

Bistability in oscillatory cortical modules

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Abstract

A bistable system exhibits two distinct response levels, so it may act as a switch. Bistability is a common feature of many dynamical systems, including single and interconnected neurons. In general, it provides a simple model mechanism for the gating of neural activity, which may be ubiquitously important for the operation of real nervous systems. Here we explore the range of conditions under which bistability is possible in recurrent neural networks. In particular, we explore whether oscillations affect the capacity of a circuit to produce bistable behavior. To this end, we simulate and compare three types of networks: one with homogeneous parameters (so individual units are identical), another with heterogeneous parameters, and a third that is forced to produce oscillatory activity. We use an evolutionary strategy to generate networks of each type that are bistable in the presence of noise. We find that all evolved networks reach a nearly equal capacity to sustain bistability in the presence of high noise, suggesting that such capacity is not greatly limited by other constraints that may be placed upon a network.

Key words: Gamma oscillations, Recurrent networks, Working memory, Genetic algorithms, Neuron models

1 Introduction

A remarkable aspect of the nervous system is the variety of dynamics that may be observed in neural activity under different conditions. If there are general principles of computation at work in the nervous system, the mechanisms embodying those principles must likewise be able to operate under

¹ Research supported by startup funds from WFUSM and by grant NS044894-01 from the NINDS.

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many conditions. For example, they must operate in the presence of network oscillations, a common feature of neural activity [10,11]. One mechanism which may be broadly important for neural computation is bistability. Our interest in this commonly observed phenomenon [2,3,5,12] stems from its importance to models of mnemonic activity and temporal integration [1,4,6], and from its potential role as a gate of neural activity [8]. However, bistability will not likely be of much use to a nervous system if networks require a narrow set of conditions for its operation. Here we assess just how narrow are the conditions required for bistability, and more specifically, the extent to which bistability can coexist with network oscillations.

We use a simple genetic algorithm [7] to evolve networks capable of bistability. One of these networks is oscillatory; the others do not oscillate, and differ by the extent of their heterogeneity across network parameters. The objective is to measure the relative degree to which the constraints on these networks help or hinder bistability's evolution, and thus to assess its robustness. In other words, is there a particular architecture that is in some sense optimal for generating a bistable switch?

2 Network equations

The network equations we use [8] are similar to divisive normalization models [9]. There are N interacting neurons whose firing rates evolve in time according to

$$\tau \frac{dr_i}{dt} = -r_i + \frac{\sum_j w_{ij} r_j + h_i}{s_i + \sum_j v_{ij} r_j^2} + \eta_i, \quad (1)$$

where r_i is the firing rate of neuron i . Recurrent excitation is mediated by excitatory synaptic weights w_{ij} , and the sum in the denominator represents divisive inhibition mediated by synaptic weights v_{ij} ; all connection weights are positive. The term h_i is an independent, external input to neuron i that comes from outside the network. The term η_i represents Gaussian noise; its standard deviation is set to $\sigma(1 + r_i)$, where σ is a constant, so it includes both additive and multiplicative components. In general, this simplified description provides a good qualitative match to the behavior of more realistic models based on integrate-and-fire neurons [8].

All results shown are for networks with 6 neurons. The three types of networks studied differed in their weight matrices and in their distributions of h and s values. Self-connections were allowed.

3 Network evolution

The evolutionary algorithm [7] was the same for the three types of network, and ran as follows. First, a population of 100 networks was generated, where the free parameters of each unit were chosen randomly from pre-specified distributions. Then all networks were simulated for 6 seconds according to Equation 1. Initial firing rates were chosen from a Poisson distribution with a mean of 2 Hz. After the first two seconds of simulation, all neurons received a transient stimulus, so their rates stepped up to about 50 Hz. The idea was that, in bistable networks, this stimulus would cause a switch from a low to a high firing rate (Fig. 1). At the end of the simulation, a fitness value was calculated for each of the 100 networks. The 6 most fit networks were then cloned multiple times to produce a new generation of 100 networks. The free parameters of the clones were varied (mutated) by small random amounts not exceeding $\pm 2\%$ of their current values. For each network type, this selection continued for a total of 2000 generations. However, the fitness typically reached a high value after about 100 generations, so the noise level σ was incremented every 200 generations.

