through vision and proprioception using dimension dependent variances. A Bayesian model has been applied to this combination in, for example, Deneve and Pouget \cite{2}. As opposed to previous works, our method allows Bayesian estimation of the modality specific distributions from the inputs. It performs a Bayesian optimal inference using the learned variances. Also, our network is significantly smaller and sparser than previous neural models of this task.

Figure 1: Results from neural inference along two perceptual dimensions: distance and azimuth. Crosses indicate the Bayesian optimal cue integration for each of three experimental conditions A, B, and C each of which have different sense/dimension dependent variances. Points indicate the output of the network clustered around the Bayesian optimal estimate.

References

Persistent activity in neural networks with dynamic synapses

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Persistent activity states (attractors), observed in several neocortical areas after the removal of a sensory stimulus, are believed to form the neuronal basis of working memory. One of the possible mechanisms that can underlie persistent activity is recurrent excitation mediated by intra-cortical synaptic connections. A recent experimental study revealed that connections between pyramidal cells in prefrontal cortex exhibit various degrees of synaptic depression and facilitation [1]. Here we analyze the effect of synaptic dynamics on the emergence and persistence of attractor states in interconnected neural networks. We show that different combinations of synaptic depression and facilitation result in qualitatively different network dynamics with respect to the emergence of the attractor states. When every attractor consists of several interconnected sub-populations with diverse synaptic dynamics, the persistent state can be made selective to the temporal profile of the stimulus in addition to its spatial characteristics. This is illustrated in the in the Figure below, where we show the activity in the network of two inter-connected subpopulations receiving identical stimulus of two different durations. For the short stimulus, the subpopulation with depressing synapses converges to the persistent state, while for the long stimulus the subpopulation with stronger synaptic facilitation is in the persistent state. This analysis raises a possibility that the framework of attractor neural networks can be extended to represent time-dependent stimuli.

Acknowledgements:

We thank Barak Blumenfeld for fruitful discussions. The work was supported by Israeli Science Foundation and Irving B. Harris Foundation.

References:

Separation of the Cortical Spectrum to Examine Large Scale Network Dynamics

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We begin with our recent experimental electrocorticographic (ECoG) findings that demonstrate focal (<1 cm) task-related change on the human cortical surface with 10 millisecond resolution (shown in figure below). By decomposing the ECoG power spectrum using Independent Components Analysis (ICA), we are able to reveal that there are different processes with fundamentally different characteristics that can be resolved on this scale. The evolution of these processes in relation to the temporal dynamics of well-characterized motor tasks reveals separable dynamics, which we attribute to distinct cortical processes. These fall loosely into two categories, those that are local and revealed by spectrally broad power law components, and those that are spectrally narrow and due to the interplay between the cortical surface and sub-cortical structures (e.g. thalamus and basal ganglia). We implement a model for this using a simplified neuronal view with recurrent input from local populations and feed-forward and feedback interactions with distant (sub-cortical) areas. This model demonstrates how the large-scale network dynamics measured by ECoG could be produced and revealed in the spectra we measure experimentally. Changes in the influence of the thalamic portion of the model explain recent experimental results which showed diminished spectral change with focal thalamic lesions in humans[1]. We also use the model to demonstrate why the low and high frequency changes in the ECoG spectrum with activity have characteristically different spatial distribution [2] and different across-channel coherence.


Correlations and population dynamics in cortical networks

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The dynamics of large recurrent networks of excitatory and inhibitory spiking neurons was extensively studied by various authors using a mean field approach. Based on a Fokker-Planck equation describing the dynamics of the membrane potential distribution for a diffusion approximation, stationary firing rates of the population could be successfully predicted. In the inhibition dominated regime and for weak external inputs dynamic states of the network were anticipated, that are characterized by irregular firing at low rates and asynchronous global dynamics—a combination of properties that is commonly attributed to cortical activity in behaving animals [1]. In numerical simulations we found, however, that networks in this regime display residual transient synchronizations leading to a strongly fluctuating population activity. This phenomenon was previously classified as a "finite size effect" that is negligible for very large networks. Here, we show that the theory is exact already for comparably small networks, if we neglect the functional segregation of inhibition and excitation. We explain why structural correlations strongly increase the impact of shared input, and how this affects the variance of the population activity. A modified two-population mean field theory indeed captures quantitative features of the population power spectra. We emphasize that it is not the antagonistic action of two neuron populations, but rather the abundant pairwise correlations ignored so far, that lead to the observed synchronicity in this regime.

Figure: Networks with cortex-like (A,C) vs. randomized distributions of synaptic signs (B,D) exhibit strong differences in their activity dynamics. (A) and (B) depict the imposed wiring schemes. Black represents positive, gray negative weights, white stands for absent synapses. Columns encode the output of neurons, rows stand for the inputs. (A) shows a network where neurons have either only excitatory or only inhibitory outgoing synapses, whereas (B) is a network where individual neurons can have both at the same time. The network topology and mean input to each neuron, however, are exactly the same in both cases. (C) shows a raster plot of 1,000 excitatory (black) and 1,000 inhibitory (gray) neurons from an (A)-type network comprising 10,000 excitatory and 2,500 inhibitory neurons, while (D) shows a simulation for the according (B)-type network. Inhibitory synapses were 6-fold stronger, all other parameters are according to [1].

Acknowledgments
Funding by BMBF grant 01GQ0420 to the BCCN Freiburg is gratefully acknowledged.

References
Sensitivity and invariance to natural stimulus variations in the neural discrimination of songs in field L of the songbird

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To correctly recognize and discriminate between natural stimuli, a sensory system must be able to deal with the natural variations in the stimuli. However, relatively little is known about the sensitivity or invariance of neural representations to such perturbations in the auditory system. Songbirds can discriminate between and recognize individuals despite natural variations in their songs. Motivated by this behavioral observation, we investigated the invariance in neural discrimination of songs in field L (the analogue of primary auditory cortex) in the zebra finch.

We examined invariance to two types of stimulus perturbations that occur naturally: 1) variations in intensity, which could be caused by a change in the distance to the source and 2) multiple renditions of the same bird's song which contain timing differences. Previously, we have quantified the accuracy of neural discrimination using a classification of neural spike trains based on the spike distance metric. Here, we investigated whether neural spike trains could be correctly classified, despite the variations in intensity and in renditions.

We found some cells that are highly sensitive to intensity and others that are intensity invariant over a broad range of stimulus amplitude. A varying amount of invariance was also observed in different field L neurons to different renditions of individual songs. Our results indicate that although some neurons in field L are sensitive to variations in intensity (n = 20) and renditions (n = 21), a subset of neurons are relatively invariant to such perturbations (n = 5, 4 for intensity and renditions, respectively). These invariant cells may contribute to the ability of songbirds to discriminate between and recognize conspecific individuals in the face of natural stimulus variations.

Acknowledgments
This work was supported by NIDCD, NIH (Grant# 1 RO1 DC007610-01A1).
Information rates and redundancy in the responses of striate cortical cells to natural movie stimuli

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When presented with simple stimuli like bars and gratings, adjacent neurons in striate cortex exhibit responses that are thought to be highly redundant. On the other hand, when presented with complex, time-varying natural scenes (i.e. movies), striate neurons exhibit high population sparseness, as well as high lifetime sparseness [1,2]. This raises the question of how much redundancy might be found in the responses of adjacent neurons to movie stimuli, and how the redundancy changes with distance between the neurons. We investigated this question by simultaneously recording the responses of groups of neurons in cat striate cortex to the repeated presentation of movies using silicon probes in a multi-tetrode configuration. The movies used in this experiment were 30 s long and were repeated 100 times.

Using the direct method [3,4], we calculated the information rates of 48 single cells, as well as 45 pairs of cells simultaneously recorded on the same tetrode (intra-group) and 53 pairs of cells recorded on tetrodes separated by at least 150 um (inter-group). For the single cells, we found a maximum mutual information rate of 20 bits/s, a minimum rate of 0.14 bits/s, with medians and quartiles at 3.6, 1.8, 6.0 bits/s respectively. The intra-group pairs had a maximum joint information rate of 15 bits/s, a minimum rate of 1.2 bit/s, and medians and quartiles at 7.1, 5.4, 9.4 bits/s. The inter-group pairs, on the other hand, had a maximum rate of 16 bits/s, a minimum rate of 1.6 bits/s, and medians and quartiles at 7.4, 5.4, 11 bits/s. The intra-group and inter-group distributions were not significantly different (two-sample Kolmogorov-Smirnov test. p=0.66).

We also used a synergy measure [5] to compare the joint mutual information rates to the sum of the individual information rates. This measure was normalized so that a value of 0 indicated independent coding, a value of -1 indicated maximal redundancy, while a value of 1 indicated maximal synergy. 27 of the intra-group pairs were synergistic (60%) while the other 18 pairs were redundant. For the inter-group pairs, 32 were synergistic (60%) while the other 21 were redundant. The median and quartiles for the intra-group pairs were 5.9x10^{-3}, -2.1x10^{-2}, 4.5x10^{-2}, while those for the inter-group pairs were 5.8x10^{-3}, -1.5x10^{-2}, 1.2x10^{-1}. A two-sample KS-test did not find any significant differences between these two distributions (p=0.53).

Our results indicate that when stimulated with natural movies, pairs of adjacent neurons encode just as much information as pairs of neurons that are separated by at least 150 um. Our results also suggest that the responses of adjacent neurons may not be as highly redundant as previously thought.

References
Model-based decoding, information estimation, and change-point detection in multi-neuron spike trains

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The neural decoding problem is of fundamental importance in computational and systems neuroscience: given the observed spike trains of a population of cells whose responses are related to a behaviorally-relevant signal \(\vec{x}\), how can we estimate, or “decode,” \(\vec{x}\)? Solving this problem experimentally is of basic importance both for our understanding of neural coding and for the design of neural prosthetic devices.

Here we introduce several decoding methods based on point-process neural encoding models (i.e. “forward” models that predict spike responses to novel stimuli). These models incorporate stimulus dependence and spike-history effects (such as refractoriness or bursting), and can also include multineuronal terms corresponding to the excitatory or inhibitory effects between cells. Importantly, these models have concave log-likelihood functions, allowing for simple, efficient fitting of the model parameters via maximum likelihood \([1, 2]\). This concavity property also applies to the stimulus \(\vec{x}\), implying that we can tractably perform stimulus decoding by maximizing the likelihood with respect to \(\vec{x}\). We present a tractable algorithm for computing the maximum a posteriori (MAP) estimate of the stimulus — the most probable stimulus to have generated the observed single- or multiple-spike train response, given some prior distribution over the stimulus. In certain cases we demonstrate that it is possible to decode very high-dimensional stimuli (e.g., \(\dim(\vec{x}) \approx 10^4\)) with minimal computational effort.

We can further exploit this concavity property by deriving a simple and accurate Gaussian approximation to the posterior distribution \(p(\vec{x}|D)\) of the stimulus \(\vec{x}\) given the observed spiking data \(D\). This Gaussian approximation allows us to: (1) quantify the fidelity with which various stimulus features are encoded; (2) develop an efficient, highly tractable method for estimating the mutual information between the stimulus and the response (interestingly, this estimator indicates that the standard linear reconstruction lower bound technique \([3]\) can lead to significant underestimation of the true information); and (3) establish a framework for the optimal detection of change-point times (e.g. the time at which the stimulus undergoes a change in mean or variance), by marginalizing over the posterior distribution \(p(\vec{x}|D)\). We show a variety of examples illustrating the performance of these estimators with simulated data.

Acknowledgments
JP is funded by an International Research Fellowship from the Royal Society; LP is supported by grant EY018003 from the NEI and by a Gatsby Foundation Pilot Grant.

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The KARMA of Hand Tracking

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The usage of machine learning algorithms to decode intended behavior from neural activity serves a dual purpose. First, these tools can be used to allow subjects to interact with their environment through a brain-computer interface. Second, analysis of the characteristics of such methods can underscore the significance of various features of neural activity, stimuli and responses to the encoding-decoding task. In this work we propose and test a machine learning method, called Kernel Auto-Regressive Moving Average, or KARMA in short, for the task of tracking hand movements, executed by a monkey in a standard motor control task, from neural spiking activity in primary motor cortex.

KARMA uses both past observations (neural activities) and past predictions (movement parameters) to make the next prediction. In the model used by KARMA one may learn to predict not only target values (hand positions) but also auxiliary features, which can be used to improve modelling of the dynamics and the prediction of the target values. For example, we predict hand velocity and acceleration and use them to better predict hand position. Other features of the task, such as distance to target, can also be estimated and incorporated into the prediction of future behavior. Unlike the standard ARMA model which is a linear model, KARMA uses non-linear similarity functions (termed kernels) to compare between tuples of (observed) neural activities and (previously predicted) motor task parameters. These kernels can be specified by the user of the algorithm to tell it how to measure the amount of similarity between pairs of tuples.

In this work we compare KARMA to several state-of-the-art methods. We used correlation coefficients (CC) between true and predicted hand positions as the measure of success. Each method was fitted with its optimal hyper-parameters by selecting the parameters that achieved best test results in 5-fold cross validation on one of 9 daily recording sessions. Results are reported on test data using 5-fold cross validation and performed on the remaining 8 sessions. We explain the differences between the methods and interpret the demonstrated superiority of KARMA (figure 1) as an indication that the algorithmic differences are important for understanding the motor control task. For example, when KARMA is implemented with an AR degree of 0 it reduces to standard support vector regression (SVR) and no longer possesses a movement model. When KARMA is used with linear kernels it reduces to ARMA and is no longer a non-linear method. We also compare KARMA with Kalman filtering (KF) which possesses both a model of state dynamics and models of system noise but lacks the kernel induced non-linearities. In figure 1, KF1 is standard KF and KF10 uses the same MA degree of 10 as KARMA. Our main conclusion is that both the nonlinear dynamics and interpretation of neural activity are key elements in the hand tracking task.

Acknowledgments

This study was supported by BMBF-DIP, GIF grant no. 1-773-8.6/2003, BSF, and by the Johnson & Johnson Fund for Innovative Science.

