Bistability in oscillatory cortical modules

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Abstract

There is vast experimental evidence indicating that cortical neurons often oscillate. Underlying mechanisms and ideas about possible functional roles have been proposed, but relatively little work has focused on the dynamics of microcircuits that oscillate. Bistability is a simple yet powerful dynamical behavior. To understand how oscillations may impact the dynamics of cortical networks, bistability was studied in simple network models that either do or do not oscillate. Simulations using rate-based models showed that bistability is more robust to noise and to inhomogeneities in neuronal parameters in networks that oscillate. Thus, oscillations may enhance important dynamical features of conventional networks.

Introduction

Although the experimental evidence showing that cortical neurons display stereotypical patterns of rhythmic activity is quite abundant, the functional significance of these patterns remains uncertain (Salinas and Sejnowski, 2001). Part of the problem is that it is relatively easy to generate oscillations in neural networks, as revealed by modeling studies; for instance, oscillations may arise simply from the recurrent connectivity inherent to single cortical columns (Bush and Sejnowski, 1996; Fuentes et al., 1996). Therefore, it is unclear whether such oscillations are fine-tuned and exploited by cortical circuits for specific functions, or whether they are largely an inevitable by-product of other organizational principles (Singer and Gray, 1995; Shadlen and Movshon, 1999).

Here I take a different approach. Perhaps the role of oscillations will become clearer if we understand better how they affect the dynamics of small networks or cortical modules. So, the idea is to start with a network that has a specific target function, and investigate whether oscillatory activity will, in some sense, help or hinder the implementation of that function. Bistability is a good candidate to begin this inquiry; first, because it is a relatively simple dynamical behavior that may arise even in randomly-connected networks; and second, because a bistable system is essentially a switch, so its potential relevance is clear — indeed, bistability is often an essential element of models of short-term memory (Durstewitz et al., 2000; Koulakov et al., 2002).

Rate-Based Network Model

The network equations I use are similar to divisive normalization models (Simoncelli and Heeger, 1998; Schwartz and Simoncelli, 2001). There are N interacting neurons whose firing rates evolve in time according to

$$\tau \frac{dR_i}{dt} = - R_i + \frac{\left(h_i + \sum_j W_{ij} R_j \right)^2}{s + \sum_j V_{ij} R_j^2} + \eta_i \, , \qquad (1)$$

where R_i is the firing rate of neuron i. The neurons are driven through excitatory synaptic weights $\boldsymbol{W}$, and the sum in the denominator represents divisive inhibition mediated by synaptic weights $\boldsymbol{V}$; all connection weights are positive. The term h_i represents an external input to neuron i that comes from outside the network and is not affected by its activity, and the term η_i represents Gaussian noise; in the simulations, Its standad deviation was set to $\sigma(1+r_i)$, so it included both additive and multiplicative components. In general, in spite of its simplicity, this description provides a good qualitative match to the behavior of more realistic models based on integrate-and-fire neurons (Salinas, 2003).

Bistability With and Without Oscillations

In the above model, regular bistability (no oscillations involved) may be obtained by setting $\boldsymbol{W}$ and $\boldsymbol{V}$ equal to two constant values, or by using random values drawn from uniform distributions (Salinas, 2003). Variability in the background rates as well as sparseness in the connections may be included as well. In this case the network can fire at either of two possible mean rates — about 4 and 40 spikes/s — and the system can shift from one to another through transient changes in the external inputs h_i; this is illustrated in Figure 1a. However, as the noise and sparseness of the network are increased, the high-rate state becomes unstable; this regime is illustrated in Figure 1b.

To generate oscillatory activity, the network was divided into six blocks and arranged as a ring, such that neurons in block 1 excited themselves and those in block 2, these excited themselves and those in block 3, and so forth; units in the last block, block 6, excited themselves and those in block 1. There were inhibitory connections within blocks, and also reciprocal connections between the following pairs of blocks: (1,4), (2,5) and (3,6). This arrangement generates robust oscillations, even when all excitatory and inhibitory connections that are non-zero have the same values (see Figure 1, legend). This is shown in Figure 1c. Partitioning into 6 blocks is not critical, as other numbers can also be used. With the correct parameters, this network has two possible states: the units can either fire at a low, uniform rate around 4 spikes/s, or may oscillate. While oscillating, the mean rate averaged over all neurons is roughly constant at about 30 spikes/s. So, although the individual rates vary continuously, in terms of the population-averaged rate the system can be considered bistable (Figure 1c).

