

Stationary bumps in networks of spiking neurons

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Abstract

We examine the existence and stability of spatially localized “bumps” of neuronal activity in a network of spiking neurons. Bumps have been proposed in mechanisms

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Funahashi *et al.* (1989). The network is bistable with the bump and the “all-off” state both being stable. Note that the neurons are not intrinsically bistable as in Camperi & Wang (1998) and the bump solutions do not arise from a Turing–Hopf instability like that studied by Bressloff & Coombes (1998) and Bressloff *et al.* (1999), i.e. there is no continuous path in parameter space connecting a bump and the all-off state. A time-stationary solution is one which corresponds to asynchronous firing of neurons where the firing rate is constant at each spatial point but the rate depends on spatial location. We show that the activity profile of the bumps of our model are the same as that of a corresponding population rate model.

However, bumps predicted by the rate model to be stable may in fact be unstable in a model which includes the spiking dynamics of the neurons. The rate model implicitly assumes asynchronous firing and only considers the dynamics of the firing rate. As the synaptic decay time is increased in the spiking network the bump can lose stability as a result of temporal correlation or “partial synchronization” of neurons involved in the bump. If the initial conditions are symmetric then this synchronization causes the input to the neurons to drop below the threshold required to keep it firing, leading to cessation of oscillation of the neurons and consequently the rest of the bump. However, for generic initial conditions or with the inclusion of noise, the bump destabilizes to a traveling wave. For fast enough synapses, the wave cannot exist. If some heterogeneity in the intrinsic properties of the neuron is included then the bump can be “pinned” to a fixed location; the traveling wave does not form and the bump loses stability to the all-off state.

This instability provides a mechanism for the termination of a bump, as would be required at the end of a memory task (e.g. the delayed saccade task discussed by Colby *et al.* (1995)): if many of the neurons involved in the bump can be caused to fire approximately simultaneously, and the synaptic time scale is short, there will not be enough input after this coincident firing to sustain activity and the network will switch to the all-off state.

2 Neuron model

We consider a network of N integrate-and-fire neurons whose voltages, v_i , obey the differential equations

$$\frac{dv_i}{dt} = I_i - v_i + \sum_{j,m} \frac{J_{ij}}{N} \alpha(t - t_j^m) - \sum_l \delta(t - t_i^l), \quad (1)$$

where the subscript i indexes the neurons, t_j^m is the m th firing of neuron j , defined by the times that $v_j(t)$ crosses the threshold which we have set to 1, I_i is the input current applied to neuron i , and $\delta(\cdot)$ is the Dirac delta function, which resets the voltage to zero. The function $\alpha(t)$ is a post-synaptic current and is nonzero only for $t > 0$. The connection weight between neuron i and neuron j is J_{ij} . The sum over m and l extend over the entire firing history of the neurons in the network and the sum over j extends over the network. Each time the voltage crosses the threshold from below the neuron is said to “fire”. The voltage then immediately resets to $v_i = 0$ and a synaptic pulse $\alpha(t)$ is sent to all connected neurons.

In our examination of bump solutions we will consider subthreshold input ($I_i < 1$) and a weight matrix that is translationally invariant (i.e. J_{ij} only depends on $|i - j|$). It is of the lateral inhibition form (i.e. locally excitatory but distally inhibitory); this type of

connectivity matrix can be shown to arise from a multi-layer network with both inhibitory and excitatory populations if the inhibition is fast, as shown by Ermentrout (1998).

We can formally integrate Eq. (1) to obtain the spike response form (Gerstner, 1995; Gerstner *et al.*, 1996; Cho, 1998). This form will allow us to relate the bump profile for the integrate-and-fire network to the profile of a rate model similar to that studied by Amari (1977). Suppose that neuron i has fired in the past at times t_i^l , here $l = 0, -1, -2, \dots, -\infty$. The neuron most recently fired at t_i^0 . We consider the dynamics for $t > t_i^0$. Integrating Eq. (1) yields

$$v_i(t) = I_i(1 - e^{-(t-t_i^0)}) + \sum_{j,m} \frac{J_{ij}}{N} \int_{t_i^0}^t e^{s-t} \alpha(s - t_j^m) ds, \quad (2)$$

