Neural Network Dynamics

Tim P. Vogels, Kanaka Rajan, and L.F. Abbott

Volen Center for Complex Systems and Department of Biology, Brandeis University, Waltham, Massachusetts 02454-9110; email: vogels@brandeis.edu

Annu. Rev. Neurosci.
2005. 28:357–76

doi: 10.1146/
annurev.neuro.28.061604.135637

First published online as a
Review in Advance on
March 22, 2005

0147-006X/05/0721-
0357$20.00

Key Words

balance, memory, signal propagation, states, sustained activity

Abstract

Neural network modeling is often concerned with stimulus-driven responses, but most of the activity in the brain is internally generated. Here, we review network models of internally generated activity, focusing on three types of network dynamics: (*a*) sustained responses to transient stimuli, which provide a model of working memory; (*b*) oscillatory network activity; and (*c*) chaotic activity, which models complex patterns of background spiking in cortical and other circuits. We also review propagation of stimulus-driven activity through spontaneously active networks. Exploring these aspects of neural network dynamics is critical for understanding how neural circuits produce cognitive function.

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INTRODUCTION

We generate most of our thoughts and behaviors internally, but our actions can be modified drastically by small changes in our perception of the external environment. Stated another way, the neural circuits of the brain perpetually generate complex patterns of activity with an extraordinarily rich spatial and temporal structure, yet they remain highly sensitive to sensory input. The majority of modeling in neuroscience is concerned with activity that is driven by a stimulus. Such models are constructed to account for sensitivity, selectivity, and other features of neuronal responses to sensory input (reviewed, for example, in Dayan & Abbott 2001). In the absence of that input, neurons in these models are typically silent. Although this approach has had considerable success in accounting for response properties in primary sensory areas, such as the early visual system, it clearly cannot account for the majority of activity in the brain, which is internally generated. This review is devoted to modeling work at the other extreme: models that produce their own activity, even in the absence of external input.

Understanding how neural circuitry generates complex patterns of activity is challenging, and it is even more difficult to build models of this type that remain sensitive to sensory input. In mathematical terms, we need to understand how a system can reconcile a rich internal state structure with a high degree of sensitivity to external variables. This problem is far from solved, but here we review progress that has been made in recent years. Rather than surveying a large number of models and applications, we illustrate the existing issues and the progress made using two basic models: a network model described in terms of neuronal firing rates that exhibits sustained and oscillatory activity and a network of spiking model neurons that displays chaotic activity.

We begin the review with a discussion of sustained responses to transient stimuli. Neuronal activity evoked by a transient stimulus often continues beyond the period of stimulus presentation and, in cases where short-term memory of the stimulus is required for a task, such sustained activity can last for tens of seconds (Wang & Goldman-Rakic 2004). Neuronal firing at a constant rate is a form of internally generated activity known as fixed-point behavior. This time-independent activity is too simple to address the issue of how complex patterns of activity are generated. On the other hand, these models provide an excellent example of the problem of making internally generated activity sensitive to external input because, to be of any use in a memory task, self-sustained neural activity must be sensitive to those aspects of the stimulus that are being remembered (Compte et al. 2000, Seung et al. 2000).

From sustained activity, we move on to a discussion of oscillations. Oscillations are a widespread feature of neural systems, and oscillating neural network models have been studied extensively (Marder & Calabrese 1996, Buzsaki & Draguhn 2004). We illustrate this form of network activity by modifying a model with self-sustained activity.

Our next topic covers large networks of spiking model neurons that display complex

chaotic activity. In these networks, excitation and inhibition are balanced so that they nearly cancel, and neuronal firing is driven by fluctuations that transiently spoil this cancellation (Shadlen & Newsome 1994, Tsodyks & Sejnowski 1995, Troyer & Miller 1997). Neuronal responses recorded in vivo are highly variable (Burns & Webb 1976, Dean 1981, Softky & Koch 1993, Holt et al. 1996, Anderson et al. 2000), and it has long been recognized that some form of "noise" has to be included if models of such responses are to match the data (see, for example, Usher et al. 1994). In models, this noise is often added from a random external source, such as a random number generator, which does not match what happens in real neural circuits. Although neurons are subject to thermal fluctuations that act like an external source of noise, it appears that most of the variability in cortical circuits comes from activity generated within the neural circuits themselves (Arieli et al. 1996). Sparsely connected networks of spiking model neurons can generate what looks like random, noisy activity without the need for any external source of randomness (van Vreeswijk & Sompolinsky 1996, 1998; Amit & Brunel 1997; Brunel 2000; Mehring et al. 2003; Lerchner et al. 2004). This is a significant achievement toward the goal of understanding the dynamics of complex neuronal activity.

Spiking network models go a long way toward solving the problem of producing complex, self-sustained patterns of activity, but they fail at accounting for the input sensitivity of biological networks. Returning to this problem, we conclude this review by examining studies of signal propagation in neural networks. For a network to be sensitive to external input, the activity generated by that input must propagate through the network. There has been considerable discussion about the different ways that information might be encoded by neural activity. To be viable, a coding scheme must support propagation of information from one brain region to another (Diesmann et al. 1999, van Rossum et al. 2002). Propagation of signals across neural networks is difficult to achieve because of two sources of instability. First, signals tend to either grow or shrink in amplitude as they propagate from one group of neurons to another. Rather precise tuning is required to prevent signals from either blowing up or decaying away before they reach their targets. This problem is well illustrated in a simple avalanche model of propagation that we review (Harris 1963, Zapperi et al. 1995, de Carvalho & Prado 2000, Beggs & Plenz 2003). Second, signal propagation in neural networks can lead to unrealistic large-scale synchronization of neuronal firing (Marsalek et al. 1997, Golomb 1998, Burkitt & Clark 1999, van Rossum et al. 2002, Reyes 2003, Litvak et al. 2003). Avoiding this problem requires the introduction of noise, which leads us back to sparsely coupled networks of spiking neurons that can generate the required noise internally. As discussed below, signal propagation and sensitivity to input remain significant challenges to our understanding of neural network dynamics.

FIRING-RATE AND SPIKING NETWORK MODELS

The power of present-day computers permits simulation of large networks, even in cases when the individual neurons are modeled in considerable detail. Of course, there is a tradeoff between the amount of detail that can be devoted to modeling each individual neuron (or each synapse, which is even more costly owing to their larger numbers) and the size and complexity of the network that can be simulated. A common compromise is to use a relatively simple spiking model, the integrate-and-fire model, to describe each neuron. This allows simulations of networks with tens or even hundreds of thousands of neurons.

Such networks are complex dynamical systems involving the numerical integration of many thousands of coupled differential equations. In computer simulations, as opposed to experiments, any variable in any neuron or

synapse of the network can be monitored and manipulated. Nevertheless, characterizing and understanding what is going on at the network level can be difficult. Furthermore, time constraints on the simulation of these systems makes it difficult to survey the complete parameter space (which typically has a high dimension) adequately (Prinz et al. 2004). Spiking models are difficult to analyze mathematically, so modeling networks often involves a second approach that uses firing rates, rather than action potential sequences, to characterize neuronal responses (Wilson & Cowan 1972, Shriki et al. 2003).