Figure 1: Win scores. Each node is an algorithm. Each directed edge tells % of time that the algorithm above achieved a better CC on test data than the algorithm below.
The tilt illusion, population decoding, and natural scene statistics

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Context exerts a dramatic influence on neural processing and sensory experience. Perceptually, the presence of contextual information at a given point can elicit striking misjudgements of local features, such as orientation and motion. This is manifest in illusions and aftereffects, which have been a topic of intensive study for decades. Perceptual illusions are most puzzling when contexts induce distortions that appear inconsistent with their statistically normative implications, as their functional role then is quite mysterious.

Here we focus on one of the best studied contextual effects, namely the influence of spatial surround on local orientation misjudgements, i.e., the tilt illusion. We build computational models that treat populations of orientation-tuned neurons in primary visual cortex in statistical terms, and link the outputs of such populations with the perceptual phenomena they appear to underpin.

Specifically, we consider neural-level models of divisive gain control. This idea has a rich mechanistic and functional pedigree. We formulate a generative version of divisive gain control as part of a well-found model of natural image statistics (so-called Gaussian Scale Mixture Models). We then ask how this model leads to changes in tuning curves, and consequently, through population decoding, to misjudgements in the tilt illusion.

Previous work has shown that in natural scenes, filters with similar orientation preferences that represent nearby locations in the image have strong statistical dependencies, and so are, correctly, members of the same divisive gain control pool. We demonstrate that through population decoding, this contextual normalization leads to tilt repulsion. However, an interesting consequence of contextual effects, as in the tilt illusion, is that the nature of the misjudgements can be either repulsive or attractive, depending on factors such as the relative angle between the center target and surrounding context stimuli. Although the repulsive effect has been most widely modeled, the (weaker but consistently present) attractive effect is also diagnostic of the system behavior. We formulate a variant of the model that obtains both attraction and repulsion. The modified model assumes a more sophisticated scheme, in which the target and spatial context filters have a probability of belonging to the same gain control pool.

Although tilt and spatial context is a particularly convenient example for which there are many diverse data, most of the underlying issues extend to other visual attributes and contextual phenomena.

Acknowledgments
We are grateful to Anne Hsu for helpful discussions. This work was supported by HHMI and the Gatsby Charitable Foundation.
Tempotron Decoding of Spike Patterns from Retinal Ganglion Cell Populations

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Vision relies on the transmission of information from the eye to central brain regions via the activity of retinal ganglion cells. This activity exhibits stimulus-dependent variations in firing rate as well as in the precise timing of spikes, which can be strongly correlated between neurons[1]. It is still unclear, however, how these response features underlie accurate and rapid analyses of complex visual images. In particular, it remains to be shown how downstream brain areas can read out the information contained in the spatio-temporal spike patterns of ganglion cells.

To address this question, we used a recently developed, biologically plausible model neuron (tempotron[2]) to decode spike trains that were simultaneously recorded from ganglion cells in the isolated salamander retina. The model is based on an integrate-and-fire neuron, which receives the recorded spike trains as synaptic input. We used the tempotron learning rule to adjust the synaptic weights, thus training the neuron to discriminate between different stimulus conditions on the basis of the spatio-temporal spike patterns in the ganglion cell population. The visual stimuli used in this study consisted of briefly presented spatial gratings for which both spatial phase and contrast level were varied independently. Retinal ganglion cells responded to these stimuli with precisely timed bursts of spikes[3].

We found that the tempotron can successfully learn to discriminate between the spatial phases or contrast levels of the presented visual stimuli. Moreover, testing the performance of the model on data that combine variations in phase and contrast showed that decoding can be performed in a contrast-invariant manner. We quantified how this performance depends on decision time, size of the considered neural population, and on spike correlations between different neurons. Our results highlight the biological plausibility of spike-timing based population codes in early visual processing.

Acknowledgments
This work was supported by the Minerva Foundation, the HFSP, the NIH, and the ISF.

References
Direct measurement of “suppression” in the LGN in the context of natural stimuli and its implications for visual coding

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Some of the greatest advances in neural coding have occurred in the visual system, where the relationship between visual stimuli and the observed neuronal activity is relatively straightforward. However, experiments that probe this relationship in more “natural” contexts have revealed many higher order aspects of visual neuron responses, such as their precise timing down to milliseconds, adaptation to contrast, and non-linear summation of multiple stimuli. Here, we describe a new modeling framework applied to LGN neuron data recorded in the context of both artificial noise stimuli and “natural” movies. The basis of this model is the familiar “LN” (linear-non-linear) cascade model based on a linear spatiotemporal receptive field (STRF), but adds a second “suppressive” STRF with different tuning properties. Extending the maximum-likelihood estimation framework proposed by [1], we simultaneously fit both spatiotemporal receptive fields using a modest amount of recording time in the context of both artificial “noise” stimuli and natural movies.

The resulting model reveals the rich computation performed by LGN neurons and accurately describes their responses to both simple (such as spatially homogeneous) and complex “natural” stimuli. [Because we use maximum likelihood estimation, the model can be applied to highly correlated stimuli (such as natural movies) as easily as to uncorrelated “noise” stimuli, permitting a direct comparison.] In addition to providing an improved prediction of the observed LGN neuron responses (i.e., significantly higher likelihood using data not included in the original fit), this “suppression model” captures much of the temporal precision observed experimentally, because the suppressive STRF is mostly overlapping but temporally delayed compared with the linear STRF. Furthermore, suppression may also be related to other “higher-order” features of LGN responses: for example, the relative strength of suppression increases with contrast, which reproduces many of the effects of “contrast gain control” [2,3]. The suppressive STRF likely derives from particular elements of retinal processing (e.g., [4]), but this modeling reveals more general computational principles that arise through commonalities in neuronal processing present across sensory areas. Thus, in accounting for several disparate higher-order elements with a tractable computational model, we can understand their role in the processing of natural vision.

Acknowledgments
This work was supported by NIH-EY05253 and SUNY Research Foundation (CW, JZJ, CIY, JMA) and NGIA Grant HM1582-05-C-0009 (NAL, GBS).

References
Spatial selectivity and theta phase precession in CA1 interneurons

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The traditional hypothesis has been that most of the information processing of neural networks is carried out by excitatory cells, which send out their axons to downstream structures. In the cortex, including in the hippocampus, inhibitory neurons are present in a lower proportion than excitatory cells and have local processes. These characteristics have led to the idea that interneurons merely modulate the global activity of the network through nonspecific suppression of excitability. However, based on their exquisite diversity and complex functional characteristics, there is now growing evidence that interneurons might play a much more refined role than initially thought.

In the CA1 region of the rat hippocampus, pyramidal cells discharge selectively when the animal is in specific locations in its environment, called the place fields of the cells. Furthermore, the firing exhibits a precise relationship with the ongoing rhythmic activity of the network: as the rat traverses a place field, spikes display progressively earlier phases relative to the theta oscillation (phase precession). Thus both rate coding and temporal coding coexist in this region, at least in the excitatory population.

The goal of this study has been to investigate the spatial selectivity and theta phase dynamics of interneurons in CA1. We recorded the activity of both excitatory and inhibitory cells using the multi-tetrode recording technique, as well as the continuous local field potential from the stratum radiatum for the theta rhythm. Rats ran repeatedly back and forth for food reward on a linear circular track. Spatial selectivity was quantified by the mutual information between the firing rate of the neurons and the location of the animal. Using this measure, inhibitory interneurons showed robust and stable spatial selectivity. As previously reported in the literature, we observed strong phase locking of interneuron firing to the theta rhythm. Furthermore, on sections of the track, the range of theta phases shifted progressively to earlier parts of the theta cycle as the rat advanced, so that a negative correlation between phase and position could be demonstrated in single interneurons. These spatially-restricted segments of phase precession coincided with local peaks in the firing rate.

These results indicate that spatial selectivity and phase precession in CA1 are not properties restricted to pyramidal cells. Rather, they may be a more general expression of a common interaction between the different inputs impinging on both excitatory and inhibitory cells in CA1 and the intrinsic characteristics of those cells. This hypothesis is discussed in the framework of a simple model of phase precession. We conclude that the role of interneurons may extend beyond a global damping of the network by participating in a finely-tuned local processing with the pyramidal cells.

Acknowledgments
This work was supported by NIH, RIKEN Institute, and The Human Frontier Science Program Organization (Long-Term Fellowship to VES).
Information theoretic quantification of neural transmission following changes in release probability

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Neurons are complex transmitting devices which encode information in terms of digital spike trains and communicate at the synapses, where the incoming spikes are converted into analog signals by elaborated nonlinear transformations. Synapses undergo long-term plasticity, which affects neuronal computation through changes in neurotransmission dynamics [1,2]. Although this observation has opened new perspectives on the biophysical basis of learning and memory [3], its consequences on the information transmission of a neuron remain only partially understood. One major obstacle is the computational complexity and the high dimensionality of the input-output space of a neuron [4], which makes it impracticable to perform a thorough computational analysis of a neuron with multiple synaptic inputs. Previously, approximations via dimensionality reduction have been attempted, but focused on the effect of an individual synapse while considering the rest of the dendritic inputs as background noise [5]. We present here an information theoretic analysis of the information processing of a neuron over a significant region of its entire synaptic input space. We focused on the cerebellar granule cell (GC), whose excitatory input space could be explored extensively. GCs have a low number of mossy fiber afferents (4.17 on average) [6], which generates a tractable number of presynaptic input combinations greatly reducing the complexity of information theoretic calculations.

With experiments and simulations, we quantified how increase neurotransmitter release probability (p), following long-term potentiation, enhanced information transmission of cerebellar GC. Our analysis showed that p shapes the neurotransmission landscape in unexpected ways. As p increased, stimulus transmission reliability did not increase monotonically. Indeed, past a certain value, further increase in p resulted in partial destruction of the original information. These findings demonstrate that synaptic plasticity sets a compromise between increased response and neurotransmission reliability. Furthermore, the spatiotemporal characteristics of the inputs determine the effect of p on neurotransmission, thus permitting the selection of distinctive preferred stimuli with different p values. These mechanisms may have important consequences on the encoding of cerebellar mossy fiber inputs and on the plasticity and computation at the next circuit stage, including the parallel fiber – Purkinje cell synapses.

References
Stimulus reconstruction from in vivo spiking activity of neuronal populations in somatosensory cortex

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Sensory stimulation leads to distributed activity across a wide population of neurons in the mammalian somatosensory cortex. It is presumed that information about the sensory stimulus is likewise distributed across a population of neurons, but it remains unknown how information content grows with the number of neurons in the observed population. We aimed to predict the onset times and angles of individual whisker deflections from the activity of simultaneously recorded layer 2/3 neuronal populations, \textit{in vivo}.

Layer 2/3 neurons located above the layer 4 barrel were bulk loaded with the calcium sensitive indicator Oregon-green BAPTA-1 AM and imaged using 2-photon microscopy (TPM). TPM allowed us to monitor both spiking and non-spiking neurons within these populations with single action-potential and single neuron resolution. In addition, this spiking activity was related back to neuron position within the somatotopic map with high (<5 µm) spatial resolution.

We then evaluated several techniques for stimulus information extraction from neuronal activity patterns, ultimately deciding on a correlation based algorithm for its simplicity and effectiveness. We used this method to predict the time and angle of whisker deflection from neuronal population activity. We found that the activity of one neuron alone allowed for prediction accuracy only slightly above chance levels. However, as the number of simultaneously recorded neurons that were included in the analysis was increased, prediction errors of both type I (false positives) and type II (undetected stimuli) decreased. We defined a measure of the total extractable information based on the mutual information of Shannon, and found that this quantity increases linearly with the number of available neurons.

Using the spatial discrimination capacity of TPM, we observed a highly significant increase in accuracy for the prediction of stimulus onset times among neuronal populations inside the barrel column, as opposed to those in the septal area between barrel columns. However, this anatomical difference was not evident for the prediction of stimulus angle. Both individual neurons and local neuron populations varied widely in the relative amounts of information they contributed about the stimulus.

By extrapolating these results to a larger population of neurons, we were able to estimate that near perfect reconstruction of stimulus onset time could be accomplished with between 175 and 201 Layer 2/3 neurons, while reconstruction of stimulus angle could be accomplished with between 244 and 291 neurons. We conclude that sensory inputs to the barrel cortex can be accurately reconstructed from a relatively small population of layer 2/3 neurons, and that stimulus features that are not available in the activity of any individual neuron can be faithfully represented by neuronal populations.
Auditory Information Coding by Cochlear Nucleus Onset Neurons

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In this paper we use information theory to quantify the information in the output spike trains of modeled cochlear nucleus onset neurons. Onset neurons have very specialized membrane properties, and they are known for their precise temporal processing. We modeled the onset neurons with a single-compartmental model including five major Hodgkin-Huxley-type ion channels. We connected them to 60 auditory nerve fibres from our inner ear model. The physiologically motivated model of the peripheral auditory system consisted of a simplified ear canal and middle ear model, a model of inner ear hydrodynamics followed by a compression stage, and sensory cells. We calculated the information carried by the spike trains of onset neurons directly, without making any assumptions on how the neurons code the sound stimuli [1].

We conclude that the maximum information transmission rate for a single neuron is up to 950 bits/s, which corresponds to approximately 5.0 bits/spike. For quasi-periodic signals like voiced speech, the transmitted information saturates as word duration increases. In general, approximately 90\% of the available information from the spike trains was transmitted within 69 ms. Information of speech concentrates at formant frequency regions. When the speech signal is masked by added pink noise, the shape of information distribution over frequency is well preserved until the signal to noise ratio drops below 0 dB. Information transmitted by the spike trains increases monotonically with the temporal resolution that is used to represent the spikes. The neurons are able to code information in a very fine time scale of approximately 20 \(\mu\)s. At 10 ms resolution, which is usually the case for most automatic speech recognition systems, information rate is only about 9\% of the one at the highest resolution in our study (\(\sim 0.02\) ms). This indicates that for automatic speech recognition systems especially in background noise, fine-grained temporal information is essential and should no longer be neglected.