In general, given the same numbers of neurons and similar mean rates, the oscillating network is considerably more robust to noise than the non-oscillating one. The network in Figure 1c, which is stable, includes twice the level of noise as that in Figure 1b, which is unstable. The oscillating network becomes unstable at much higher noise levels than the non-oscillating one. The difference in robustness is even more evident when the networks are sparse (not shown). Currently, I am systematically exploring how this effect depends on network parameters, and plan to investigate whether the same phenomenon is observed in networks of spiking neurons. It would be extremely interesting if oscillations could be arranged so that they increased the stability of more realistic networks.

In conclusion, there are some neural functions that can be implemented either with or without oscillatory neurons. Creating a switch is one of them, and oscillations seem advantageous for this purpose. Perhaps there are other cases in which similar results apply. This would provide some valuable insight into the functional properties of rhythmic activity in the cortex.

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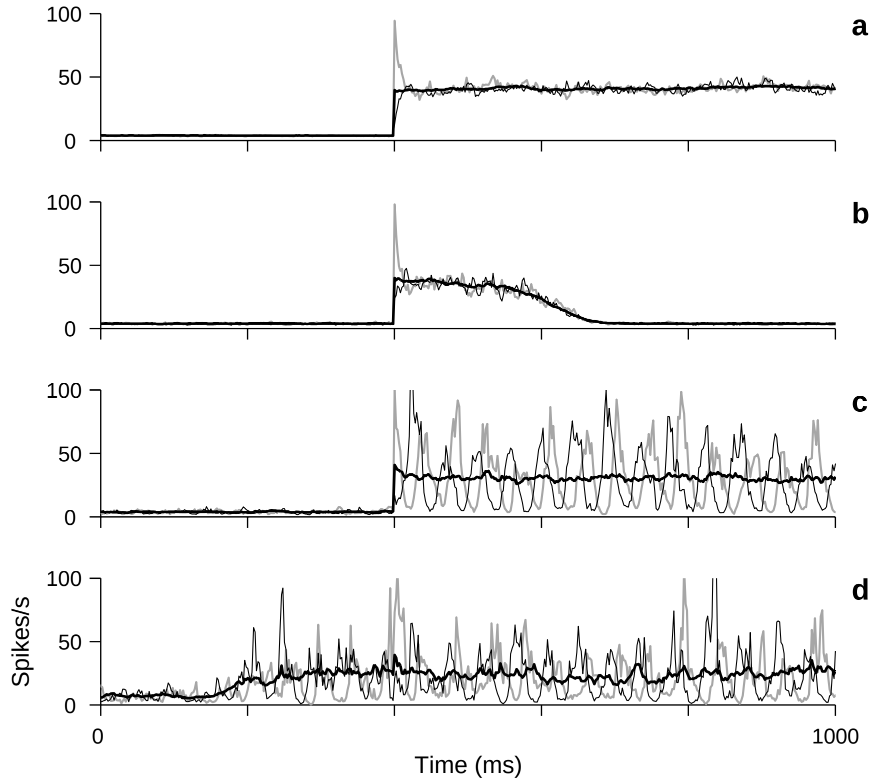

Figure 1. Two bistable networks. Sixty neurons were coupled using Equation 1. Gray and thin black lines show the firing rates of two individual neurons in each network; thick black traces indicate population-averaged rates. In all panels, at t=400 ms all rates were instantaneously increased. **a, b,** Bistability with uniform connections. Here W_{ij}=0.0177 and V_{ij}=0.00024 for all neurons and all connections ($i \neq j$). In **a** and **b**, σ=0.02 and σ=0.04, respectively. With high noise levels the high-rate state becomes unstable and decays spontaneously. **c, d,** Bistability in an oscillating network subdivided into 6 blocks, as described in the text. For all non-zero connections, W_{ij}=0.082 and V_{ij}=0.003. In **c** and **d**, σ=0.08 and σ=0.14, respectively. In this network the two states remain stable at much higher noise levels. Other parameters were: s=40, τ=5 ms, N=60, Δt=0.2 ms. Self-connections were always eliminated.