Firing-Rate Networks

In a firing-rate network, each neuron is described at time t by a firing rate $r_i(t)$ for neuron i, where $i = 1, 2, \ldots N$ labels the N neurons of the network. Each firing rate relaxes with a time constant τ_r to a steady-state value given by a function F that describes the relationship between firing rate and input current for the neuron. The input current for neuron i is the sum of the input from sources outside the network such as sensory input, denoted by $I_i(t)$, and a term describing input from other neurons within the network. The resulting dynamic equation is

$$\tau_r \frac{dr_i}{dt} = -r_i(t) + F\left(I_i(t) + \sum_{j=1}^{N} \mathcal{J}_{ij} r_j(t) + \Theta\right), \qquad 1.$$

where $\mathcal{J}_{ij}$ describes the strength and type (excitatory if $\mathcal{J}_{ij} > 0$ and inhibitory if $\mathcal{J}_{ij} < 0$) of the synapse from presynaptic neuron j to postsynaptic neuron i. The constant Θ acts as a current bias that can induce spontaneous firing if it is positive or suppress firing if it is negative. The time constant τ_r determines how quickly the firing rate can change. For the network shown in **Figures 1** and **2** (see Sustained Activity, below), $\tau_r = 10$ ms.

The assumption behind Equation 1 is that, on average, the input from a given presynaptic neuron is proportional to its firing rate (the factor r_j in Equation 1) and that the total synaptic input is obtained by summing the contributions of all the presynaptic neurons (the sum over j in Equation 1). A number of different forms can be used for the firing-rate function F, but we restrict our discussion to one simple form,

$$F(x) = \begin{cases} x & \text{if} \quad x \geq 0 \\ 0 & \text{if} \quad x < 0, \end{cases} \qquad 2.$$

which assumes a linear relationship between firing rate and current but accounts for rectification, i.e., the fact that firing rates cannot be negative.

To examine the activity generated internally by the model of Equation 1, we set $I_i = 0$ for all i. This spontaneous activity is then determined by the values of the synaptic weights $\mathcal{J}_{ij}$ for all i, j pairs; the constant Θ; and, in some cases, the initial state of the network. We consider different forms for the synaptic weights that generate different types of internally generated activity. To probe the input sensitivity of these networks, we can transiently activate the external inputs and examine what happens.

Integrate-and-Fire Networks

In addition to network models described by firing rates, we discuss networks constructed from a simple model of a spiking neuron, the integrate-and-fire model. In the integrate-and-fire approach, network neuron i is described by a membrane potential V_i. Although the model generates action potentials, it contains no biophysical spike-generating mechanism. Instead, action potentials are generated by a simple rule: An action potential occurs whenever the membrane potential reaches a threshold value V_{th}, and immediately thereafter the membrane potential is reset to a value V_{reset}. Refractoriness can be imposed by holding the membrane potential to this value for a time, the refractory period, following the spike. The network model shown in **Figure 3** (see Chaotic Spiking Networks, below), for example, uses a refractory period of 5 ms.

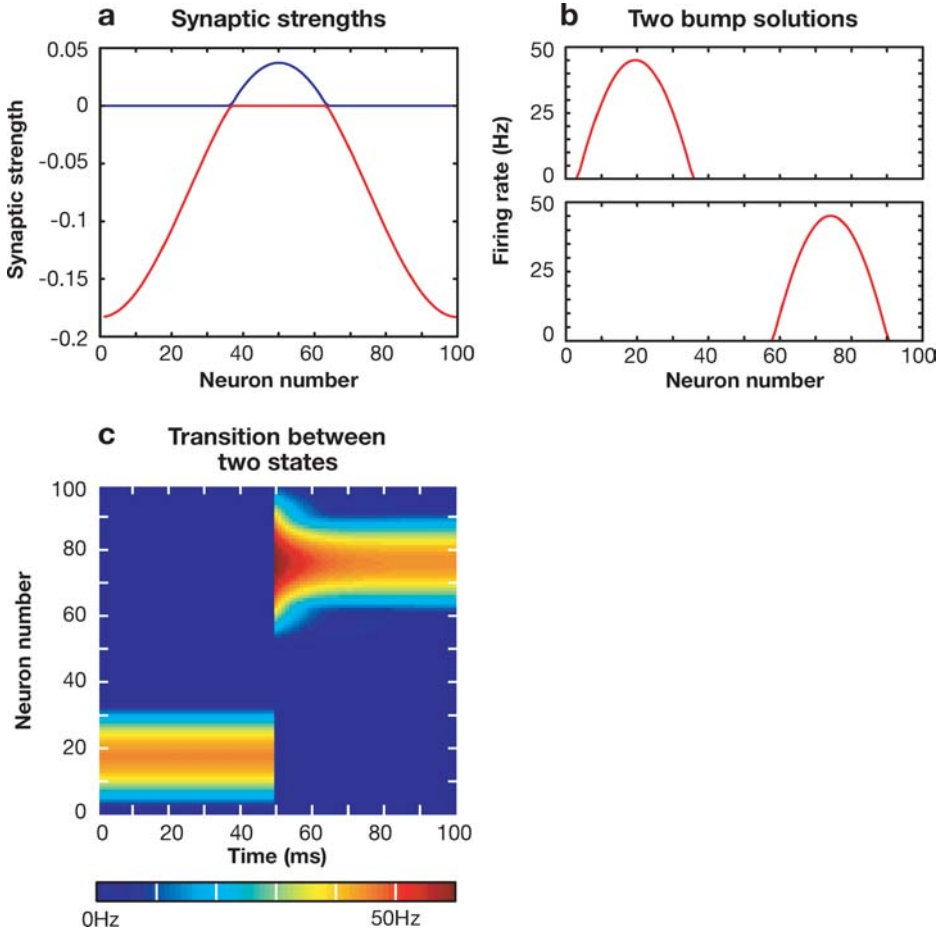

Figure 1

Sustained network activity in a bump configuration. (*a*) The distribution of excitation (*blue line*) and inhibition (*red line*) for a network neuron. These lines indicate the strength and sign of the synaptic weight linking neuron 50 to the other neurons in the network indicated by the value on the horizontal axis. (*b*) Two bumps centered around different neuronal populations. Both plots indicate the firing rate for 100 network neurons. The top panel shows a bump of activity centered around neuron 20, and the bottom a similar bump centered around neuron 75. (*c*) Activity of 100 network neurons as a function of time. A bump of activity centered around neuron 20 was perturbed at time 50 ms to shift it to a bump centered around neuron 75, after a transient.

When an action potential occurs, the time of the spike, denoted by t_i^a, is recorded. The superscript a refers to which particular action potential fired by neuron i occurred at time t_i^a. In other words, the sequence of action potentials generated by neuron i is described by the firing times t_i^a for $a = 1, 2, \ldots$.