Acknowledgments
We thank Alexander Borst and Spavieri Deusdedit for helpful discussions. This work was funded by the German Federal Ministry of Education and Research (reference number 01GQ0443).

References

Simultaneous Optimization of Clustering and Dimension Reduction for Neural Population Activities

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Recently, there has been an increase in the need to 'read out' information from the single-trial activities of many neurons. This is useful to develop brain-machine interfaces (BMI). To construct better BMI, it is critical to visualize the information that neurons encode. Clustering and dimension reduction are useful visualization methods. However, there remain two problems that we are concerned. One problem is that the dimension of population activity vectors (PVs) which consist of individual neural activities is high. The other is that the number of data is usually small because of few experimental conditions. Clustering for neural population activities has troubles in overfitting and high computational complexity. In this study, we consider a case that high-dimensional noises with large variances exist as shown in Fig.1. In this case, usual dimension reduction methods might not extract meaningful signals in a low-dimensional space. To solve these problems, we developed a new algorithm to optimize clustering and dimension reduction simultaneously. The proposed probabilistic model was a product of a mixture of two-dimensional Gaussians and 43-dimensional spherical Gaussian noises (Fig.1). Since the spherical Gaussian assumption was violated for the neural data, we applied whitening to make the variances of all components of PVs equal. To avoid enlarging the components with too small variances, we applied principal component analysis to project the PVs to 10-dimensional vectors. We estimated the parameters of the Gaussian mixture by variational Bayes (VB), and optimized basis vectors which determined a two-dimensional subspace by steepest ascent method to maximize free energy of VB. We used the activities of 45 neurons recorded individually in the monkey inferior-temporal cortex while 38 visual stimuli (geometric shapes and faces of humans and monkeys) were presented \cite{1} as test data. A PV for each stimulus consisted of mean activities of 45 neurons within a 50-ms sliding time window. To compare the effect of the whitening, we show the 38 PVs projected into the two-dimensional subspace within 90-140 ms and 140-190 ms time windows without whitening (a) and with whitening (b). The points represent the PVs for human faces (red), monkey faces (blue), and shapes (green), respectively. The ellipses represent the resulting clusters. Although 4 clusters were assigned for monkey faces within the 140-190 ms window in (a), 3 clusters were assigned in (b). Individual clusters in (b) were separated much more clearly than (a). These results indicate our algorithm is very useful to visualize the information that many neurons encode.

\begin{figure}[h]
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\includegraphics[width=\textwidth]{fig1.png}
\caption{Fig.1 Probabilistic model. Fig.2 Clustering results in subspaces: (a) without whitening, (b) with whitening.}
\end{figure}

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Extreme Synergy in a Retinal Code

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Humans and other primates require between 50-200 msec to process visual scenes, a period over which even strongly stimulated retinal ganglion cells are likely to generate no more than a few to a few tens of spikes above background levels. If the variance in the number of spikes scales roughly as the mean, the luminance signals conveyed by individual ganglion cells would be subject to random fluctuations of 20% to 50%, a noise level seemingly incompatible with the acuity of visual perception. Here, we use computer-generated spike trains to demonstrate that dramatic increases in signal to noise may be achieved by utilizing the information encoded by pairwise oscillatory correlations between retinal neurons. Realistic spatiotemporal correlations were produced by modulating the instantaneous firing rates of all stimulated ganglion cells by a common oscillatory input (central frequency = 80 Hz, HWHM = 10 Hz) whose temporal structure was consistent with measured retinal field potentials. Principal Components Analysis (PCA) was used to simultaneously analyze the pairwise spatiotemporal correlations present in local neighborhoods containing several hundred ganglion cells, representing thousands of distinct cell pairs. Our results suggest that rather than operating as independent encoders, ganglion cells may utilize an extremely synergistic code in which the messages transmitted by any one neuron can only be accurately interpreted within the context of the concurrent firing activity across a large group of surrounding elements.

Reconstruction of a simple visual stimulus. Raw data consisted of a 16×16 grid of computer-generated spike trains, 100 msec in duration, with a mean baseline firing rate of 25 Hz. The mean firing rate of the central 10×10 patch was increased by 2Xs, to 50 Hz (panels A,C) or 4Xs to 100 Hz (panels B,D). A,B) Rate-based reconstructions. Pixel brightness was proportional to the number of spikes in the corresponding cell. As predicted, the rate-based reconstructions were relatively noisy. C,D) Correlation-based reconstructions. Correlations were computed between all pairs of spike trains. The magnitude of the correlation between any given pair was determined by the integral of the time-dependent correlation function over all temporal lags. The amplitude of each spike event was weighted by the concurrent local field potential band-pass filtered between 60-100 Hz. Reconstructed images were given by the 1st principal component (eigenvector with the largest eigenvalue). Percent correct foreground/background discrimination using an ideal observer: A) 76%, B) 90%, C) 93% D) 100%. Right Column: Average cross-correlogram between all cell pairs, expressed as a fraction of the asymptotic value.
To Spike or Not to Spike: Optimal Change-Detection in Single Neurons

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Survival in a non-stationary, potentially adversarial environment requires animals to detect sensory changes rapidly yet accurately, two oft competing desiderata. Neurons subserving such detections are faced with the corresponding challenge to discern “real” changes in inputs as quickly as possible, while ignoring “noisy” fluctuations. Mathematically, this is an example of a change-detection problem that is actively researched in the controlled stochastic processes community. In this work, we utilize sophisticated tools developed in that community to formalize an instantiation of the problem faced by the nervous system, and characterize the Bayes-optimal decision policy under certain assumptions. Focusing on the specific problem of a neuron detecting a hidden (Bernoulli) rate change in its input spike train, we demonstrate that the optimal strategy corresponds to an information accumulation and decision process that bears remarkable resemblance to the dynamics of a leaky integrate-and-fire neuron. This correspondence suggests that neurons are optimized for tracking changes in its input statistics. It sheds new light on the computational import of intracellular properties such as resting membrane potential, voltage-dependent conductance, and post-spike reset voltage. We also explore the influence that factors such as timing, uncertainty, neuromodulation, and reward should and do have on neuronal dynamics and sensitivity, as the optimal decision strategy depends critically on these factors. We also examine the implications of this optimization framework, in which the timing of every single input and output spike plays a critical role, in the regime of high firing rates – in this latter case, the objective function is equivalent to maximizing the difference between stimulus-evoked firing rate and spontaneous firing rate. More generally, the mathematical framework introduced in this work is useful for formalizing not only neuronal decision problems, but also time-pressed decision-making at all levels of systems and cognitive behavior.

Acknowledgments
We thank Bill Bialek, Peter Dayan, Savas Dayanik, and Sophie Deneve for helpful discussions. Funding is from an NIH NRSA institutional training grant.

References
Capacity of Populations: Implications for Neural Prosthetics

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An important consequence of Shannon’s rate-distortion theory is that information capacity determines the ultimate coding fidelity of any system, encompassing any fidelity measure. Using point process models for neural populations, we explored how innervation of and within a population affects capacity [1]. Our results showed that the capacity of parallel Poisson channels is proportional to the population size. We conjecture that just as in the single channel case, our Poisson result bounds the capacity of jointly defined collections of point processes that more accurately model neural activity. Somewhat surprisingly, our capacity result applies regardless of whether each channel has a separate input or whether every channel shares a common input. We interpret this result to mean that whether neurons in a population have individual innervation or a common innervation has no effect on the population’s ability to represent information.

In contrast, aggregating the population’s outputs dramatically reduces capacity. Specifically, we considered how summing the component Poisson processes to produce a composite signal affects capacity. While we could not derive an analytic result, our numerical results suggest that the capacity of an aggregated population is less than twice the capacity of an individual neuron regardless of population size. Any subsequent filtering or the addition of recording noise can only reduce capacity further; hence, our results represent the largest possible capacity that unsorted extracellular recordings or gross recordings of neural activities can have. Because the capacity is so dramatically reduced, the information encoded by the population cannot be accurately determined from its aggregated output by any means.

These two cases—a neural population having a single, common input and an aggregated recording from any population—model two common neural prosthetic situations. The first describes electrical stimulation situations, such as cochlear implants, in which each electrode excites multiple neurons. The second models the use of gross recordings, such as EEGs and unsorted extracellular recordings, to effect motion of a missing limb. Our capacity results suggest that electrical stimulation faces no fundamental barriers to creating viable replacement sensory or motor inputs. On the other hand, using gross recordings for controlling motion must somehow surmount the limitations that our capacity results indicate must be present. This capacity barrier can be lifted in two ways. If the original constituents could be untangled from the aggregate using spike sorting techniques, no capacity decrease would occur. Alternatively, recent work has shown that feedback can increase capacity, though the results do not indicate by how much [2]. Thus, visual feedback may play a crucial role in enabling artificial limb motion guided by neural control.

Acknowledgments
ING supported by a NSERC Fellowship.

References
Balanced inputs cause ‘firing irregularity clamp’ regardless of large rate fluctuation

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Cortical neurons show highly irregular firing patterns, suggesting that this irregularity may be important for cortical function and that there are mechanisms to actively maintain it. It is not known how this irregularity is maintained and, especially, how much background synaptic activity and intrinsic membrane properties affect firing irregularity.

In many previous studies, the irregularity has been characterized by the coefficient of variation of interspike intervals, $C_V$. However, $C_V$ does not necessarily reflect the irregularity of a spike train if firing rate changes over time. For instance, $C_V$ becomes large when the firing rate of a regular spike train is modulated. We need another mathematical measure which is sensitive only to the irregularity of neuronal firing, but not to the rate modulation. For that purpose, we previously studied the decomposition of the two factors. To be precise, we modeled spike generation as the gamma process, which is a natural extension of the widely-hypothesized Poisson process, and suggested using the ‘shape parameter’ orthogonal to the firing rate as a measure for the spiking irregularity [1].

In this paper, we characterize the irregularity of spike output in response to synaptic inputs in computational models and real cells recorded by whole-cell patch-clamp technique. We found that when excitatory and inhibitory synaptic inputs are balanced or co-tuned, the spiking irregularity varies moderately irrespective of changes in the firing rate. The results suggest that the two dimensions may be functionally decoupled in the information representation by neurons. The degree of irregularity depends on cell’s intrinsic properties and the effective reversal potential $V_r$ of synapses. However, it remains unchanged over time within a balanced regime. Since evidence is accumulating for balanced excitation and inhibition [2], our results may achieve a novel insight into neural code. We briefly argue how the present finding may facilitate the information decoding in the brain machine interface.

\begin{figure}[h]
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\includegraphics[width=\textwidth]{figure1.png}
\caption{Firing rate and regularity for two cortical neurons for various net synaptic conductances.}
\end{figure}

Acknowledgments
This work was supported in part by grants from JSPS (No. 18020007).

References
Maximum entropy modeling of multi-neuron firing patterns in V1

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Understanding the activity of a network of neurons is challenging due to the exponential growth in potential interactions as the network size increases. In the visual cortex, the firing activity of pairs of neurons is correlated over a few tens of milliseconds, but the source and significance of these correlations is controversial. Correlations may reflect genuine interactions between pairs of neurons or driving by a common input.

One way to investigate the structure of neuronal correlations is maximum entropy modeling. Maximum entropy modeling generates canonical joint firing distributions that are consistent with a certain set of constraints but are otherwise as unstructured as possible. In particular, maximum entropy models can be formulated from constraints derived from pair-wise interactions, or alternatively, from a common-input model. Recently, maximum entropy techniques have been used to study the structure of multi-neuron firing patterns in the retina (Schneidman et al. 2006 and Shlens et al. 2006); in this context, pairwise-interactions appear to account for multineuronal firing patterns. Here, we implement a similar analysis of multi-neuron firing patterns from tetrode recordings in the primary visual cortex of the anesthetized macaque.

One caveat to multi-neuron analyses of tetrode recordings is that when neurons fire within a millisecond of each other, spikes can be misclassified or dropped, leading to a systematic underestimate of simultaneous events. We (conservatively) correct for this underestimate, by postulating that correlations on the order of a millisecond are no stronger than correlations on the order of ten milliseconds.

As in the retina, we find that weak pair-wise interactions between neurons imply significant departures from independence in multi-neuron firing patterns, and lead to a prevalence of simultaneous multi-neuron activity. We also find that a simple common-input model, with constraints on the probability that a neuron fires when any other neuron fires, also captures much of the observed departures from independence. We derive Bayesian estimates of likelihood ratios for the pair-wise and common-input models and show that, for a range of priors, the pair-wise model is more likely than the common-input model. Thus, it appears that in V1, at least within the range of a hundred microns, most of the structure in multi-neuron firing patterns can be explained on the basis of interactions between pairs of neurons.

Support: GM7739 and NEIITEO7138 (IEO), 2RO1EY9314 (JDV)
An Encoding Transition in the Concurrent Encoding of Frequency and Amplitude Modulation in Human Auditory Cortex

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Complex natural sounds (e.g., animal vocalizations or speech) can be characterized by specific spectrotemporal patterns whose components change in both frequency (frequency modulation, FM) and amplitude (amplitude modulation, AM). The neural coding of AM and FM has been widely studied in humans and animals, but typically with either pure AM or pure FM stimuli. The neural mechanisms employed to perceptually unify AM and FM acoustic features remain unclear. Using stimuli with simultaneous sinusoidal AM (at rate $f_{AM} = 37$ Hz) and FM (with varying rates $f_{FM}$), magnetoencephalography (MEG) is used to investigate the elicited auditory steady state response (aSSR) at relevant frequencies ($f_{AM}$, $f_{FM}$, $f_{AM} \pm f_{FM}$). Previous work [1] demonstrated that for sounds with slower FM dynamics ($f_{FM} \lesssim 5$ Hz), the phase of the aSSR at $f_{AM}$ tracked the FM; in other words, AM and FM features were co-tracked and co-represented by ‘phase modulation’ encoding. This study explores the neural coding mechanism for stimuli with faster FM dynamics (up to 30 Hz), demonstrating that at faster rates ($f_{FM} \geq 5$ Hz), there is a transition from pure phase modulation encoding to a single-upper-sideband (SSB) response (at frequency $f_{AM} + f_{FM}$) pattern. We propose that this unexpected SSB response can be explained by the additional involvement of subsidiary amplitude modulation encoding responses, simultaneously to, and in quadrature with, the ongoing phase modulation. These results, using MEG to reveal a possible neural encoding of specific acoustic properties, demonstrate more generally that physiological tests of encoding hypotheses can be performed non-invasively, and on human subjects, complementing invasive, single-unit recordings in animals.