The fitness function was a product of three terms designed to satisfy three conditions: (1) that the mean prestimulus firing rate of each network stayed near a predetermined target rate of 4 Hz, (2) that the firing rates were not exceedingly high at any time during the simulation, and (3) that there was a clear separation between mean pre- and post-stimulus firing rates. This is the key for obtaining bistable behavior, and was quantified using the classic d' measure from signal detection theory: $d' = (r_{post} - r_{pre}) / \sqrt{\sigma_{post}^2 + \sigma_{pre}^2}$, where r_{pre} and r_{post} are the mean rates of one network before and after the stimulus, respectively; σ_{pre} and σ_{post} are the corresponding standard deviations. The mean rate of a network was obtained by averaging the rates of its 6 neurons. The d' was computed for each of the 100 networks in every generation. Larger values were obtained for networks in which the stimulus provoked a more sustained change in the average rate. Through the selection process, d' values increased progressively from one generation to the next until robust bistability was obtained.

4 Bistability in homogeneous, heterogeneous and oscillatory networks

In homogeneous networks, neurons were connected all-to-all but were identical. All excitatory synapses had equal strength, and the same occurred for inhibitory synapses. Thus, in effect, each network had only 4 free parameters that were initialized and mutated independently during evolution: h , s , the strength of excitatory synapses w , and the strength of inhibitory

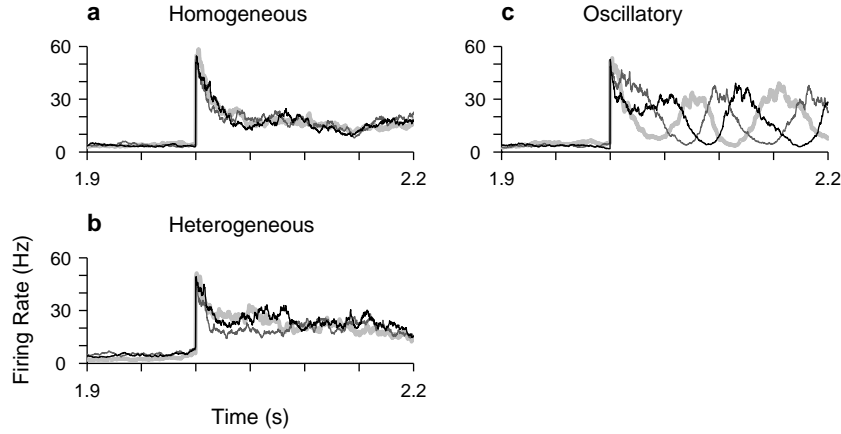


Fig. 1. Bistable behavior in the 3 network types. Each graph shows the firing rate of 3 of the 6 neurons in a network as a function of time, for 300 ms around the stimulus. All networks are shown at generation 790 of their evolution. (a) Traces from a homogeneous network in which all units have the same parameters. (b) Traces from a heterogeneous network in which all parameters may be different across units. (c) Traces from an oscillatory network in which the connection matrices had symmetries that made them prone to oscillate.

synapses v .

Fig. 1a shows the firing rates of 3 neurons over 300 ms around the time of stimulation. The neurons belong to the most fit homogeneous network of generation 790 of the evolution. Prior to the stimulus, the firing rates hover around 4 Hz; following the stimulus and the associated transient, the rates are sustained at around 20 Hz. This network thus exhibits bistability. However, by this point in the evolution, the noise was so high that not even the most fit network exhibited bistability every time it was simulated. This is illustrated in Fig. 2a. Here, the same network from Fig. 1a was simulated 100 times under identical conditions (but different instances of the noise). Each row in Fig. 2 corresponds to one trial; the grayscale intensity indicates the mean firing rate at each point in time, which was computed by averaging the rates of the 6 neurons. The trials (rows) have been ordered by mean prestimulus firing rate. On about 40% of the trials the network switched spontaneously from the low-rate to the high-rate state before the stimulus. Thus, the switch failed in about 40% of the attempts. Note, however, that the probability of failure is a monotonic function of the noise level (Fig. 2d). The key observation is that approximately the same failure rate was obtained for all network types (Figs. 2a-c).