The membrane potential in the subthreshold range of the integrate-and-fire model is described by a simple resistor-capacitor circuit or, equivalently, by the equation

$$\tau_m \frac{dV_i}{dt} = V_{rest} - V_i(t) + \Theta + I_i(t) + \sum_{j=1}^{N} \mathcal{J}_{ij} \sum_{t_j^a < t} f\left(t - t_j^a\right) \qquad 3.$$

for neuron i. Here, τ_m is the membrane time constant, V_{rest} is the resting membrane

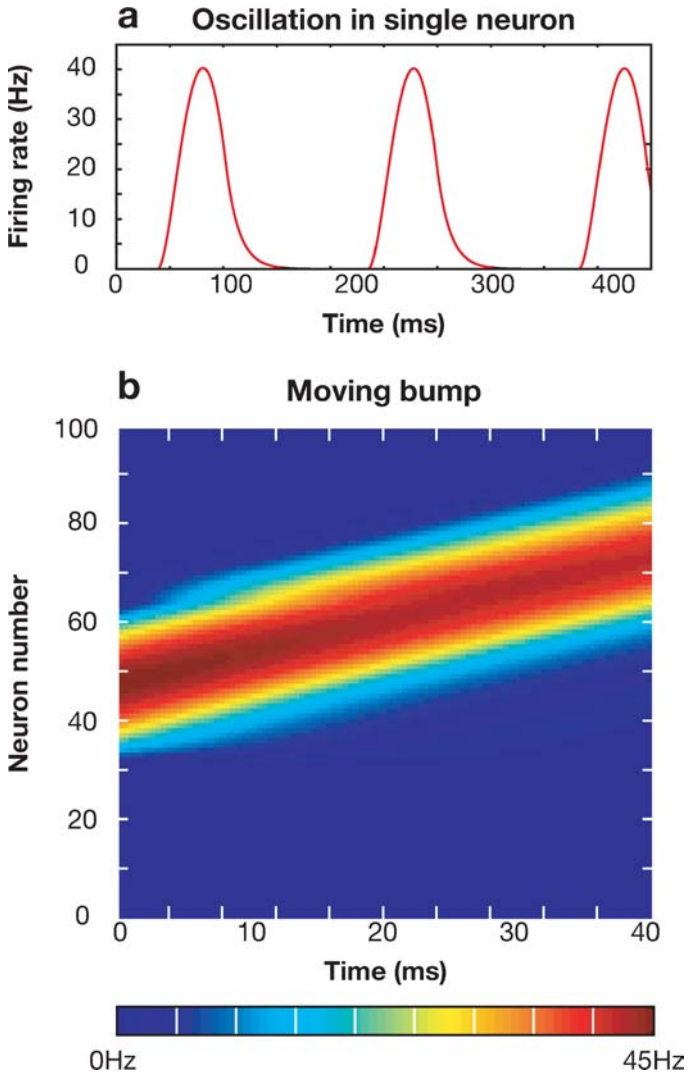

Figure 2

Oscillatory network activity produced by a traveling bump of activity. (*a*) The firing rate of one neuron as a function of time. (*b*) The activity of the entire population of 100 neurons as a function of time. The angled stripe indicates the traveling bump.

potential of the neuron, and Θ is a bias current similar to what appears in Equation 1. As in the case of a firing-rate network, the total input current, given by the last two terms in Equation 3, consists of an external input, $I_i(t)$, and input coming from the other neurons within the network. For the networks shown in **Figure 3**, $\tau_m = 20$ ms, $V_{rest} = V_{reset} = -60$ mV, $V_{th} = -50$ mV, and $\Theta = 15$ mV. For excitatory connections, $\mathcal{J}_{ij} = 1.6$ mV and for inhibitory connections, $\mathcal{J}_{ij} = -8.7$ mV.

The interaction of neurons through chemical synapses arises when presynaptic action potentials produce transient changes in the conductance of the postsynaptic neuron. This can be duplicated in an integrate-and-fire network. However, in the models we review a simplification is made: The postsynaptic effect of a presynaptic action potential is modeled as current injection into the neuron, rather than as a change in its conductance. The synaptic current generated in this way depends on the timing of the presynaptic action potentials. The second sum in the double sum within Equation 3 adds up the contributions from all the action potentials fired by neuron j prior to the time t when the membrane potential of neuron i is being evaluated. The factor $\mathcal{J}_{ij}$ describes, as in the case of firing-rate networks, the strength and type of the synapse from neuron j to neuron i. The function f describes the time course of the postsynaptic current evoked by a presynaptic action potential and, in the examples we show, it takes the form

$$f(t) = \begin{cases} \exp(-t/\tau_s) & \text{if} \quad t \geq 0 \\ 0 & \text{if} \quad t < 0. \end{cases} \qquad 4.$$

For the network in **Figure 3**, $\tau_s = 5$ ms for excitatory synapses and $\tau_s = 10$ ms for inhibitory synapses. As in the case of firing-rate networks, the internally generated activity of the integrate-and-fire network depends on the values of the synaptic weights used in the model and on Θ.

FORMS OF NETWORK DYNAMICS

The long-term behavior of dynamical systems is typically classified into four categories: fixed, periodic, quasi-periodic, or chaotic (Strogatz 1994). Fixed or, more properly, fixed-point dynamics means that the system is in a state in which the variables do not change over time. Periodic behavior refers to a time-varying asymptotic state over a particular interval that repeats indefinitely. Quasi-periodic behavior is nonrepeating because it is composed of two or more periodic patterns of activity with incommensurate frequencies.

Incommensurate means that the ratio of the frequencies is an irrational number, which implies that the phase relationship between the different periodic patterns changes on every cycle forever. Finally, chaotic activity is nonrepeating and is characterized by extreme sensitivity to initial conditions. Stable fixed, oscillatory, or chaotic states are often called attractors because nearby states are drawn to them over time.

The dynamic states we have outlined can be linked to activity patterns of obvious importance to neuroscience. The sustained activity characteristic of short-term memory (Wang & Goldman-Rakic 2004) resembles fixed-point behavior, but with an important twist. A system with a single fixed-point attractor, meaning that all initial states end up with the same time-independent pattern of activity, is useless as a memory device. Memory requires the final state of the system to retain some trace of its initial state; this is how sensitivity to the remembered stimulus is expressed in the final state of the system. Thus, memory models require multiple fixed points, each one used to retain a different memory. If a continuous parameter related to the stimulus, such as its position or size, is to be remembered, the memory model must contain a continuum of