Acknowledgments
We are grateful to Jeff Walker for his excellent technical assistance. This work was supported by NIH grant R01 DC05660.

References
Time-evolving neural codes underlie odor perception in an insect

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Understanding how perception arises from sensory information processing in the brain requires correlating stimulus-evoked neural activity with behavioral assays of perception. We examined the relationship between odor representation and behavioral response in a relatively simple animal, the hawkmoth (\textit{Manduca sexta}). In insects, odorants are detected at the antenna by olfactory receptors which relay their responses to the antennal lobe (AL) for further processing. There, the odor code is shaped through interaction between two intrinsic neuron types: the excitatory projection neurons (PNs) and the inhibitory local neurons (LNs). The processed code is transmitted to the Kenyon cells (KCs) in the mushroom body (MB), a structure associated with memory.

We used many odors including pure chemicals and plant essential oils over a wide range of concentrations, as well as a range of pulse durations from 100 ms (as moths would encounter in an odor plume in flight) to 4 sec (as encountered when sampling food from, and learning about, flowers). All odor stimulus conditions reliably evoked local field potential (LFP) oscillations in the MB, indicating strongly synchronized neural activity. Intracellular recordings from PNs (n=15) and LNs (n=31) in the AL showed that their odor-evoked spikes were phase-locked to the LFP oscillations, and that LNs usually fired shortly after PNs (cell types confirmed by dye injection). Subthreshold membrane potential oscillations in PNs and LNs were highly correlated with the LFP oscillations, consistent with an oscillation mechanism in the AL arising from excitatory inputs from PNs to LNs and inhibitory feedback from LNs to PNs at each oscillation cycle. Local injections into the AL of picrotoxin (blocker of inhibitory transmission) reversibly abolished oscillations recorded in the MB. These results indicate that odor information is encoded in the oscillatory and synchronous firings of PNs, as in the locust.

Next, we examined how the PN olfactory code is transformed in the MB. Seventeen intra- and 78 extracellular recordings from KCs revealed very sparse spikes that were phase-locked to the LFP oscillations, indicating that KCs are sensitive to the oscillatory synchrony of their inputs. KCs responded preferentially to the onset of brief odor pulses (< 1 sec), and to onset and offset of long pulses (4 sec). Long odor pulses, commonly used in conditioning paradigms, elicited spikes in ensembles of KCs that differed between odor onset and offset, indicating that odor representations in the MB evolved over the course of the stimulus-evoked response. This suggested odor perception may also vary over time.

Moths were classically conditioned in a proboscis extension reflex (PER) paradigm so that either the onset response (evoked by short odor pulses, N=49) or the offset response (evoked by long odor pulses, N=59) overlapped with sucrose reward. Moths trained with the short pulses (500 ms) later responded equally well to short and long test pulses, whereas moths trained with the long pulses (4 sec) responded best to a long test pulse, but significantly less often to a short test pulse. Thus, moths can distinguish the odor onset from offset, consistent with the time-varying odor representations in the MB.

\textbf{Acknowledgments}

The Japan Society for the Promotion of Science (00169, 70510) to I.I. Joint NIH-NIST postdoctoral fellowship award by National Research Council to B.R. Intramural support from NICHD to M.S.
Explicit Object Representation by Sparse Neural Codes

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Highly sparse representations of objects in the visual environment in which individual neurons display a strong selectivity for only one or a few stimuli (such as familiar individuals or landmark buildings) out of on the order of 100 presented to a test subject have been observed in the human medial temporal lobe (MTL), a brain area believed to be crucial to the formation of new semantic memories [1, 2]. The process by which more distributed representations earlier in the visual pathway are transformed to produce such highly selective and invariant units results in information represented only implicitly by the pattern of light impinging on the retina and in the firing of neurons in early visual areas being made explicit at the level of MTL. This “sparsification” may be an important design principle underlying the structure of this brain region.

We apply a modified version of the model of Olshausen and Field [3], in which a network of nonlinear neurons generates a sparse representation of its inputs through an unsupervised learning process, to the outputs of a biologically plausible model of the human ventral visual pathway [4]. We train this system on real-world images from multiple categories taken from the Caltech-256 dataset. This training is carried out in an entirely unsupervised manner, without specifying image categories or even the number of categories present. Although the underlying constraint in the model is merely to produce a sparse representation of its input set, units emerge that respond selectively to specific image categories such as faces and airplanes. The sparseness constraint thus facilitates the formation of explicit representations of image categories, despite the category information being represented only implicitly in the input images.

Acknowledgments

We thank Thomas Serre and Minjoon Kouh of MIT for providing the visual system model used here as well as assistance with its operation, and Richard Murray, Jerry Marsden, and Pietro Perona at Caltech for valuable feedback. This work was funded by a Fannie and John Hertz Foundation Fellowship (to S.W.), as well as by grants from the ONR, NIMH, and NGA.

References


Recovery of Stimuli Encoded with Hodgkin-Huxley Neurons

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In the reverse correlation method [1] to neural encoding, the neural system is treated as a black box and both the input stimuli and output spike trains are assumed to be observable. Based on the correlation between the input and the output, the black box is identified as the kernel of a Wiener filter. When investigating problems arising in olfactory coding, an explicit characterization of odor stimuli is, however, not available. In addition, sensory systems are exposed to unknown stimuli in real-time. Under these conditions, investigations of sensory encoding of natural stimuli assume that only the spike train is observable and the neural system can be described as a non-linear dynamical system. The Hodgkin-Huxley neuron is the model of choice.

A non-linear perturbation analysis shows that the system of ordinary differential equations describing the Hodgkin-Huxley neuron with a weak stimulus accepts a solution consisting of a phase shift term and a small perturbation term. We derive a recovery algorithm that extracts information about the stimulus contained in the phase shift term and is embedded in the perturbation term. Results are obtained for both Hodgkin-Huxley neurons with deterministic and stochastic gating variables, respectively.

We show that a Hodgkin-Huxley neuron with deterministic gating variables is I/O equivalent with a project-integrate-and-fire (PIF) neuron with a variable threshold sequence. The PIF neuron integrates a projection of the stimulus onto the phase response curve that is, in turn, modulated by a phase shift process. The phase shift process is described by a differential equation that is stimulus driven. The PIF neuron generates a spike whenever a threshold value is achieved; the values of the threshold sequence are explicitly given. In the absence of the small perturbation term, the stimulus is tangentially coupled into the limit cycle of the Hodgkin-Huxley neuron and the PIF neuron reduces to an integrate-and-fire neuron [2], [3]. Building on the I/O equivalent PIF neuron, we provide a stimulus recovery algorithm and evaluate its performance.

We extend these results to noisy Hodgkin-Huxley neurons. This calls for generalizing the phase response curve to the case where the gating variables are modeled as stochastic processes. We provide a stochastic differential equation that describes the phase shift process and reduce the noisy Hodgkin-Huxley neuron to a stochastic analog of the PIF neuron obtained in the deterministic case. Finally, we provide an algorithm for stimulus recovery based on observing the spike train generated by a noisy Hodgkin-Huxley neuron.

Acknowledgments
The work presented here was supported in part by NIH under grant number 1 R01 DC008701-01 and in part by NSF under grant number CCF-06-35252.

References
Using cortical timing information to guide behavior

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It is well established that animals can exploit the fine temporal structure of some stimuli; for example, interaural time differences of less than one millisecond are used for spatial localization of sound. It is also clear that cortical neurons can lock with millisecond precision to the fine temporal structure of some stimuli. However, it has been difficult to establish whether the fine temporal structure of cortical responses can be used in a behavioral context to guide decisions. Indeed, in the case of spatial localization of sound, the relevant interaural time differences cues are processed below the level of the cortex by means of specialized circuitry.

We have therefore adopted a direct approach to probe the precision with which cortical timing information can be used to guide behavior in the rat. To bypass subcortical auditory pathways, we stimulate primary auditory cortex directly, using transient biphasic current trains delivered via chronically implanted intracortical microelectrodes. The behavioral paradigm we use is a two-alternative choice task in which stimulus 1 consists of the simultaneous stimulation of two intracortical sites (A & B), and stimulus 2 consists of sequential stimulation of the two sites separated by a brief interval dt (A - dt - B). After the subjects are trained to perform to criterion (1-2 weeks) with the initial long interstimulus interval (dt > 50 msec) for stimulus 2, we probe the subjects' psychophysical threshold by reducing dt, until the subjects can no longer distinguish between the two stimuli. Our initial experiments indicate that the cortex can make use of information on a time scale as short as 10 ms, and possibly much less.

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Adaptation and context dependent coding across the whisker pathway

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Neurons in barrel cortex show prominent adaptation to repeated stimuli. We have recently found that barrel cortex adaptation causes the representation of a given whisker movement to depend on the movement’s context [1]. We recorded single-neuron responses to continuous, rapidly varying, stochastic whisker movement stimuli in anesthetized rats, and analyzed stimulus-response relationships using spike-triggered covariance methods. In every neuron with rate adaptation, input-output tuning functions rescaled following changes in stimulus statistics (high versus low variance). These changes in gain matched input-output functions to the stimulus range and allowed neurons to maintain the amount of information conveyed about stimulus features, thus enhancing whisker movement encoding.

Here we explore how adaptation to continuous, rapidly varying stimuli is generated in the whisker pathway. Do rate adaptation and gain rescaling arise cortically, or are they present at subcortical stages? We performed extracellular recordings of single-neuron responses in the anesthetized VPM thalamic nucleus. Neurons showed a wide diversity of behaviors – rate adaptation ranged from completely absent to strongly prominent. Conversely, units recorded in the trigeminal ganglion did not adapt to rapidly varying stimuli. We are analyzing whether thalamic adaptation involves gain rescaling, as in cortex.

What mechanisms can account for adaptive gain rescaling? While contributions of synaptic dynamics to barrel cortex adaptation are well characterized, less is known about the role of intrinsic membrane properties. Using whole cell recordings in acute slices, we found that intrinsic properties can account for adaptive gain rescaling, but only when stimuli provide net depolarization. Taken together, our results suggest that adaptation to stimulus statistics in barrel cortex is the result of the interplay between synaptic and intrinsic mechanisms acting at several stages in the pathway.

Acknowledgments
We are grateful to Marco Brambilla for help with spike sorting. This work was supported by: Human Frontier Science Program Grant RG0043/2004-C, EC Marie Curie International Reintegration Grant MIRG-CT-2004-511273, Royal Society Joint Project Grant, Royal Society Research Grant.

References
Auditory alerts caused by changes in unattended sounds

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An important function of the auditory system is to alert animals to changes in their environment. Phenomena such as mismatch negativity (MMN), changes in detection threshold and changes in reaction time are associated with rare deviant sounds set amongst common standards [1]. Here, we focus on the range and impact of certain changes in unattended sounds on the perception of other, attended sounds, interpreting such changes as potentially containing a distracting, “alerting” quality, related to informational masking [2]. The eventual goal of this research is to find which changes in distributions generating stochastic sounds do and do not cause auditory alerts.

We tested the distracting quality of changes in an unattended sound by asking subjects to discriminate between two frequencies of regularly presented tone pips, while simultaneously presenting the sound of interest as a spectrally well-separated, task-irrelevant auditory stream. The impact of changes in the task-irrelevant stream on the performance in the discrimination task could then be studied. This design is related to a previously proposed distraction paradigm in which there is no unattended sound and the task-irrelevant changes (such as a change in volume) occur in the tone pips of the discrimination task themselves [3].

We present psychophysical results showing the time-varying extent of the distracting quality of a change in the unattended sound (see figure below). In some cases, this works symmetrically: a rare instance of sound A within common sound B is distracting, whereas a rare instance of sound B within common sound A is also distracting. Thus change, rather than identity, of the unattended stimulus is responsible for the distraction.

Grand average results on pilot data from six subjects (two of whom were not naive). Blue: average performance away from deviants. Red: average performance near deviants. Black and gray: temporal variation of performance near deviants. The standard sound in one condition was the deviant in the other condition. These sounds were harmonic stacks differing in distribution of power in each harmonic.

Acknowledgments
We thank Torsten Marquardt for discussions. Supported by the Gatsby Charitable Foundation.

References
Modeling Sounds with Gaussian Modulation Cascade Processes

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The processing of sensory input is intimately linked to its statistical structure, and this relationship can be used to derive computational models of sensory processing. For instance, one approach is to devise a model for the sensory data that captures the observed statistical structure through latent variables, and then to view sensory processing as inference under this model. This approach has had greatest success in modeling visual processing of static images. In audition things are rather more difficult, first because we need models with an explicit temporal dimension, and second because sounds are transformed into a time-frequency representation at the cochlea. Here, we introduce a new generative model for the dynamic Fourier components of sounds called the Gaussian Modulation Cascade Process (GMCP).

The GMCP takes inspiration from traditional ideas of amplitude demodulation where the goal is to represent a waveform as a product of a slowly varying envelope and quickly varying carrier. This idea can be extended by demodulating the envelope, forming a demodulation cascade. Empirically, this is found to be an efficient representation of sounds, as each process in the cascade captures structure at a different time-scale. Interestingly the modulators are found to be self-similar in this case. An alternative generalisation of amplitude demodulation is to first pass the sound through a filterbank and then to demodulate each channel independently, forming a modulation filterbank. Analysing natural sounds in this way shows amplitude modulation (AM) is present over a wide range of time-scales, and that it is strongly correlated across widely separated frequency channels. The AM statistics show an interesting invariance: they are channel independent [1].