In heterogeneous networks, neurons were connected all-to-all and all their parameters were subject to mutation during evolution. Thus, the value of every synapse was allowed to vary independently, as were the h and s val-

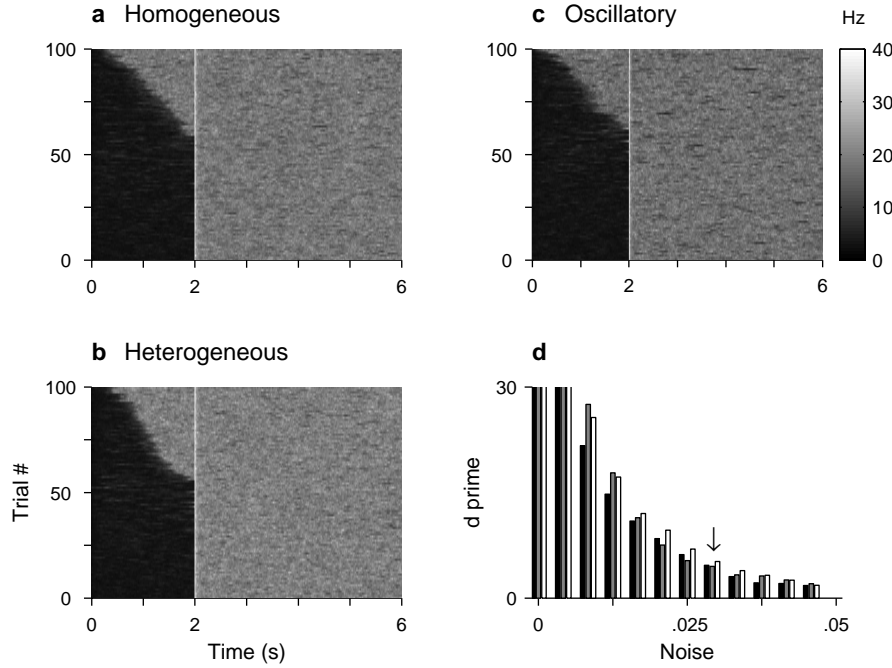


Fig. 2. Failure rate of the three types of network. Panels a–c show 100 simulations of the same three networks used in Fig. 1. Each row corresponds to one simulation trial. The x-axis is time, and the mean firing rate of the network (averaged over its 6 neurons) is indicated by the gray level. For display purposes, trials were sorted by the pre-stimulus rate. An increase in firing rate before the stimulus is a failure of the switch. (a) Homogeneous network. (b) Heterogeneous network. (c) Oscillatory network. (d) Comparison of d' values for different amounts of noise; σ varies along the x-axis. As a reference, the d' in panels a–c goes from 0.1 to 16, with an average of 5. The arrow points to the noise level used to produce panels a–c. As noise increases, d' decreases at about the same rate for the three networks. Black bars, oscillatory network; gray bars, homogeneous network; white bars, heterogeneous network.

ues for each neuron. In total, for each heterogeneous network there were 84 independent parameters. Evolution of such networks resulted in significant heterogeneity across all parameters. Also, the mean firing rates of individual neurons could differ quite noticeably from each other. Fig. 1b shows the firing rates of three neurons from a heterogeneous network after 790 generations of evolution. This network behaves similarly to the homogeneous network pictured above it; in particular, it fails with about the same frequency (Figs. 2a,b).

To generate oscillatory activity, the neurons in each oscillatory network were arranged in a ring, such that neuron 1 excited itself and neuron 2, neuron 2 excited itself and neuron 3, and so forth; neuron 6 excited itself and neuron 1. In addition, each neuron inhibited the neurons 2, 3, and 4 places ahead of it on the ring. Such networks were highly prone to oscillate.