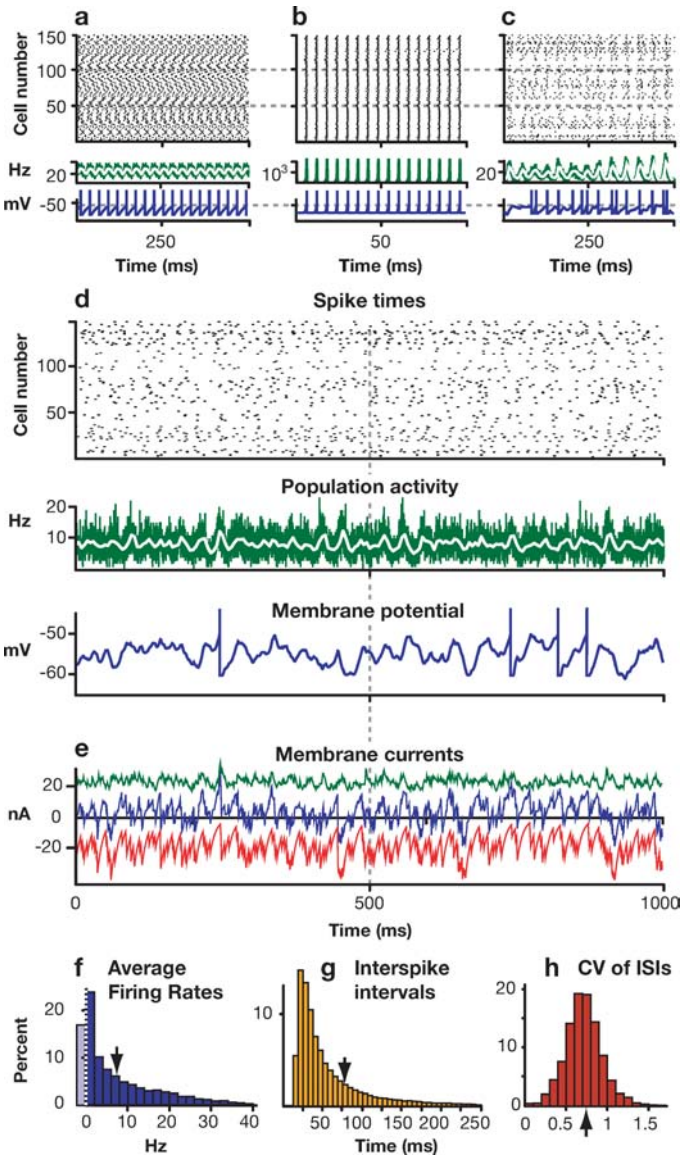

Figure 3

Different forms of activity in a network of spiking model neurons. In panels *a–d*, the top plot is a rastor showing spikes produced over time by 150 of the 10,000 network neurons, the middle plot shows the average firing rate of the entire population (green for 0.1 ms binning and white for 5 ms binning), and the bottom plot shows the voltage trace of a single representative neuron. (*a*) Asynchronous regular activity. The individual neurons fire regularly, but the population rate is roughly constant. (*b*) Synchronous regular activity. Both the individual neurons and the population rate oscillate. (*c*) Synchronous irregular activity. Individual neurons fire irregularly, but the population activity is oscillatory. (*d*) Asynchronous irregular activity. The individual neurons fire irregularly, and the population rate is roughly constant. (*e*) Plots of the excitatory (*green curve*) and inhibitory (*red curve*) currents into the neuron shown above (plotted against time) illustrate that the total current (*blue curve*) is made up of roughly canceling components. (*f*) A histogram of the time-average firing rates of the network neurons. The average firing rate for the entire population, indicated by the arrow, is 8 Hz. (*g*) A histogram of the interspike intervals (ISIs) of the network neurons with the average indicated by the arrow. (*h*) A histogram of the coefficients of variation (the standard deviation of the ISIs over their mean) for the network neurons, with the arrow indicating the average.

fixed points configured along what is called a line attractor, which is just a line of fixed-point attractors. We illustrate a model of this general type in the following section.

Periodic dynamics is obviously connected to the many oscillatory states seen in neural recordings (Marder & Calabrese 1996, Buzsaki & Draguhn 2004). A stable periodic state is also called a limit cycle because it involves cyclic activity that describes the limiting behavior, in time, of many nearby initial states. A model with a continuous line of fixed-point attractors that loops back on itself can easily be turned into an oscillator simply by making the system move around on this loop, a situation we illustrate below.

Although periodic oscillations are frequently seen in cortical recordings (Buzsaki & Draguhn 2004), the overall activity is extremely complex and nonrepeating. The fact that this activity appears to involve superimposed oscillations at many different frequencies (Penttonen & Buzsaki 2003, Leopold et al. 2003) might suggest that the total activity is quasi-periodic, constructed from many different incommensurate oscillations. However, nonrepeating dynamical systems constructed from large numbers of oscillatory elements tend to be chaotic rather than quasi-periodic (Ott 2002). Therefore, the overall activity is more likely to be modeled by a chaotic system, and we review a spiking model of this type below.

Sustained Activity

To sustain their own activity, a group of neurons must feed back enough excitation to each other to maintain the firing that is the source of that excitation. At the same time, sufficient inhibition must be present to prevent the excitatory feedback from producing runaway activity. It might appear that precise parameter adjustment would be required to balance the runaway effects of excitation and the suppressive effects of inhibition, but this is not necessarily the case. In firing-rate models with short-range excitation and long-range inhibition (a so-called Mexican hat configuration), the balance needed for stability can arise automatically. Consider what happens when a group of neurons that excite each other locally are activated. If the excitation is strong enough, more neurons will be recruited into this active group and its size will grow. The number of active excitatory inputs received by a single neuron in this group will grow initially as more neurons become excited, but then it will saturate when all of the neurons within the range of its excitatory connections are already active. On the other hand, the number of active inhibitory inputs will continue to grow at this point because of the longer range of the inhibitory connections. At some point, as the group of active neurons grows, the amount of inhibition will catch up to and then surpass the amount of excitation (provided the inhibition is strong enough) and, at this point, the active group will stop growing and stabilize. In this way, the growth of the active group to an equilibrium size adjusts the balance of excitation and inhibition automatically without requiring fine tuning of parameters (Hansel & Mato 1993; Ben-Yishai et al. 1995, 1997; Hahnloser et al. 2003).

Such a model can be constructed using the network model of Equation 1 by choosing the synaptic weights appropriately (Ben-Yishai et al. 1995, 1997; Hansel & Sompolinsky 2000). For this purpose, we set the weight for the synapse from neuron j to neuron i to

$$\mathcal{J}_{ij} = -\mathcal{J}_0 + \mathcal{J}_2 \cos\left(\frac{2\pi(i-j)}{N}\right), \qquad 5.$$

where $\mathcal{J}_0$ and $\mathcal{J}_2$ are constants. For the network shown in **Figures 1** and **2**, $N = 100$, $\mathcal{J}_0 = 0.073$, $\mathcal{J}_2 = 0.11$, and $\Theta = 20$ Hz. The patterns of excitation for one particular neuron (given by the positive part of $\mathcal{J}_{ij}$ for $i = 50$ and the full range of j values) and inhibition for the same neuron (given by the negative part of $\mathcal{J}_{ij}$) are plotted in **Figure 1*a***. The pattern of short-range excitation and long-range inhibition discussed in the previous paragraph is readily apparent. As a

consequence of this configuration, the model has a time-independent steady-state solution consisting of a "bump" of activity, as seen in **Figure 1*b,c***.

An important feature of this model is that it has not one, but a multitude of bump configurations. The synaptic weights given in Equation 5 do not change if we make the transformations $i \rightarrow i + c$ and $j \rightarrow j + c$, where c is any integer. This symmetry implies that if the model has one bump solution (which it does), it must have a whole family of such solutions. Two of these are shown in **Figure 1*b,c***. For any given bump, there is one neuron that fires faster than all the others, and any one of the N neurons in the network can play this role. Thus, there are at least N different bump states.