We believe the interesting structure in the statistics of AM suggests that it might provide an efficient representation of natural sounds. Indeed the auditory system appears to listen attentively to AM [2]. This motivates a new generative model that combines the modulation cascade and modulation filterbank. The model comprises a hierarchy of latent variables, with each level representing a different time scale of AM (though there can be several components in each level). Each latent is a smooth Gaussian Process, $p(x_{k,1:T}^{(m)}) = GP(0, C_{1:T})$. The observations, which are the sine and cosine coefficients of a Short Term Fourier Transform of a sound, are formed by a sum of products of latent variables and generative weights,

$$p(y_t | x_{1:M}^{(1:M)}, g_{k_1:k_M}, \sigma_y^2) = \text{Norm} \left( \sum_{k_1:k_M} g_{k_1:k_M} \prod_{m=1}^M x_{k,m,t}^{(m)}, \sigma_y^2 I \right).$$

Promisingly, samples from the GMCP resemble natural sounds for a wide range of parameter settings. Furthermore, due to the structure of the non-linearity, inference and learning is relatively simple. We show that there are a family of efficient variational EM learning algorithms that perform well when we know ground truth. Finally we show some preliminary results on natural sounds.

Acknowledgments
We thank Pietro Berkes for all his help. This work was supported by the Gatsby Charitable Foundation.

References
“The Whole Rat Catalog” – relating form and function in the rat vibrissal array

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When a rat ‘whisks’ against an object, different whiskers, each with different shapes and mechanical properties, contact different parts of the object, either simultaneously, or with varying time delays [1]. Thus, a complete understanding of how form and function are related in the vibrissal array must include a detailed knowledge of the spatio-temporal sequence of sensory input across the array. Our long term goal is to obtain the spatiotemporal patterns of sensory input that result from the rat’s natural exploratory behaviors. With current video techniques, this goal is virtually impossible, because each whisker must be tracked individually. The goal is more realistic if the position and velocity of the head and a few whiskers can be fed to a computational model that “fills in” the rest of the array. As a first step towards this objective we have constructed “The Whole Rat Catalog” (WRC), a complete 3-dimensional (3D) model of the rat head that includes the positions, shapes, and orientations of the whiskers.

Whiskers were plucked from four female Sprague-Dawley rats and scanned using a standard flatbed scanner. To the eye, the majority of the vibrissae appeared to lie flat in a plane. However, a closer inspection revealed that many of the whiskers actually had a small amount of curvature out of the plane. It was found that typically, the proximal 70–80% of the length of the whisker lay in a plane, while the most distal 20 – 30 % curved slightly out of the plane. A coordinate-free or parametric representation of the whisker shape was then employed in order to describe the 2D shape without reference to Cartesian coordinates. In a coordinate-free representation of a plane curve, the shape of the curve is described by specifying the curvature $\kappa(s)$, at each point, as a function of the arc length $s$. In the absence of any a priori model for $\kappa(s)$, we assumed a quadratic form: $\kappa(s) = as^2 + bs + c$. We obtained excellent fits to the data by this method. A very strong correlation was found between the coefficients, and to a very good approximation, $b = -a$, and $c = 1 + 0.2b$.

To determine the three-dimensional (3D) position and orientation of each vibrissa on the rat's head, a high resolution volumetric scan of the head and whisker array was obtained with a 3D laser scanner. The 3D whisker orientation was then quantified by matching the 2D scan data with the corresponding 3D volumetric data. The 3D orientation of the whiskers could be defined using three angles: $\Theta$ (rostral-caudal), $\phi$ (dorsal ventral), and $\psi$ (rotational). All three orientation angles were found to vary smoothly across the array. In the WRC, we have measured 17 different parameters relating to the position and orientation of the whiskers on the mystacial pad. We examined correlations between all non-identical pairs of these parameters. For four pairs, we observed “strong” correlations, i.e. with $|r| > 0.8$, which are described in our poster. In future work, we plan to insert realistic whisker dynamics into this model.

Acknowledgments
We thank Neel Naik and Myron Kim for data collection. This work was supported by NSF grant IIS-0613568

References
Three cell types in the avian primary auditory area field L

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Natural auditory signals such as speech and birdsong vary greatly in their volume and dynamic range, yet auditory neurons can only encode the spectro-temporal modulations in these signals over a limited range. We used reverse-correlation techniques to study the spectro-temporal encoding properties of neurons in field L, the avian analog of primary auditory cortex in two regimes: a loud volume (63dB) and a soft volume (30dB). We found three types of cells that differed in their physiology, in the extent of their spectral and temporal filters, and in the way these filters depended on the volume of the stimulus. The first type had responses that were narrowly tuned in both spectrum and time. At loud volumes, these cells showed increases in both spectral sideband inhibition, and temporal inhibition, making them more sensitive to spectral and temporal differences in this regime. These cells typically had narrow spike waveforms, high spontaneous and driven firing rates, and short refractory periods. The second type of cell had filters that were also narrow in time, but were broader in their spectral sensitivity. These cells showed an increase in temporal but not spectral inhibition at the loud volume, suggesting that these cells are specialized for encoding temporal modulations. These cells shared many of their physiological properties with the first type of cell. The third type of cell had much broader spike waveforms, lower firing rates, and longer refractory times. These cells were narrowly tuned in frequency but had much longer integration times. As a population, these cells did not show significant changes in their receptive fields with volume, although this may be due to poorer filter estimates due to their lower firing rates. The first and second types of cell were found only in a restricted central area of our dorso-ventral penetrations, suggesting that these cells are located in the auditory subfield L2a, which receives direct input from the thalamus. The third type of cell was more broadly distributed, but was found primarily in fields L1 and L3, which flank L2a and receive their input from it. These data suggest that field L shows some spatial segregation of cell types specialized for encoding of temporal and of spectral modulations, and that changes in receptive field shape with volume may reveal the stimulus dimensions for which neurons are specialized.

Acknowledgments
This work was supported by HHMI and NIH.
Natural scenes in vibrissa-mediated active touch

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Sensory information must pass through peripheral sensory organs. As such, understanding how their embodied, physical properties shape neural representation is central to understanding perception. Moreover, in many cases active sensor control refines processing even before the onset of neural activity (e.g., altering contact force and velocity during touch). We are exploring these principles in the rodent vibrissa (whisker) system, with which rats can perform high-precision tactile tasks, using a combination of body, head and "whisking" movements to engage objects of interest with their vibrissae.

Mechanical resonances are a prominent componenet of vibrissa signal transduction in plucked vibrissae, anesthetized animals with piezo stimulation, and in awake animals performing discrimination tasks. Here we address the detailed character of inputs to the afferents (at the vibrissa base), and how these inputs are neurally represented. Individual micromotions can significantly exceed velocities and accelerations typically employed in acute physiology experiments. Further, freely behaving animals choose to contact surfaces in a way that expresses a coarse frequency gradient across multiple vibrissae. In general the pattern of motions is dominated by “stick-slip-ring” events on coarse surfaces and smoother oscillations (due to friction) on flat surfaces. We have initiated simultaneous facial EMG and cortical single-unit recording with the task videography, to relate sensor properties to the animal’s behavioral choices and neural activity.

Acknowledgments
We thank Howard Eichenbaum for consulting on behavioral methods, Emery Brown for consulting on data anlysis, and Elizabeth Sievert and Jamie Mehringer for assistance with animal training. This work was supported by NIH 5 F32 NS045415 (J.T.R.), NIH R01-NS045130 (C.I.M), NSF 0316933 (C.I.M.). J.T.R. holds a Career Award at the Scientific Interface from the Burroughs Wellcome Fund.
A model of the encoding of mechanical variables by rat vibrissal trigeminal ganglion neurons

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Rats rely strongly on tactile information from their vibrissae (whiskers) to explore their environment, but the fundamental mechanical parameters encoded by the vibrissal system have yet to be completely quantified. Mechanoreceptors located in the whisker follicle sense whisker deflection and convey this information to primary sensory neurons in the trigeminal ganglion (Vg). The responses of Vg neurons have been studied using passive ramp and hold deflections [1], white noise stimuli [2], and artificially induced whisking [3]. We hypothesized that the following mechanical variables are encoded by Vg neurons: whisker deflection angle, the angular velocity, the moment and its first temporal derivative, all measured at the base of the whisker. Here, we test this hypothesis using a generalized integrate-and-fire model of Vg cells responding to combinations of these mechanical variables. The model consists of a stimulus dependent current, which is a summation of mechanical variables multiplied with direction-dependent gains, a spike history dependent current, and a Gaussian white noise current. We compared simulation results with previously published data from several labs. Our model was able to reproduce the qualitative features of spike trains and PSTHs to all three stimulus paradigms mentioned above. The figure compares results of the model with published experimental data for passive stimulation (left) and artificial whisking (right).

References

Neural Feature Layers Can Establish Correspondences In Physiological Time

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We describe a neural network model able to rapidly establish correspondences between neural feature layers. There are good reasons to assume that the brain performs correspondence-based invariant object recognition [1]. In the technical domain, this represents state-of-the-art object and face recognition technology (e.g. [2]). The inherent task of finding corresponding points in different images of the same object has to be solved in very short time intervals in order to account for physiological object recognition times below 100 ms [3].

As input we use natural images which are overlaid by a regular grid. The surrounding of a grid-point excites subpopulations of a cortical column model [4,5] via Gabor-like receptive fields (RFs) (compare [1,6]). Thus, the neural activity distribution within such a feature column encodes the image texture at a grid-point, and a layer of feature columns encodes the whole image. We use two layers of feature columns to represent two different images of the same object. To find corresponding points, each feature column is paired with a model column whose neural subpopulations control the connections to the other layer, i.e., they realize dynamic links [6]. The subpopulations of these control columns are excited by both, similarities between activity distributions of pairs of feature columns, and by the activities in neighboring control columns. The latter implements a topological constraint for potential connectivities.

Given a pair of images, the system converges from a state of all-to-all connectivity between the layers to a state of neighborhood preserving one-to-one connectivity. In simulations convergence is shown to be very fast, corresponding to times of about 50 ms and below if translated to physiological times. Using different pairs of natural grey-level images, we verify that the final one-to-one connectivity states connect corresponding points.

We have extended the model to a full object recognition system by adding a third gallery layer which stores representations of a multitude of memorized images. Recognition is fast (about 100 ms) and, e.g., images of faces can be recognized on the basis of more than 1000 stored identities. A previous neural model of correspondence-based recognition [6] had problems with the neural evaluation of feature similarity and with speed. The model [7] is fast but did not attempt to cope with different feature types.

Acknowledgments: We gratefully acknowledge funding by the Gatsby Charitable Foundation, the Hertie Foundation, the Volkswagen Foundation, and the EU project FP6-2005-015803.

References

Signatures of signal and noise in a model of PO map formation
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It has been proposed that early in cortical development, orientation maps emerge from (electrical) pattern formation [1]. To explore this possibility, we have built a large-scale neuromorphic model of early V1 that consists of a two-layer network of recurrently-connected silicon neurons with short-range excitation and long-range inhibition [2]. The neurons in our network receive isotropic afferent inputs. When the recurrent feedback is tuned to be sufficiently strong, bump-like patterns of neural activity form across the network; these bumps, which are seeded by random component heterogeneity, serve as the scaffold of the map (Fig. A). Similar to animal maps, our chip has smoothly changing orientation domains (because the bumps have spatial extent) that repeat at regular intervals (because the bumps are periodic).

Here, we show that the way in which a bump aligns itself to the stimulus (in a 10ms frame) determines whether that bump contributes to robust selectivity. First, we identify a bump (defined as a contiguous region of activity in a frame), and measure its axis of orientation (when fit to an ellipse). Next, bumps are segregated into an aligned channel, which corresponds to bumps that are parallel with the stimulus (Fig. B, green), and a non-aligned channel, which corresponds to all other bumps (Fig. B, red). Finally, we compare the similarity index (SI) between the converged PO map (created from a long experiment) with PO maps created by sampling frames from the aligned channel (Fig. C, green) and the non-aligned channel (Fig. C, red); a SI of 1 indicates the PO maps are identical, whereas a SI of 0.5 indicates random maps.

Our results show that aligned bumps do not contribute to orientation selectivity (noise) while non-aligned bumps provide robust selectivity (signal). We believe this relationship exists because aligned bumps are driven by direct stimulation and are therefore equally active for all orientations (non-selective). Non-aligned bumps, on the other hand, are driven by recurrent interactions, which can be orientation selective due to biases introduced by the network’s unique scaffold. We propose that activity imaged from early V1 should be analyzed in a similar manner to determine if electrical pattern formation plays an important role in map development.

A Different gratings elicit different bump patterns, resulting in a PO map. B Aligned (green) and non-aligned (red) bumps in a 10ms frame. C Similarity between map from A and channel-specific maps.

References
Natural image statistics predict organization of retinal ganglion cell arrays

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Ganglion cells comprise about ~15 distinct types whose arrays each cover the retina completely and independently. Within an array, one cell's dendrites typically extend to its neighbors somas. Consequently, receptive fields overlap to a degree that merges the individual receptive fields into a flat sensitivity surface. But is this organization optimal for signaling natural scenes? Statistical regularities in natural scenes determine how spatial information is integrated optimally. The shape of individual receptive fields has been predicted by balancing the trade-off between increasing signal-to-noise ratio and reducing redundancy. We followed an analogous approach to determine the optimal spacing of the arrays.

We recorded from pairs of neighboring brisk-transient cells (guinea pig) to measure the overlap of dendritic and receptive fields. Since the ON and OFF subtypes form independent mosaics with different densities, we measured them separately. When neighboring cells were dye-injected, their dendritic fields were seen to overlap. OFF cells overlapped slightly more than ON cells. Confocal microscopy confirmed that the dendritic tips of one cell approximately reached the soma of its neighbor.

Spatial receptive fields were mapped using a random checkerboard stimulus and fit to a difference-of-Gaussians function. The mean spacing (receptive field center separation in units of $\sigma$) between ON centers was $2.0 \pm 0.6 \sigma$, and between OFF centers it was $1.8 \pm 0.5 \sigma$, where $\sigma$ denotes the standard deviation of the center Gaussian. The surround gain (relative to the center) averaged 0.73 (ON) and 0.80 (OFF); the surround size (relative to center) averaged 1.45 (ON) and 1.36 (OFF). In subsequent analyses, we used the average spatial filters (ON and OFF) obtained from this reverse-correlation analysis to model the array's responses to natural images.

