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 $1/N$. 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.