The existence of multiple bump states allows the network to retain a memory of its initial pattern of activity, as shown in **Figure 1*c***. Here, the population of neurons started out in a state with activity centered around neuron 20. Halfway through the simulation, we changed the state of the system and created a new pattern of activity centered around neuron 75. Thus, in this case, the system maintains a memory of one pattern of activity for half the simulation and then of another pattern of activity thereafter.

The model shown in **Figure 1** provides a useful description of short-term memory because it combines a simple form of self-sustained activity with sensitivity to external input. However, there is a price for this success. The model maintains sensitivity to input through the imposition of a symmetry, and anything that breaks this symmetry, even slightly, will spoil that sensitivity. Various remedies have been proposed for the sensitivity of these models to small symmetry-breaking effects (Camperi & Wang 1998, Compte et al. 2000, Seung et al. 2000, Tegner et al. 2002, Renart et al. 2003), but the general issue of reconciling self-sustained activity and sensitivity to input is not completely resolved even in the simple case of fixed patterns of activity.

Oscillations

Oscillations and synchrony in neural networks have received an enormous amount of attention (Ermentrout & Cowan 1979, Marder & Calabrese 1996, Gray 1994, Laurent 1996, Rinzel & Ermentrout 1998, Traub et al. 1999). We do not attempt to review the vast literature on this subject, but instead treat oscillations as a step toward understanding more complex, nonperiodic activity. To illustrate one mechanism through which network oscillations can arise, we modify the model of sustained activity introduced in the previous section to make it oscillate.

Network oscillations often arise from a dynamic interplay of excitatory and inhibitory populations of cells (Wilson & Cowan 1972), with inhibition playing a particularly important role (Traub et al. 1989, 1997; Golomb & Rinzel 1993; Wang & Buzsaki 1996; White et al. 1998; Brunel & Hakim 1999; Whittington et al. 2000). In the model we use to illustrate network oscillations, a periodic pattern of activity is set up in each neuron by turning the steady-state bump of the previous section into a traveling wave. One way to do this is to introduce adaptation into the neurons of the model (Hansel & Sompolinsky 2000). As the active neurons adapt, the bump of activity moves to recruit neurons not previously active. Another way to produce a moving bump of activity is to modify the synaptic weights of Equation 5, replacing them with

$$\mathcal{J}_{ij} = -\mathcal{J}_0 + \mathcal{J}_2 \left(\cos\left(\frac{2\pi(i-j)}{N} \right) - \omega\tau_r \sin\left(\frac{2\pi(i-j)}{N} \right) \right). \qquad 6.$$

The parameter ω, which is set to $\omega = 40$ radians/s for **Figure 2**, determines the speed of propagation of the moving bump or, equivalently, the oscillation frequency of the individual neurons in the network. Note that these synaptic weights retain the symmetry that existed for the model of sustained activity discussed in the previous section.

The resulting pattern of activity is shown in **Figure 2**. **Figure 2*a*** shows the firing rate of

a single neuron plotted as a function of time, indicating the periodic, oscillatory nature of the activity. Each neuron in the network has an oscillating firing rate, but with a different phase depending on when the moving bump sweeps past it. The entire moving bump is shown in **Figure 2*b***, with the firing rate plotted against time for all of the neurons in the network.

Chaotic Spiking Networks

The large number of synaptic connections received by cortical neurons does not, at first sight, appear to be consistent with the high degree of variability in cortical responses (Softky & Koch 1993). Naively, one would expect a neuron with n synaptic inputs, each of strength g, to receive a total synaptic input of order gn. If we think of the strength factor g as the probability that a given presynaptic action potential evokes a postsynaptic response, we must require the total synaptic input (gn) to be of order 1, otherwise the postsynaptic neuron would fire much more rapidly than its presynaptic partners within the network. In a recurrently connected network, such a situation is inconsistent because each neuron plays both presynaptic and postsynaptic roles. This condition requires g to be of order $1/n$. For synaptic inputs that fluctuate independently, the variance of the total synaptic input is proportional to g^2n, which for $g \sim 1/n$ is of order $1/n$. With n being approximately 10,000, this argument would suggest that synapses should be quite weak ($g \approx 0.0001$) and that the variance of the total synaptic input should be quite small.

The argument of the preceding paragraph is clearly incorrect for cortical circuits. Where they have been measured, synapses between cortical neurons have been found to be much stronger than the estimate obtained above (Song et al. 2004), and cortical neurons are highly variable in their responses, suggesting that the input variance is much larger than of order $1/n$. Instead, cortical synapses seem to have a strength of order $g \sim \sqrt{1/n}$, which makes the input variance, g^2n, of order 1 (van Vreeswijk & Sompolinsky 1996, 1998). The reason that cortical neurons do not experience runaway firing is that the total synaptic input is not of order $gn \sim \sqrt{n}$ as suggest above, but of order 1 because of a balance between excitatory and inhibitory inputs. The order-of-magnitude estimate given above did not take into account such a cancelation, but this appears to be what happens in cortical circuits (Shadlen & Newsome 1994, Tsodyks & Sejnowski 1995, Troyer & Miller 1997). This realization has important implications that we now explore, and it represents an important advance in our understanding of cortical dynamics.

In the previous sections, we considered model networks in which the individual neurons are described by firing rates. We now discuss networks of spiking neurons. The activity of spiking networks has been divided into four classes depending on how the individual neurons fire and how the activities of the different neurons relate to each other (Brunel 2000). Individual neurons are classified as firing in either a regular or an irregular pattern. At the network level, the neurons may either synchronize their firing or fire asynchronously. **Figure 3** shows examples of each of the four possible combinations of these attributes for a network of 10,000 integrate-and-fire model neurons, 80% of which are excitatory and 20% inhibitory (meaning that they inject positive and negative exponentially decaying pulses of current into their target postsynaptic neurons, respectively).

Individual neurons in the example of **Figure 3*a*** fire at a steady rate in a periodic pattern, but, in this case, they fire asynchronously because they are uncoupled and were started with random initial conditions. This is a rather trivial example of an asynchronous regular state; more interesting cases also exist (Brunel 2000). Weakly coupled networks can also exhibit such asynchronous regular activity.

In **Figure 3*b***, excitatory synapses between regularly firing neurons have caused the spikes

to synchronize, producing synchronous regular network activity. As the excitatory and inhibitory currents are brought into a more balanced configuration, the individual neurons start to fire in irregular patterns, as seen in panels c and d of **Figure 3**. The difference between these panels is that there is partial synchrony in the case of **Figure 3*c***, as can be seen by the oscillations in the average firing rate of the population of neurons shown in the middle trace of this panel, whereas the population activity in the case of **Figure 3*d*** is asynchronous. A transition between synchronous and asynchronous states with irregular firing occurs, for example, when Θ is decreased or inhibition is increased (Brunel 2000).