Ganglion cells were modeled as summing directly from cones, whose output signal-to-noise ratio was determined from vesicle release rates at different light intensities, assuming Poisson vesicle release. Intensities were chosen from a standard database of natural images. Relative surround size, surround gain, and the absolute distance between cells were fixed to match physiology. For this array, increasing receptive field size had two effects: SNR increased (as more cones were summed), and redundancy increased (as receptive fields overlapped more). These two effects competed so that information in the array peaked at spacings of 1.8 $\sigma$ (ON) and 1.7 $\sigma$ (OFF), within the error of the measured values. These results were robust to variations in absolute spacing, surround gain, surround width, and cone SNR.

Acknowledgments
This work was supported by NIH grants EY08124 and EY016607, and NSF grant IBN-0344678.
About the Triangle Inequality in Perceptual Spaces

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Perceptual similarity is often formalized as a metric in a multi-dimensional space. Stimuli are points in the space and stimuli that are similar are close to each other in this space. A large distance separates stimuli that are very different from each other. This conception of similarity prevails in studies from color perception and face perception to studies of categorization. While this notion of similarity is intuitively plausible there has been an intense debate in cognitive psychology whether perceived dissimilarity satisfies the metric axioms. In a seminal series of papers, Tversky and colleagues have challenged all of the metric axioms [1,2,3].

The triangle inequality has been the hardest of the metric axioms to test experimentally. The reason for this is that measurements of perceived dissimilarity are usually only on an ordinal scale, on an interval scale at most. Hence, the triangle inequality on a finite set of points can always be satisfied, trivially, by adding a big enough constant to the measurements. Tversky and Gati [3] found a way to test the triangle inequality in conjunction with a second, very common assumption. This assumption is segmental additivity [1]: The distance from A to C equals the distance from A to B plus the distance from B to C, if B is “on the way”. All of the metrics that had been suggested to model similarity also had this assumption of segmental additivity, be it the Euclidean metric, the $L_p$-metric, or any Riemannian geometry. Tversky and Gati collected a substantial amount of data using many different stimulus sets, ranging from perceptual to cognitive, and found strong evidence that many human similarity judgments cannot be accounted for by the usual models of similarity. This led them to the conclusion that either the triangle inequality has to be given up or one has to use metric models with subadditive metrics. They favored the first solution. Here, we present a principled subadditive metric based on Shepard’s universal law of generalization [4].

Instead of representing each stimulus as a point in a multi-dimensional space our subadditive metric stems from representing each stimulus by its similarity to all other stimuli in the space. This similarity function, as for example given by Shepard’s law, will usually be a radial basis function and also a positive definite kernel. Hence, there is a natural inner product defined by the kernel and a metric that is induced by the inner product. This metric is subadditive. In addition, this metric has the psychologically desirable property that the distance between stimuli is bounded.

Acknowledgments
This work was supported by the Max Planck Society.

References
Extraclassical Responses in V1 Modeled via Modulated Cortical Conductances

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Two competing phenomenological models of extraclassical spatial summation in V1 are the difference-of-Gaussians (DoG) and the ratio-of-Gaussians (RoG) which argue for subtractive or divisive normalization, respectively, as the basis for a variety of extraclassical response properties, such as surround suppression and contrast-dependent receptive field growth. Problematic with these models, however, is that they are somewhat removed from the neurophysiology and thus do not lend themselves to inferring underlying mechanisms. Simulations of an anatomically and physiologically detailed large-scale spiking neuron model, which we have previous developed [1], indicate that the interaction between excitatory and inhibitory cortical conductances may be at the root of the these extraclassical phenomena and that both subtractive and divisive effects of cortical inhibition are involved. Moreover, Anderson et al showed, using intracellular recordings from cat, that cortical conductances are oscillatory [2], with stronger modulation in the inhibitory conductance. Based on these two observations, we developed a modulated cortical conductance (MCC) model which explicitly captures the observed modulations in the cortical conductances and also accounts for length tuning in the membrane potential. We fit our model to experimental intracellular data (Figure 1A), and compare these fits to those for the RoG and DoG models. We show that our model produces fits as good as, if not better than, these two phenomenological models (Figure 1B), while also providing a more explicit mechanistic explanation for extraclassical spatial summation in V1 neurons.

Acknowledgments
We thank Jeffery Anderson for providing intracellular data. This work was supported by ONR grant N00014-01-1-0625.

References

Figure 1: (A) Example fit of MCC model to experimental data. Points represent data, curves are the fit. Fits for (upper) excitatory conductance, (middle) inhibitory conductance and (lower) resultant membrane potential, generated from the fitted excitatory and inhibitory conductances, using the equation $V_m = (g_E V_E + g_I V_I + g_L V_L)/(g_E + g_I + g_L)$, with reversal potentials $V_E = -0 \text{ mV}, V_I = -80 \text{ mV}, V_L = -66.8 \text{ mV}$. (B) Resultant $\chi^2_N$ for the three models (MCC, DoG, RoG), for data taken from 22 neurons. The DoG and RoG models are fit to the membrane potential while MCC is fit on the conductances and the membrane potential is computed from these fits. In all cases the $\chi^2_N$ is relative to the membrane potential. Axes are normalized so that the total $\chi^2_N$ for all three models is equal to 1. The distance of a point from each bounding axis represents the normalized $\chi^2_N$ for the fit to that model. A point in the center of the triangle represents a neuron that is fitted equally well by the three models, while a point lying in a subregion represents a better fit for one of the three models (total number of neurons best fit by each model is given by n). The size of a point scales with the total $\chi^2_N$ error of all three models. Responses for high contrast gratings are indicated by filled points, and those for low contrast gratings are unfilled.
From perception to action: specific role of the Parietal Reach Region (PRR)


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The PRR of the Posterior Parietal Cortex (PPC) seems to play a role in gating the nervous system to either adjust an old motor program under a new context, or bypass the learning. Prior to movement onset a given cell in this region responds very differently when the pending reach is new from when is automatic (observed in 33/35 cells). We describe two distinct types of cells (in 140 cells from 2 monkeys), useful to form a gating mechanism to correctly select the initiation of the action. This gating signal must be linked to the geometry of the space-time for action initiation, i.e. in what direction of space to start moving, and how far and for how long to follow that direction before starting to stop. This information is in place prior to the onset of movement and the availability of sensory motor feedback. It is relevant as soon as an object in space is perceived as a target for action. As the hand approaches that object the initial time to reach the peak velocity changes as a function of the action’s context. Yet in monkeys and humans reaching the same spatial location through very different trajectories and different τ’s does not alter a geometric symmetry. Across differently curved trajectories and the straight lines joining their starting and ending points two ratios are kept invariant. The partial length of the curve up to the point of maximum bending summed with the corresponding straight line length (perimeter) divided by the total sum of the curve’s and the line’s lengths spans a distribution with maximum always centered at ½. Likewise the ratio of their enclosed partial to total area is about ½. Normally the difference between these 2 ratios is very small. Across different contexts the slope and the intercept of the regression line best fitting these distributions are similar within monkeys and humans. This is the case whether the action is new or already a motor program. It would seem that this is just a mechanical constraint or some inevitable byproduct of the arm’s geometry. Yet we show that this measure is under neural control as not only does it break down when the parietal system is compromised but also it gets fixed when the appropriate feedback is provided. For this geometric symmetry an important parameter to know a priori is τ. In parietal patient S.W. the abnormally high variability of τ (as compared to 9 age-matched normal subjects) leads to large initiation errors that result in excess trajectory bending when he points forward in the dark. This in turn increases the initial perimeter (length) component in the ratio thus breaking the symmetry. When an allocentric cue (vision of the target location) is provided his system binds τ to the space for action, repairs the initiation of the motion and recovers the symmetry. In contrast when an egocentric cue (vision of his moving hand only) is provided τ is not fixed, and neither is the symmetry. His egocentric frame of reference is severely impaired. This work highlights the role of the parietal system in the initiation and guidance of voluntary reaches, and a specific way in which the early perceptual system sets the stage for the later motor system.
A model of extra-classical surround suppression in the lateral geniculate nucleus (LGN)

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We have developed a large scale spiking neuron model of LGN constrained by anatomical and physiological data taken from monkey magno and parvo layers and cat layer A X-cells. Here we present simulations that address extra-classical surround suppression as well the direction tuning of this suppression for stimuli composed of drifting gratings. The suppression we observe in the model is exclusively generated by inhibitory inter-neurons and agrees well with experimental data. Its mechanism relies on the retinotopy and LGN cell density in the model, but does not require more subtle features such as extra-classical surround suppression of retinal ganglion cells, synaptic depression/facilitation, adaptation, cortical-LGN feedback etc. The direction tuning of the surround suppression observed in the model is generated by a combination of the stimulus discontinuity at the aperture-annulus border, sparseness of the LGN connectivity and sparsity in visual space. The model predicts that a difference in sparseness of the LGN connectivity may explain the difference in the degree of surround orientation tuning observed in monkey and cat.

Acknowledgments
This work was supported by ONR Grant N00014-01-1-0625.
Modeling Learning and Adaptation Induced Plasticity of Orientation Tuning in V1

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Hubel and Wiesel demonstrated that primary visual cortex (V1) is the first stage in the visual pathway where cells respond to the orientation of a stimulus. However, there is still controversy over how this property arises. Feed-forward models propose that orientation tuning arises from the alignment of inputs from the LGN to V1. The modified feed-forward model (MFM) is an updated version that includes anti-phase intracortical inhibition to maintain contrast invariance. By contrast, the recurrent model (RM) proposes that LGN inputs are only broadly tuned for orientation and are sharpened through recurrent intracortical connections. We have recently shown that although the MFM is applicable to simple cells, the RM produces complex cells when cells with different receptive field phases are included in the model. We have also developed a modified recurrent model (MRM) which adds anti-phase inhibition to the RM in order to preserve a cell’s receptive field phase. However, the MRM still sharpens a broadly tuned feed-forward input through a recurrent cortical mechanism. Thus, the question still stands: do simple cells achieve sharp orientation tuning through a feed-forward mechanism (such as the MFM) or through a recurrent intracortical mechanism (such as the MRM)?

One fruitful way to address this issue is to examine these models from the standpoint of plasticity. Orientation tuning has recently been shown to be plastic in two different paradigms. Learning an orientation discrimination task has been shown to 1) sharpen orientation tuning curves near the learned orientation and 2) modestly broaden tuning curves far from the learned orientation, while adaptation has been shown to 1) broaden tuning curves near the adapted orientation, 2) modestly sharpen tuning curves far from the adapted orientation, and 3) skew tuning curve peaks away from the adapted orientation. We have previously modeled all of these changes using the RM. Here, we compare the MFM, the RM, and the MRM in order to assess how well each model can reproduce the plasticity data. Learning and adaptation in the orientation domain have both been found to lead to a suppression of neural activity for cells whose preferred orientation is near the learned or adapted orientation. Suppression of firing may be either pre-synaptic (e.g., via synaptic vesicle depletion) or post-synaptic (e.g., via receptor desensitization). For the MFM, the RM, and the MRM, we explore the effects of pre and post-synaptic reductions in both excitatory and inhibitory cells in order to assess how well each of the three orientation models may account for the published learning and adaptation data. We find that the RM and the MRM are better able to do so than the MFM. Two key features are found to be required for plasticity: 1) a feed-forward input from the LGN that is broadly tuned for orientation, and 2) recurrent intracortical connections that sharpen the feed-forward tuning. These two features are prominent in the RM and MRM and absent in the MFM. Our work suggests that 1) complex cells that achieve sharp orientation tuning in a recurrent fashion (such as in the RM) will show all aspects of learning and adaptation-induced plasticity, and 2) the extent to which the MRM verses the MFM is applicable at the simple cell level may be assessed by the degree of observed plasticity in simple cells.
Timing Perisaccadic Visual Processing Using Multi-modal Temporal Order Judgments

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Unlike the auditory, or (for the most part) olfactory and somatosensory systems, the human visual system takes input in brief and discrete samples. In spite of this, we are able to act smoothly and perceive the visual world as temporally and spatially continuous. How the visual system deals with the spatial problem architecturally has received considerable attention, however its temporal dynamics (or alternatively how we solve the problem’s temporal component) has only of late been given serious consideration. That we know relatively little is evidenced by the discovery that for a period (~70 ms) immediately before a saccade, a pair of flashed stimuli will be perceived as having happened in the ‘wrong’ order. We establish experimentally that unimodal auditory stimuli are not subject to this distortion and then use an audio-visual temporal order judgment paradigm to determine why and how the illusion occurs in vision. By examining changes to the multi-modal point of subjective simultaneity we are able to discern that the processing of a single visual stimulus is altered as a function of when during saccade generation the stimulus occurs. Our latest results indicate that visual processing during earlier periods (80-40 ms pre-saccade) is slower when compared to processing during later periods (40-0 ms pre-saccade), suggesting that visual temporal continuity may be maintained by differentially varying speed of processing.

Acknowledgments
This work was supported by a Canadian Natural Sciences and Engineering Research Council Scholarship and NSF CAREER Grant 0133996.

References

Coherence of local field potentials in monkey primary visual cortex in the context of a relative disparity judgment task.

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The temporal binding model states that coupling of neuronal signals on a millisecond time scale serves to flexibly bind groups of neurons into functional assemblies. Within this framework neurons can, for identical stimuli, be part of different assemblies depending on the global percept. Alternatively, strength of signal coupling might be unaffected by the global percept and merely reflect the visual stimulus and the underlying anatomical cortical connectivity. We examined temporal binding of neuronal signals in a globally unambiguous scene-segmentation task with stimuli that could locally, on the spatial scale of neurons in primary visual cortex (V1), be either ambiguous or not.