Because all neurons were identical, in effect there were only 7 independent parameters that varied during evolution: h and s , which were the same for all neurons, the two excitatory weights, and the three inhibitory weights. Fig. 1c shows sample firing rate traces from one such network. Like the others, this one has a stable low-rate state around 4 Hz and a high state around 20 Hz, but when the network is in the high-rate state, the neurons oscillate. This network again fails with about the same frequency as the other two (Figs. 2a-d).

5 Discussion

Fig. 2d illustrates more broadly the relationship between bistability and noise for the three networks in this figure. Each bar represents the mean value of d' for a given network type at the specified noise level. A high d' corresponds to situations where spontaneous transitions are rare, so the failure rate is low; fewer failures are seen when the pre- and post-stimulus mean rates are more separated. This figure shows that the separation between the pre- and post-stimulus firing rates is not very different between the three networks for any level of noise. In general, we found that our evolution algorithm consistently led to similar performances across the three kinds of networks. Similar results were observed when we varied several of the algorithm's parameters, such as the mutation rate, the numbers of generations and the precise form of the fitness function. Other quantities, such as the initial distributions of network parameters, the number of units in a network, or the simulation time, did not have major effects either.

Our results suggest that the various constraints we have placed on these networks do not differentially limit their capacity for bistability. Thus, there does not seem to be a 'best' way for constructing a bistable neural circuit, at least within the range of possibilities we have explored. This is somewhat surprising, even within this restricted range, because the number of effective degrees of freedom varied quite drastically between the three network types (from 4 to 84). Regarding oscillations, their mere presence does not seem to hinder or enhance a network's capacity for bistability. These results highlight the ease with which bistability may be achieved in recurrent neural networks, and suggest that it is a highly robust mechanism for gating information flow and for combining a switch with other neural functions or dynamics [8].

References

- [1] D. Durstewitz, J.K. Seamans, T.J. Sejnowski, Dopamine-mediated stabilization of delay-period activity in a network model of prefrontal cortex. *J. Neurophysiol.* 83 (2000) 1733–1750.
- [2] P. Heyward, M. Ennis, A. Keller, M.T. Shipley, Membrane bistability in olfactory bulb mitral cells. *J. Neurosci.* 21 (2001) 5311–5320.
- [3] S. Kalitzin, B.W. van Dijk, H. Spekreijse, Self-organized dynamics in plastic neural networks: bistability and coherence. *Biol. Cybern.* 83 (2000) 139–150.
- [4] A.A. Koulakov, S. Raghavachari, A. Kepecs, J.E. Lisman, Model for a robust neural integrator. *Nat. Neurosci.* 5 (2002) 775–782.
- [5] R.H. Lee, C.J. Heckman, Bistability in spinal motoneurons in vivo: systematic variations in persistent inward currents. *J. Neurophysiol.* 80 (1998) 583–593.
- [6] Y. Loewenstein, H. Sompolinsky, Temporal integration by calcium dynamics in a model neuron. *Nat. Neurosci.* 6 (2003) 961–967.
- [7] M. Mitchell, *An Introduction to genetic algorithms*, MIT Press, Cambridge, MA, 1998.
- [8] E. Salinas, Background synaptic activity as a switch between dynamical states in a network, *Neural Comput.* 15 (2003) 1439–1475.
- [9] O. Schwartz, E.P. Simoncelli, Natural signal statistics and sensory gain control. *Nat. Neurosci.* 4 (2001) 819–825.
- [10] M.N. Shadlen, J.A. Movshon, Synchrony unbound: a critical evaluation of the temporal binding hypothesis. *Neuron* 24 (1999) 67–77.
- [11] W. Singer, C.M. Gray, Visual feature integration and the temporal correlation hypothesis. *Annu. Rev. Neurosci.* 18 (1995) 555–586.
- [12] B. Zhang, R.M. Harris-Warrick, Calcium-dependent plateau potentials in a crab stomatogastric ganglion motor neuron. I. Calcium current and its modulation by serotonin. *J. Neurophysiol.* 74 (1995) 1929–1237.