Asynchronous states have received considerable attention as candidates for the background activity seen in cortical and other neural circuits (Abbott & van Vreeswijk 1993, Destexhe 1994, Brunel & Hakim 1999, Fusi & Mattia 1999, Gerstner 2000, van Vreeswijk 2000, Hansel & Mato 2002). The key features that permit the existence of an asynchronous network state with irregular firing of the individual neurons that are illustrated in panels d–h of **Figure 3** are (*a*) a balance of excitation and inhibition, as indicated by **Figure 3*e***, and (*b*) sparse connectivity (van Vreeswijk & Sompolinsky 1996, 1998; Amit & Brunel 1997; Brunel 2000; Lerchner et al. 2004). For the example shown in **Figure 3**, neurons were connected randomly with a connection probability of 1.5%. Asynchronous irregular activity can also arise in sparsely connected networks with local patterns of connectivity (Mehring et al. 2003). In all cases, the sparseness of the connectivity means that large numbers of neurons are required to achieve this type of activity. The example of **Figure 3** is based on synapses that inject current into their postsynaptic targets, but asynchronous irregular activity can also arise from conductance-based synapses, although the firing of individual neurons tends to be considerably more burst-like in this case.

The asynchronous irregular state of network activity is quite remarkable. Note that the highly irregular voltage trace for an individual neuron of the network shown in the bottom panel of **Figure 3*d*** arises in this model without the addition of any external source of randomness (i.e., no random number generator is used in the simulation). As shown in panel *f* of **Figure 3**, the network neurons display a roughly exponentially distributed range of firing rates. The spiking statistics of the network show an exponentially distributed range of interspike intervals (except for short intervals forbidden by the refractory period imposed on the neurons) and a range of values of the coefficients of variation (standard deviation divided by the mean) of interspike intervals for the individual neurons (**Figures 3*g*** and **3*h***, respectively).

It is possible to investigate the asynchronous irregular state through analytic calculations, not merely by simulation (van Vreeswijk & Sompolonsky 1996, 1998; Amit & Brunel 1997; Brunel 2000). This analysis is based on self-consistent mean-field calculations. The idea underlying these calculations is that neurons in a closed network receive inputs from other neurons with firing statistics similar to their own. The self-consistent calculation involves determining the firing statistics of a neuron receiving a total synaptic input characterized by a particular mean and variance (Ricciardi 1977, Tuckwell 1988, Brunel & Sergi 1998). Self-consistency is then imposed by demanding that the assumed mean and variance match what would be obtained by summing synaptic inputs from a set of presynaptic neurons with the computed postsynaptic firing statistics. These calculations provide an accurate description of what happens in computer simulations of model networks, such as that shown in **Figure 3**.

Given that cortical connectivity is sparse and that cortical background activity is of the asynchronous irregular form, the fact that sparsely connected model networks with balanced excitation and inhibition produce such a pattern of activity lends further support to the idea that excitation and inhibition are in a balanced configuration within cortical

circuits. Balancing two opposing influences in this way is an odd approach from a computational perspective. A standard warning in numerical calculations is to avoid subtracting two large numbers that are close to being equal because the answer obtained in such a case is sensitive to small errors in the calculation of either of the large numbers. Yet this appears to be exactly how cortical circuits operate and, indeed, the result is highly variable responses. Why would the system have evolved to operate in this way? One proposed answer is that networks in a balanced configuration can respond more rapidly to inputs than those with unbalanced excitation and inhibition (Tsodyks & Sejnowski 1995, van Vreeswijk & Sompolinsky 1998). Another suggestion is that the large input variance produced by a balanced network is not merely a source of noise. Instead, having comparable levels of mean and variance for synaptic inputs permits two types of signals to be transmitted simultaneously within these circuits, one (the mean) that drives neuronal responses and the other (the variance) that serves to modify neuronal gain (Chance et al. 2002) and can evoke rapid responses (Silberberg et al. 2004). Finally, as we discuss in the following section, high variance is important for supporting stable signal propagation.

SIGNAL PROPAGATION

Cognitive processing requires that signals propagate reliably through multiple regions of the brain. Achieving stable signal propagation in neural networks is a difficult problem. After introducing some of the problems associated with signal propagation, we discuss two proposed modes of propagation, synfire chains and firing-rate propagation.

As activity propagates through a network, action potentials tend to synchronize, and avoiding network-wide synchronization of activity requires noise (Marsalek et al. 1997, Golomb 1998, Burkitt & Clark 1999, Diesmann et al. 1999, van Rossum et al. 2002, Reyes 2003, Litvak et al. 2003). In early models, this noise was introduced from an external source, such as a random-number generator (Diesmann et al. 1999, van Rossum et al. 2002), but more recent studies have used the asynchronous irregular state discussed in the previous section to provide the variability needed to prevent large-scale synchronization (Mehring et al. 2003, Aviel et al. 2003, Vogels & Abbott 2004). However, noise, whether externally or internally generated, does not necessarily remove all synchronization. Forms of signal propagation can be distinguished by whether or not they involved synchrony. Synchrony plays a critical role in synfire propagation, whereas for firing-rate propagation synchronization destroys the signal.

Avalanche Model

We begin our discussion of signal propagation by discussing a highly simplified model that is, nevertheless, useful for illustrating basic issues relevant to signal propagation in neural networks. This model, known as the avalanche model (Harris 1963, Zapperi et al. 1995, de Carvalho & Prado 2000), is defined by the following rule: When a neuron fires an action potential, a spike is evoked in each of its n postsynaptic target neurons with probability p. The same rule is then applied to any of the postsynaptic neurons that fired owing to the first application of the rule. Each firing is treated as an independent event (certainly an unrealistic assumption, especially for late stages of the propagation chain). By applying this rule to a single initial neuron, then to all the neurons that the initial neuron caused to fire, and then to all the neurons that subsequently fire, the model can be iterated sequentially, describing the propagation of a neuronal signal.

The average number of neurons that fire at the second stage, after the single initial neuron has fired, is pn. At the next stage, the average number of firing neurons is $(pn)^2$ because each of the pn neurons firing at the second stage induces an average of pn neurons to fire at the third stage. At stage s, the average number of neurons that fire is $(pn)^s$. This simple

calculation illustrates one major issue in signal propagation. Signals tend either to decay, which happens in the avalanche model if $pn < 1$, or to blow up, which happens if $pn > 1$. To maintain stable average propagation over multiple stages, the probability of evoking an action potential must be adjusted so that pn is close to 1. This feature of propagation in the avalanche model is illustrated in **Figure 4*b*** for subcritical ($pn < 1$), critical ($pn = 1$), and supracritical ($pn > 1$) cases.

Although choosing $pn = 1$ stabilizes the average level of propagation from stage to stage, there are large fluctuations from trial to trial. The red sequence in **Figure 4*a*** shows a case where one neuron firing at stage 1 evokes one neuron firing at stage 5. Although this represents the average behavior, it is actually quite rare. The blue sequence in **Figure 4*a*** is an example of a propagation failure, and the green sequence shows a propagation explosion. A failure can occur, for example, if the first neuron does not activate any other neurons, which makes the second stage silent. Such failures obviously make the wave of propagating activity die out. If the number of activated neurons at the second stage is larger than average, the system becomes prone to sequential increases, and the propagating activity tends to explode. **Figure 4*c*** shows the percentage of successful propagations (meaning that at least one neuron fired) at various stages of a critical avalanche. Note that beyond 3 stages, propagation fails more than 50% of the time. **Figure 4*d*** shows the number of activity explosions. This is highly sensitive to the value of pn, but even for the critical case, there are a fair number of explosions beyond layer 5.