The stimuli, two overlapping rectangles (∼ 6.5° × 2°) together forming a cross, were presented binocularly with a Wheatstone stereoscope. The horizontal rectangle was presented with either crossed or uncrossed disparity to mimic stimulus configurations with either the horizontal or the vertical rectangle in front. In the locally unambiguous condition the surfaces consisted of random-dot patterns. In the locally ambiguous condition the surfaces of the rectangles were homogeneous, i.e., task-relevant disparity information was restricted to the vertical borders of the rectangles. We recorded local field potentials (LFP) with a 2 × 8 microelectrode array from the upper layers of V1 while a macaque monkey performed a relative disparity judgment task. Stimuli were positioned so that half of the RFs were located each on the overlapping part of the rectangles and the branch of the horizontal rectangle, respectively. The RFs located on the overlapping part could either code the horizontal or the vertical rectangle, depending on the relative disparity of the two rectangles. LFP coherence was calculated for all pairs of simultaneously recorded units.

We compared LFP coherence of pairs of recording sites when both sites coded the same versus different objects (horizontal versus vertical rectangle in front). In the locally unambiguous condition coherence was reduced by 38% ± 2% (mean ± standard error, p < .0001, Wilcoxon Signed Rank Test) in the α- and β-band ∼ 160 – 300 ms after stimulus onset when the recording sites coded different objects. This reduction was drastically attenuated (3% ± 2%, p < .01) in the locally ambiguous situation. Contrary to our expectations, modulation of coupling strength in the γ-band was not observed in any case.

In summary, coherence of LFP is strongly influenced by the local stimulus configuration but covaries only weakly with the global disparity cues in cases with locally ambiguous stimuli. This could be explained by selectivity of lateral connections to absolute disparity preference. Thus, our results suggest that signal coupling might support the formation of certain percepts in situations with locally unambiguous stimuli, while different global percepts do not influence signal coupling in V1 when locally identical stimuli are presented.

Acknowledgments
Supported by DFG GRK 885 and FOR 560.
Learning Invariant and Variant Components of Time Varying Natural Images Using a Sparse, Multiplicative Model

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A remarkable property of biological visual systems is their ability to infer structure within the visual world. In order to infer structure, a useful representation should separate the invariant from the variant information [1, 2]. Invariant information is important for determining ‘what’ we are seeing, recognizing objects and interpreting scenes; while variant information captures the ‘where’ or ‘how’ information, the transformations of objects. It has been hypothesized that biological visual systems represent ‘what’ and ‘where’ visual information in two separate cortical processing streams [3]. How do biological systems decompose visual information into separate invariant and variant representations?

To explore such a decomposition, we present a model that learns to separate the invariant from the variant part of time varying natural movies. We first reformulate the sparse coding model [4], in which images are represented as a generative model of linear over-complete bases with sparse causal variables, so that images are instead represented in terms of a multiplicative interaction between two sets of causal variables. One set of variables is constrained to change slowly over time (the invariant representation), and the other set of variables is allowed to change quickly over time and is encoded as a phase angle (the variant representation). These variables effectively decompose the original sparse coding variables into invariant and variant representations.

After training on natural image sequences, the learned basis functions are similar to those produced by the original sparse coding model: Gabor-like functions that are spatially localized, oriented and bandpass. However, the multiplicative decomposition produces both invariant components with slowly changing responses, which indicate the presence of a visual shape, and variant components in the form of processing phase angles over time, which indicate their transformations. The model thus predicts two classes of cells in primary visual cortex that form the beginnings of the ‘what’ and ‘where’ cortical streams. Moreover, our model’s decomposition provides a starting point for the construction of hierarchical models that capture the global structure and interaction of the ‘what’ and ‘where’ representations.

Acknowledgments
This work was supported by NGA grant MCA 015894-UCB and NSF grant IIS-06-25223.

References
Surrounding Modulation in Consistent Perception of Border-ownership among Various Shapes

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A number of cells in monkeys’ V2 and V4 are selective for border-ownership (BO) that indicates the direction of figure with respect to the border [1]. A notable character of the cells that appears to be crucial for natural image processing is the consistent determination of BO for various stimuli. Each cell has preferred shapes, and is not capable of determining BO for all stimuli (incomplete cue-invariance), but it rarely shows contradictory BO for different stimuli (consistency).

We propose that surrounding regions (SR) localized asymmetrically with respect to the classical receptive field [2] are essential for the cortical mechanism underlying the BO-selectivity [3]. The major concern for the model with surround modulation is consistency among stimuli, because such a simple mechanism may signal contradictory BO depending on stimuli. To investigate the robustness of the model, and the essential factors for the valid and consistent determination of BO, we generated 300 model-cells with their SRs given randomly, and carried out the simulations of the model cells with pseudo-random block-stimuli that approximate all possible shapes including occlusion. The model reproduced major characteristics of BO-selective neurons including incomplete cue-invariance and consistency among various shapes. Our multiple regression analyses indicated that the major characteristics of surround modulation apparent in V1, such as suppression dominance and orientation dependence, are crucial for the correct determination of BO.

To compare further the model characteristics and human perception, we measured psychophysically the reaction time for the detection of BO for the block stimuli, and compared the rank of reaction time with the rank of consistency computed from the 300 model-cells. The rank of model consistency shows good agreement with the rank of reaction time. These results indicate that the model based on the surrounding modulation reproduces the consistent determination of BO among various shapes.

Acknowledgments
This work was supported by grant-in-aid from the Brain Science Foundation and the Okawa Foundation. HN is supported by JSPS (KAKENHI for JSPS fellows, 17.7216).

References

Fig.1 Consistency of the model for stimuli with different degrees of complexity. Seventy-six units that showed perfect BO consistency for all of twelve 4-block-stimuli continue to show high consistency for more complex stimuli of 6- and 8-block stimuli (a total of 112). Lines connect the same model cell. A few examples of stimuli are shown at the bottom. The model is robust in that it shows consistent BO while the complexity of the shape is increased.
Task Dependence of Image Statistics at the point of gaze in a natural wooded environment

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Theories of optimal coding propose to understand early sensory processing of stimuli as being adapted to the statistics of the signals naturally occurring when interacting with the environment [1, 2, 3]. Relating this approach to vision, the regularities of natural image sequences have been investigated, eg. [4,5]. But, given that perception is active, the stimuli at the retina are dependent on oculomotor control and therefore on the executed task [6]. How do different tasks affect the statistics of image features at the fixation location? In the past a number of studies have shown that features at fixation locations are different from those selected randomly in natural scenes [7,8]. Those results were obtained by subjects looking at briefly presented static images of natural scenes subtending a limited visual angle in a laboratory environment while mostly executing the so-called ‘free-view’ task. How do these results transfer from the laboratory environment to real natural environments in which subjects execute natural goal directed behavior?

In order to address this question, eye movements of human subjects acting in a natural wooded environment were tracked with a custom-made portable eye tracker. An HD-video camera mounted on a bicycle helmet recorded the visual scene with a digonal field of view of 75 degrees. This high-resolution video allowed for the accurate analysis of visual features at fixation location versus locations chosen randomly within the visual scene. Three subjects each executed a search task, a ‘free-view’ task and a walking task. Each task had duration of approximately 90 seconds. The eye tracker was calibrated between trials.

Here we report results from the analysis of the spatiotemporal autocorrelation functions obtained from the natural scene sequences separately for the three different tasks and sets of image patches chosen according to three random sampling methods. The data show significant statistical differences between the tasks. We therefore conclude that theories of optimal coding of sensory stimuli should take into account explicit task influences.

References
Why Don’t We See Color At Night?

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Introduction. Rod photoreceptors mediate vision at low light levels while cones take over at high light levels. With rare exceptions [1], the rods within a single retina contain identical photopigment and cannot support color vision, while cones generally come in several classes each with different spectral tuning. The presence of multiple cone types enables color vision at high light levels. Why is it usually advantageous not to have color vision at night?

Van Hateren [2] analyzed the properties of optimal front-end filters for a model visual system. He showed that as signal-to-noise ratio (SNR) drops with overall light level, the degree of spectral opponency (a marker for color vision) in the optimal filters also decreases. We adopted the same general approach, but studied a model visual system built on an explicit representation of the retinal receptor array.

Methods. The model visual environment consisted of discrete images that varied over N pixels in one spatial dimension. The images had two color bands, which we refer to as “L” and “M.” The statistics of the image ensemble were specified by a multivariate normal distribution with known mean and covariance. The distribution was separable in space and color, with equal mean and variance in the two color bands. The image was transduced by a model retina with K < N receptors. Either an L- or an M-sensitive receptor was placed at each location. An L receptor’s response was given by the optically-blurred L-band image at the receptor’s spatial location plus normally-distributed additive noise, and similarly for M receptors.

We estimated the two-band color image from the array of receptor responses in a manner that minimized the expected squared estimation error [3]. We compared the expected error, taken over many draws from the image ensemble, for various choices of L/M arrangement on a regularly-spaced receptor array. Optical blur was commensurate with receptor spacing, and the image ensemble was specified with high correlations between color bands and between neighboring pixels.

Results. When receptor noise had equal variance for L and M, the optimal arrangement was alternating L and M receptors, independent of overall SNR. Real receptors with different spectral sensitivities, however, have different intrinsic noisiness [4]. When the relative noise variance for M was lower than for L, the alternating arrangement remained optimal at high overall SNR but an all-M arrangement became best as overall SNR decreased. This result (dichromatic retina best at high SNR and monochromatic retina best at low SNR) provides an optimality explanation for the design of most biological retinas.

Acknowledgments. This work was supported by NIH grant RO1 EY10016.

References. 
One dimensional measures of higher-order image structure predict human performance at discriminating complex form

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Higher-order image statistics describe complex and potentially more informative aspects of visual scenes such as corners or intersections. Such features are not accurately described until sets of spatial interactions between four or more points are taken into account [1]. The encoding of such image structure by the visual system cannot be studied with traditional, typically 2\textsuperscript{nd}-order tools such as gratings. Moreover, higher-order spatial correlations are difficult to quantify and to control experimentally. The present research overcomes such difficulties by extending the pioneering texture approach of Julesz [2].

A large battery of textures recently proposed by Maddess and co-workers [3, 4] were employed. The test battery consisted of 21 collections or ensembles each containing individual textures generated by the same set of mathematical rules. Importantly, the average third-order (and lower) correlation functions (3CFs) of each ensemble are not significantly different from zero, as is also the case for evenly distributed noise patterns (pixel values assigned randomly and with equal probability). In order to discriminate such ensembles from each other and from noise patterns one must learn ensemble specific higher-order features. A two alternative forced choice (2AFC) psychophysical study was conducted to determine the average discriminability of each of the 21 ensembles in 24 subjects. Data yielded psychometric functions (PFs) that gave the mean probability of correctly discriminating a given texture ensemble from noise patterns. PFs were compared with higher-order measures of image information (entropy) to gain insight into how subjects may be detecting statistical structure within each of the ensembles. Results suggest that histogram-like entropy statistics based on the occurrence of n-pixel (n \(>\) 5) combinations along single or multiple (depending on learning and viewing time) one dimensional horizontal strips within textures were sufficient to accurately capture human performance. The best \(R^2\) fit between PFs and horizontal entropy measures was 0.97. These findings may suggest how local filter information may be pooled across space to confer higher-order sensitivity.

Acknowledgments

This work was supported by the ARC Centre of Excellence in Vision Science. Grant no: CE0561903

References


Mechanisms of learning and attention in the auditory system of the barn owl

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One of the most fascinating properties of the brain is its ability to learn: its ability to alter its functional properties as a consequence of the interactions of an animal with the environment. The influence of experience on the brain is strong especially during early life and is modulated throughout life by the internal state of the animal. Attention, in particular, has a powerful modulating effect on learning. I will discuss a well-studied example of these principles: The effects of experience and attention on sound localization and auditory spatial processing in the barn owl.
Spikes in the Auditory Forebrain: Surprise, Not Intensity

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High-level sensory neurons encoding natural stimuli are not well modelled by linear filters operating on the time-varying stimulus intensity¹. Nonlinear neural models predict marginally better, but they often fail to advance our understanding of the neural code, since they can be difficult to interpret². We modelled auditory neurons in Caudal Mesopallium (CM), a secondary forebrain area of the male zebra finch, with linear filters convolved not with stimulus intensity, but with stimulus surprise. Surprise was quantified by taking the logarithm of how probable the stimulus was given its recent history, and by separating louder- and quieter-than-expected stimulus features, as follows:

$$Surprise = \begin{cases} -\log(P(S|D)) + \log(P(S_{ML}|D)) & \text{if } S < S_{ML}, \ 0 & \text{otherwise} \\ -\log(P(S|D)) + \log(P(S_{ML}|D)) & \text{if } S > S_{ML}, \ 0 & \text{otherwise} \end{cases}$$

(1)

$S$ is the stimulus now, $D$ is the stimulus’ recent history, and $S_{ML}$ is the most likely stimulus given the recent history. Representing the stimulus using Equation 1 instead of a spectrogram, predictions of neural responses to conspecific song improved by an astounding 57%. This improvement could be attributed neither to the gain control mechanisms we know to be present in the cochlea, nor to the separation of louder- and quieter-than-expected events.

We found the coding scheme CM uses for a type of synthetic auditory noise can be better understood if we assume CM is tuned to represent song even when noise is being played. Our results are easily interpretable: a spike in CM indicates a specific degree of surprise given the expectation of hearing song.

Acknowledgments
We thank S. M. N. Woolley and T. Fremouw for data acquisition. This work was supported by NIH grants MH59189 and DC07293.

References

Spike timing-dependent plasticity and the didactic reorganization of cortical receptive fields.