The large fluctuations that we have discussed cause the number of neurons activated by a critical avalanche to have a power-law distribution (Harris 1963, Zapperi et al. 1995, de Carvalho & Prado 2000), which agrees with what is seen in multielectrode data from organotypic cultures or slices (Beggs & Plenz 2003). Although the avalanche model is an oversimplified description, it highlights two basic points. First, tuning is required so that, on average, propagation neither dies out nor explodes. Second, even if this critical condition is met, large fluctuations can cause frequent failures and occasional explosions.

Synfire Chains

We have already mentioned that the spiking of different neurons tends to synchronize as signals propagate through a network. As long as this synchronization can be kept from spreading across the entire network, it can provide an effective method for transmitting signals (Salinas & Sejnowski 2002). This idea is the basis of propagation along synfire chains (Abeles 1991), which are groups of neurons coupled in a feedforward manner that support synchronous signal propagation (Herrmann et al. 1995). **Figure 5*a*** shows an example of a feedforward chain in which every neuron of a given layer makes synapses onto every neuron of the next layer. Signal propagation along such synfire chains has been studied extensively in network models (Aertsen et al. 1996, Diesmann et al. 1999, Cateau & Fukai 2001).

By signal propagation, we mean the transmission of activity along specific pathways across a neural network, not the activation of an entire network. Noise is essential in a network that supports synfire activity to prevent synchronous activation from spreading beyond the specified synfire chain. Stable propagation in a network receiving noisy input from an external source is illustrated in **Figure 5*b***. This propagation is subject to the same types of fluctuations seen in the avalanche model, leading, for example, to failures of propagation as in **Figure 5*c***. In these networks, synfire signals can travel through a number of embedded feedforward layers, provided they are large enough (Diesmann et al. 1999). Propagation requires a critical level of activity in the initial layer-1 pulse packet seen in **Figure 5*b***, and during propagation the level of synchrony stays at a constant value determined by the level of noise.

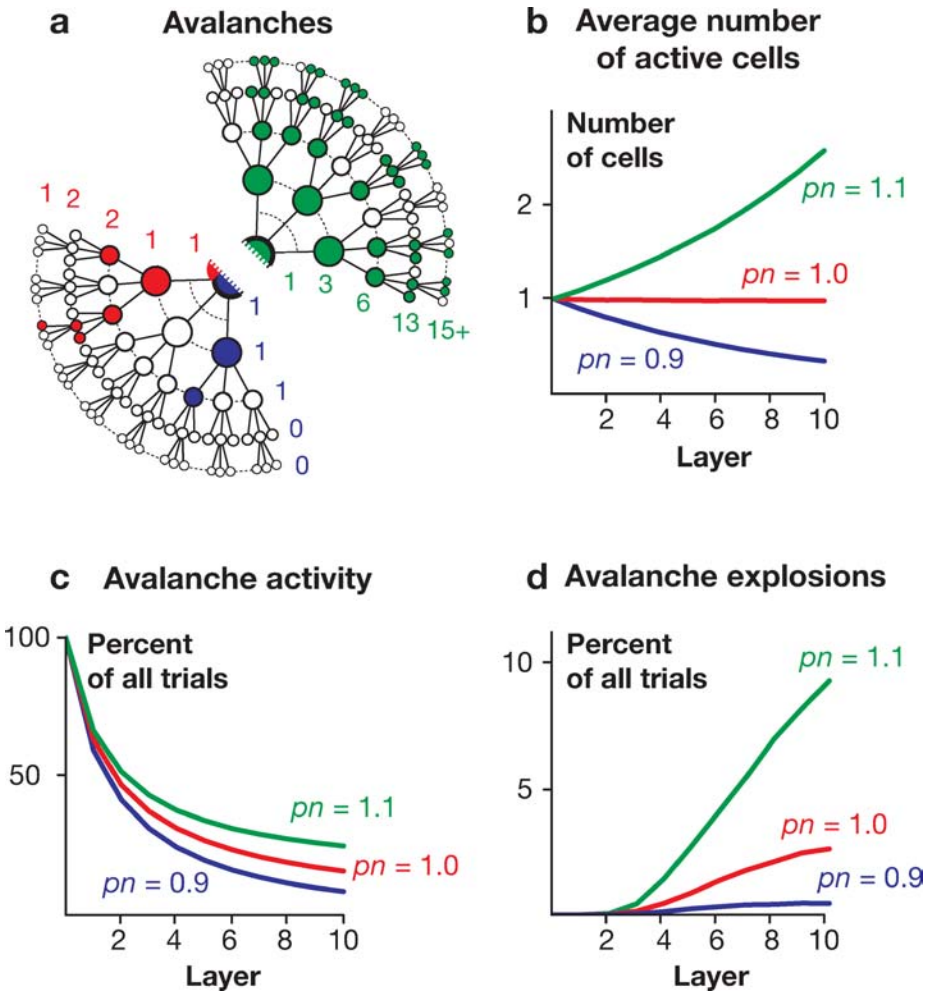

Figure 4

The avalanche model. (*a*) Avalanches develop from the center of the graphic and travel outward. Systems with $pn > 1$ (*green*) are likely to show sharply increasing numbers of active cells in consecutive layers. When $pn = 1$ (*red*), the system is more likely to propagate activity without explosive multiplication of active cells in higher layers. $pn < 1$ frequently leads to an eventual extinction of the activated wave (*blue*). (*b*) Average number of activated cells per layer in 10^4 independently activated avalanches. Avalanches with $pn > 1$ show an exponential increase in the number of active cells in higher layers. When $pn = 1$, the average number of active cells is constant, and with $pn < 1$ it declines to zero exponentially. (*c*) Distribution of avalanche run lengths. The run length is the number of layers before the avalanche stops. Higher values of *pn* lead to longer-surviving avalanches. (*d*) Occurrence of events with more than 10 active cells in a single layer for the same trials as in *c*. Higher values of *pn* increase the number of such "explosions."

As mentioned above, the synfire propagation seen in **Figures 5*b*** and **5*c*** occurs in a network that receives noise input from an external source. A more realistic approach is to generate noise within the network through the mechanism reviewed in the previous section. This has been done by embedding synfire chains (i.e., constructing specific feed-forward synaptic pathways) in large, sparsely connected networks of integrate-and-fire

neurons (Mehring et al. 2003, Aviel et al. 2003). Signal propagation has been achieved in such networks when they are large (**Figure 5*d***), but only for very specific sets of parameters. Consistent, stable propagation is problematic. These difficulties arise because, unlike the situation with external noise, synfire activity interacts with the chaotic background activity in these networks, and this interaction can be destructive to both the propagating signal and the background activity. Similar to what can occur in the avalanche model, synfire propagation can set off large-scale synchronization within the network, as seen in **Figure 5*e***. Furthermore, through the over-excitation of the inhibitory cell population these "synfire explosions" can subsequently silence the network completely