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The precise nature of the synaptic plasticity that governs neuronal receptive field properties \textit{in vivo} is not known. V1 neurons that have their receptive fields eclipsed by a circumscribed retinal lesion subsequently form ‘new’ receptive fields on intact retina outside the lesion. We studied the specific directions in which these receptive field ‘shifts’ occur, and compared them to those produced by a network model of V1. We observed that the \textit{in vivo} receptive fields rarely shifted towards the closest available region of intact retina. This result is surprising, since it is inconsistent with the expectation that neurons respond to feedforward input loss by potentiating their strongest available intracortical connections [1, 2]. Furthermore, even when these receptive fields were separated by large distances prior to lesioning, creation of the lesion caused them to shift in a correlated, convergent manner. The V1 model represented a 2D topographic arrangement of neuron populations with narrow feedforward and broad intracortical input connections that were constrained by electrophysiological and anatomical data. These connections were modulated by both homeostatic plasticity (eg ‘synaptic scaling’ [3]) and homosynaptic plasticity (LTP/LTD). A detailed comparison of our empirical and simulation results revealed that the \textit{in vivo} receptive field shifts we observed are consistent with synaptic modifications at V1 intracortical connections that are dependent upon the temporal order of pre- and post-synaptic spikes (spike timing-dependent plasticity) and are inconsistent with modifications that depend only on the temporal correlation between these spikes (correlation-dependent plasticity). Consistent with previous theoretical work [4], our results indicate that spike timing-dependent plasticity drives receptive field shift convergence by creating competition between neurons for the control of spike timing within the network. In our model the spatial scale of this competition is controlled by the network’s homeostatic balance of excitation and inhibition, revealing a novel means by which the theorised ‘didactic’ capacity of spike timing-dependent plasticity to transfer response properties between neurons [4] can be effectively switched on and off.

\textbf{Acknowledgments}
Support contributed by: BMBF 10025304 (Germany), ARC (Australia).

\textbf{References}
Unraveling fine-scale and cell-type specificity of cortical circuits

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We have studied primary visual cortex to better understand how neural circuits give rise to perception. We have found that cortical circuits are extremely precise, such that different neuron types, and even neighboring neurons of the same type, are connected differently. For example, different types of inhibitory neurons with overlapping dendritic arbors receive connections from different cortical layers. And neighboring excitatory neurons only receive common input from the same presynaptic neurons in the minority of cases when they are directly connected to each other. This fine-scale and cell type-specific organization implies that studies of relationships between circuits and function should match this level of organization. To test hypotheses about contributions of specific cell types to neuronal responses and to perception, we have developed methods to allow reversible inactivation of selected cell types. We find that expression of an insect neuropeptide receptor which couples to GIRK channels can be used to selectively, quickly, and reversibly eliminate the activity of neurons in vivo. This methods allows tests of the role of particular cell types within the intact, functioning neural network. To allow the circuitry of specific neurons to be more directly linked to function we have developed a method that allows the neurons directly presynaptic to a single neuron to be labeled genetically. This method is compatible with functional characterization of the postsynaptic neuron and future development should also allow functional characterization of the presynaptic cells by expression of genetically encoded activity sensors.
**Functional constraints do not cause observed correlations between maximal conductances in an identified neuron**

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Neurons typically express many different types of voltage-gated channels. The density of these channels, their kinetics, and their spatial distribution determine how the neuron behaves. While the density of channels in a particular identified neuron can vary widely, the behavior of that cell in a network is often tightly conserved [1]. Naively, this seems paradoxical. However, if different conductances are correlated, this could resolve the apparent paradox. In the stomatogastric ganglion (STG) of the crab, *Cancer borealis*, recent work has shown that the expression levels of many voltage-gated channels are correlated [1,2,3]. While it is tempting to conclude that these correlations are necessary for the cell’s behavior to be tightly constrained, it is not at all clear that this is the case. We wanted to understand whether the observed correlations are necessary for these neurons to function properly.

We investigated this question by constructing a population of multicompartment models of the LP neuron. Each member of this population had maximal conductances drawn randomly, independently, and uniformly from a range that roughly matched the observed biological range. We generated, simulated, and automatically classified the behavior of ~240,000 model neurons. We then filtered this population, selecting only those neurons whose behavior was consistent with the behavior of the LP cell. This was done by measuring six different properties in each model cell and comparing their values to those in biological LP cells. The six measurements were: resting membrane potential, tonic firing rate, input resistance, phase of spike onset, spike-frequency within the burst, and slow-wave oscillation amplitude. These quantities have all been measured in biological LP cells, and model LPs were considered “admissible” if they were within two standard deviations of the mean value of these measurements. Of the original ~240,000 models, 131 qualified as admissible LP models.

The data on mRNA expression levels show strong positive correlations between the levels of four channel genes: shab (Kd), shaw (Kd), shal (A) and IH (h). (All pairs were correlated.) We looked for correlations between the corresponding channels in the model population of 131 cells, but failed to find any such correlations. The lack of correlations in the model suggests that the observed correlations are not necessary for a neuron to function as a proper LP neuron. This implies that the correlations found in the data may be present for reasons not related to electrophysiological function per se. For instance, they could reflect constraints imposed by the architecture of channel expression regulation.

**Acknowledgments**

We thank J.M. Goaillard and D.J. Schulz for helpful discussions. This work was supported by NIH NS50928 (ALT), and NIH MH46742 and the McDonnell Foundation (EM).

**References**


Synchronized excitation and inhibition during spontaneous and sensory evoked response in the rat barrel cortex

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The firing of a cortical neuron is shaped by the fine balance and timing of excitatory and inhibitory inputs [8, 6, 5]. Yet, the instantaneous correlation between excitation and inhibition during spontaneous or evoked response remained unknown. In fact, due to the lack of such data some studies even assume that these two inputs are uncorrelated (or independent), e.g., see [7, 4]. The scarcity of experimental data is explained by the fact that extracellular recordings are not able to directly address this question, while the intracellular recordings can only present an average picture, by calculating the synaptic conductance from the averaged data obtained at different voltages [1, 8].

In this work we demonstrate a new approach which allows to present adequate real-time picture of the correlation between excitatory and inhibitory inputs to cortical cells. It is based on simultaneous intracellular recording from pairs of nearby neurons that receive similar synaptic inputs. We have performed a series of such recordings in the barrel cortex of halothane anesthetized rats (the spontaneous activity in this preparation is similar to the activity observed in awake animals [3, 2]). To find the extent of correlation between inhibition and excitation during spontaneous activity, the cells’ membrane potential was recorded when both cells were hyperpolarized (activity dominated by EPSCs), depolarized (activity dominated by IPSCs) and when one cell was depolarized and the other hyperpolarized (in both possible combinations). A marked correlation between the cells’ membrane potentials was observed in the first two cases. In addition, high (negative) correlation was observed between the hyperpolarized membrane potential of one cell and the depolarized membrane potential of the other. Together these observations imply that spontaneous EPSCs and IPSCs of individual cells are also highly correlated. The observed high correlation is due to two main factors. First, there exists a high temporal correlation between the EPSPs and IPSPs. In addition, the amplitudes of the excitatory and inhibitory events are also strongly correlated. In some pairs we also examined the correlation between excitation and inhibition in single trials during whisker stimulation. A strong correlation between the excitatory and inhibitory sensory evoked inputs of the cells was found, though for trials with small evoked EPSPs almost no inhibition was observed. Our results indicate that a strong coupling exists in the cortex between excitation and inhibition during both spontaneous activity and evoked responses. They also suggest that inhibitory inputs are evoked only when strong excitation is measured. These findings demonstrate the strength of our experimental approach in revealing the instantaneous excitatory-inhibitory dynamics of cortical activity.

References
A neural mechanism for decision-making, or how I learned to stop worrying and love the bound

Michael N. Shadlen

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With little sophistication, the spike rates from sensory neurons can be used to approximate useful statistics for decision-making. In the context of deciding between two sensory hypotheses, a simple difference in spike rate between sensory neurons with opposite selectivity is proportional to the log likelihood ratio in favor of one sensory interpretation over another. I will describe neural recording experiments that demonstrate the use of such a difference during decision-making in a 2-alternative direction discrimination task. The accumulation of this difference to threshold (a.k.a., “the bound”) explains the speed and accuracy of simple decisions. A new probabilistic classification task, similar to the “weather prediction task” reveals a direct representation of log probability in parietal cortex. And, if time permits, I will explain how the brain uses elapsed time to decode such probability. Interestingly, the neural computations that underlie such decision-making were anticipated during WWII by Alan Turing and Abraham Wald. Turing applied this tool to break the German navy’s Enigma cipher, while Wald invented the field of sequential analysis. In addition to mathematical elegance and winning wars, our experiments suggest that this computational strategy may lie at the core of higher brain function.
Role of serotonin in delayed reward choice in humans

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Although deregulation of the neuromodulator serotonin has long been implicated in disorders such as depression and impulsivity, its normal function in the human brain has remained enigmatic. In animals, decreased serotonin levels increase impulsive choice[1,2], presumably via an increase in the rate of discounting[2], which renders large delayed rewards less valuable than small immediate rewards. Here, we studied the effect of serotonin manipulation in humans in computer tasks in which subjects must choose between a more immediate small reward and a large delayed rewards at each trial; in these tasks, each choice affects the time remaining for later trials, and the delays vary at each trial.

We first studied the shape and the steepness of the reward discounting function adopted by our subjects in the control serotonin condition. We demonstrated that most of our subjects adopted exponential discounting in this experiment[3]. Further, we showed analytically that exponential discounting, with a decay rate comparable to that used by our subjects, maximized the total reward gain. Our results suggest that the particular shape and steepness of temporal discounting is determined by the task that the subject is facing, and question the notion of hyperbolic reward discounting as a universal principle.

Then, by using a computational model of delayed reward choice learning, we estimated the parameters governing the subjects’ choice behavior in low, normal, and high serotonin conditions. We found an increase in the rate of discounting of delayed rewards in the low serotonin condition compared to the control and the high serotonin conditions. Neither the speed of learning of the reward values, nor the variability of choice were affected by serotonin levels, however. Our findings confirm the role of serotonin in evaluating delayed rewards in humans, a role previously suggested in animal studies.

Finally, we performed a fMRI experiment to elucidate the neural mechanisms of serotonin in the evaluation of delayed rewards. A model-based analysis showed that the activity of the ventral part of the striatum correlated with reward prediction at shorter time scales, and that this activity was stronger at low serotonin levels. In contrast, the activity of the dorsal part of the striatum correlated with reward prediction at longer time scales, and this activity was stronger at high serotonin levels. Our result suggests that serotonin controls the time scale of reward prediction by differentially regulating striatal activity.

Acknowledgments
This work was supported by CREST, and by grants NIH P20 RR020700-02 and NSF IIS 0535282 to NS.

References
Credit Assignment with Bayesian Reward Estimation

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Evidence suggests that neurotransmitter dopamine is involved in the process of learning viso-motor behaviors¹. Moreover, reinforcement learning (RL) algorithms have been formulated that characterize well the neuronal signals of dopaminergic neurons in response to the occurrences of stimuli associated with rewards and the delivery of the rewards across learning². Such algorithms have been successful in modeling those responses in cases where only a single variable describes the current state of the world. But most of the time, multiple goals have to be pursued simultaneously. This problem has proven to be intractable for even small numbers of goals because of the exponential growth of the state space. One solution to this problem is to realize a single RL algorithm that uses a high dimensional state space with compositions of RL algorithms that utilize lower dimensional state spaces. Such an approach allows composite visuo-motor behaviors to be synthesized from simpler such behaviors. However taking such an approach introduces problems of its own. First, an action selection mechanism has to decide which action to choose, given that the different algorithms may suggest different actions at the same time. Secondly, given the total observed reward, the organism has to learn what fraction of this belongs to each algorithm. Sprague³ showed in simulation that individual behaviors can be learned in combination by reinforcement learning. However that simulation assumed that the rewards associated with the individual behaviors were known. In practice this is an unreasonable assumption for biological systems where only the total reward for the composite behavior is likely to be available. One would like to learn the contributions from the different behaviors from the obtained total reward. This is a long-standing credit assignment problem in learning. Chang et al.⁴ showed that an estimate for individual rewards could be obtained if the total reward was assigned to each behavior and the variations in that reward were assumed to be noise. This model made sense in their setting, which had the individual behaviors embedded in different agents, but had problems in that the resultant reward estimates could have a constant bias and be suboptimal.

We showed that the credit assignment problem has a solution when all the behaviors are embedded in the same agent⁵. This allows us to model reward not as a globally broadcasted number⁴, but as a consumable entity. The difference is that in the latter case, the individual reward estimates must add up to the total reward estimate whereas in the former case any reward not assigned to an individual behavior is assumed to be entirely noise. In our algorithm, each behavior only needs to know which subset of other behaviors is simultaneously active and their reward estimates. It can then keep a running estimate of its share as its current estimate adjusted by the total instantaneous reward minus the estimates of the concurrent behaviors. Simulations using a standard multiple Predator–Prey problem showed that when the order that the behaviors update is chosen randomly, the estimated reward for each behavior converges to its true value. We have extended this result to show that: 1) It can be formulated as a temporal difference (TD) algorithm 2) Even when the algorithm chooses a compromise (suboptimal) action, individual rewards are learned correctly and 3) Standard Bayesian cue combination can be used in this setting to weight estimates in the TD formulation according to their inverse variance. Simulations using this new weighting exhibit very fast convergence.

References
Just decide: Computational studies of intertemporal choice in humans and monkeys

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Over the last 5 years the basic architecture for general purpose decision-making in the primate brain has begun to emerge. Growing evidence suggests that circuits of the basal ganglia and the frontal cortex place subjective valuations on the actions available at any instant in time. A second operation, likely in the parietal cortex, selects one of these actions for execution. These empirically observed operations parallel the operations of standard economic theory in which the expected utilities of options are compared during a discrete choice. Confirming that neural circuits represent a quantity like expected utility has been complicated, however, by the fact that under many conditions expected utility and choice are tightly correlated. Our recent studies of inter-temporal choice in both humans and monkeys seem to have overcome this limitation. By studying the subjective values of delayed rewards we have been able to disassociate subjective value from choice under a range of conditions. Our studies of humans using fMRI suggest that the basal ganglia and frontal cortex do explicitly represent a quantity like expected utility. Our single unit studies in monkey parietal cortex suggest that when monkeys make choices early activity (that following the presentation of the available options) represents the subjective value (not choice probability) of those options. Late activity (the activity that immediately precedes action), in contrast, appears to encode choice. These data support the notion that an abstract subjective value, of the type required by axiomatic models of efficient choice, are represented in the primate nervous system. They also suggest that the posterior parietal cortex lies within the choice circuit itself and that single unit studies of this area visualize the operation of a decision-making circuit in action.
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