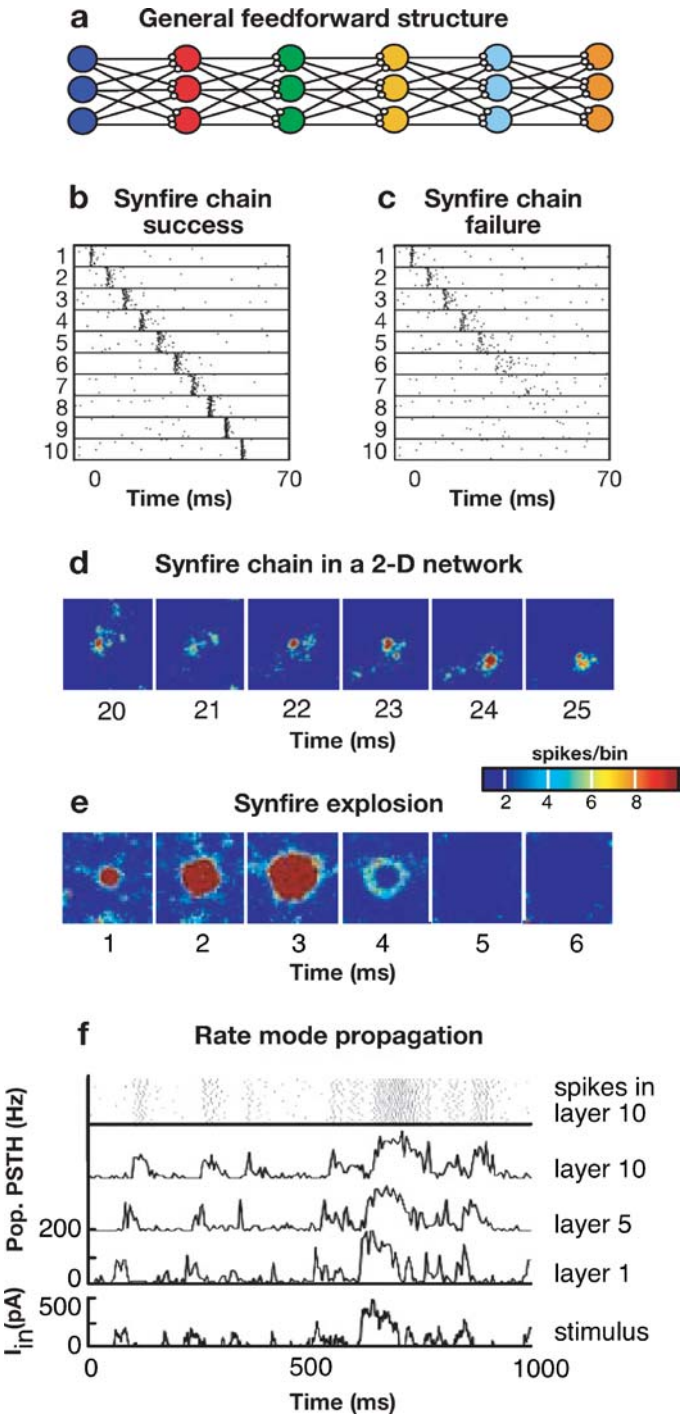

Figure 5

Signal propagation. (*a*) General layout of a synfire chain with all-to-all coupling in the feedforward direction between neighboring layers of neurons. (*b*) Propagation of a synfire wave through a feedforward network with added noise. A group of cells is activated in layer 1. This evokes activity that propagates through all layers with a time lag of approximately 5 ms per layer. (*c*) A propagation failure. The synfire wave dissolves into background activity and fails to propagate. (*d*) Synfire propagation in a two-dimensional, locally coupled, sparse, balanced network with an embedded synfire chain. Six frames show the activity of the network at different times indicated below the plots. Activity propagates from the center of the network to the lower right corner. The rest of the network is quiescent. (*e*) Activity in the same network for different initial conditions. Now the synfire event evokes a large shock wave, affects the majority of cells, and ultimately silences all network activity. (*f*) Firing-rate propagation in a feedforward network with added noise. The lowest plot shows the current injected into layer 1 of the network to evoke activity. The plots above this show the firing rates in various layers of the network, and the top plot is a raster of the spikes produced in the 20 cells of layer 10. The network accurately propagates the activity from layer 1 to 10. Panels were adapted from previously published figures: *b* and *c* (Diesmann et al. 1999), *d* and *e* (Mehring et al. 2003), and *f* (van Rossum et al. 2002).

(Gutkin et al. 2001, Mehring et al. 2003). To prevent this, the perturbation in network activity caused by the synfire chain must be diluted either by embedding it in a very large network or by introducing some form of canceling inhibition (Aviel et al. 2003).

Propagation of Firing Rates

Signals can also propagate through networks in the form of transiently elevated or depressed firing rates, rather than as waves of synchronized firing. This requires a feedforward structure similar to a synfire chain (**Figure 5*a***), but more noise to prevent synchronization even within the groups of neurons carrying the signal (Litvak et al. 2003). As shown in **Figure 5*f***, firing-rate propagation has been demonstrated in feedforward networks receiving external noise (van Rossum et al. 2002). The network used for **Figure 5*f*** (van Rossum et al. 2002) consists of 200 integrate-and-fire neurons organized in 10 layers, in which every neuron of one layer synapses on to every neuron of the next. Signal propagation through all 10 layers is observed when a sufficiently strong input is fed into layer 1.

There are actually two different modes of propagation within this network, depending on the level of externally applied noise. Without external noise, the network shows an all-or-none response. The otherwise silent input layer fires only when stimuli succeed in driving the membrane potential above threshold. All neurons of that layer then fire simultaneously and their activity evokes a traveling wave through the layers of the network similar to a synfire chain (Abeles 1991). When noise is introduced, network behavior changes. Noise was adjusted to maintain an average firing rate of 5 Hz. At optimal noise levels, all neurons desynchronize, and their membrane potentials hover slightly below threshold. Both small and large stimuli are now transmitted because the number of neurons driven to fire is proportional to the amplitude of the stimulus. Graded signals are reproduced accurately and in an approximately linear manner across 10 layers with a minimum of 20 cells in each layer.

As in the case of synfire chains, it is important to study the propagation of firing rates in networks with internally generated noise. Preliminary indications are that firing rates can indeed be propagated along embedded feedforward chains in large networks of sparsely connected integrate-and-fire neurons of the type reviewed in the previous section (Vogels & Abbott 2004).

DISCUSSION

To understand neural network activity in behaving animals we must account for both internally generated activity and activity evoked by external stimuli. The history of neuroscience is full of examples in which stimulus-evoked activity has been successfully modeled. This review has covered models that describe three forms of internally generated activity: persistent, oscillatory, and asynchronous irregular. Networks that self-sustain activity without being sensitive to external stimuli are useless in shaping behavior in response to environmental cues. On the other hand, networks in which stimulus-driven responses are not accompanied by internally generated activity cannot sustain useful forms of signal propagation. Although there is much to be done in the separate modeling of both internally and externally generated activity, the bigger challenge is to reconcile these two forms of activity and construct models in which they coexist synergistically.

ACKNOWLEDGMENTS

Research was supported by the National Science Foundation (IBN-0235463), an NIH Pioneer Award, and the Swartz Foundation.

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