By breaking up the integral in (2) into two pieces we obtain

$$v_i(t) = I_i(1 - e^{-(t-t_i^0)}) + \sum_{j,m} \frac{J_{ij}}{N} \int_{t_i^0}^t e^{s-t} \alpha(s - t_j^m) ds$$

The parameter β affects the rate at which the post-synaptic current decays. Noise is added to the network as current pulses to each neuron of the form

$$I_{\text{rand}}(t) = 6(e^{-10t} - e^{-15t})$$

here $t \geq 0$. The arrival times of these pulses have a Poisson distribution with mean frequency 0.05 and there is no correlation between pulse arrival times for different neurons.

3 Existence of the bump state

We examine the existence of bump solutions to the spike response system described by (4). A bump solution is spatially localized with spatially dependent average firing rate of the participating neurons. The firing rate is zero outside the bump and rises from zero at the edges to a maximum in the center. The firing times of the neurons are uncorrelated, so the bump is a localized patch of incoherent or asynchronous firing. The state coexists with the homogeneous non-firing (all-off) state.

It is convenient to define the activity of neuron i as

$$A_i(t) = \sum_l \delta(t - t_i^l), \quad (9)$$

here the sum over l is over all past firing times. Our activity differs from the population activity of Gerstner (1995) which considers the activity of an infinite pool of neurons at a given spatial location. We can then rewrite the synaptic input (5) in terms of the activity as

$$u_i(t) = \sum_j \frac{J_{ij}}{N} \int_0^\infty \epsilon(s) A_j(t-s) ds \quad (10)$$

Consider stationary asynchronous solutions to the spike response equations. Many authors have studied the spatially homogeneous asynchronous state with various coupling schemes (Abbott and van Vreeswijk, 1993; Treves, 1993; Gerstner, 1995, 1998, 2000). Our approach is similar to that of Gerstner (1995, 1998, 2000). We first rewrite the activity as

$$A_i(t) = A_i^0 + \Delta A_i(t), \quad (11)$$

here

$$A_i^0 = \lim_{\tau \rightarrow \infty} \frac{1}{\tau} \int_0^\tau A_i(r) dr. \quad (12)$$

Substituting (9) into (12) then yields $A_i^0 = \lim_{\tau \rightarrow \infty} n(\tau)/\tau$, here $n(\tau)$ is the number of times neuron i fired in the time interval τ . Thus, A_i^0 is the mean firing rate of neuron i .

We now insert (11) into (10) to obtain $u_i(t) = u_i^0 + \Delta u_i(t)$ here

$$u_i^0 = \sum_j \frac{J_{ij}}{N} A_j^0, \quad (13)$$

and

$$\Delta u_i(t) = \sum_j \frac{J_{ij}}{N} \int_0^\infty \epsilon(s) \Delta A_j(t-s) ds \quad (14)$$

(recall that $\int_0^\infty \epsilon(s) ds = 1$). We define the asynchronous state to be one here $\Delta u_i(t)$ is zero in the limit of infinite network size N . In the asynchronous state the input to neuron i is a constant and given by u_i^0 . This implies that the firing times of the neurons are uncorrelated. For a finite system, $\Delta u(t)$ will contribute fluctuations which scale as $N^{-1/2}$.

We now derive the self-consistent equations for the asynchronous state. Substitute $u_i(t) = u_i^0$ into (4); the local firing period $(A_i^0)^{-1}$ will be given by

$$v_i((A_i^0)^{-1} + s, s) = 1 = I_i - [I_i + u_i^0]e^{-(A_i^0)^{-1} + u_i^0}. \quad (15)$$

Solving (15) yields

$$A_i^0 = G[u_i^0] \quad (16)$$

here

$$G[z] = \begin{cases} 0, & z \leq 1 - I \\ -1/\ln \left[\frac{I+z-1}{I+z} \right], & z > 1 - I \end{cases} \quad (17)$$

(A plot of $G[z]$ can be seen in Fig. 2.) This form is similar to the usual neural network rate equation, (e.g. Amari, 1977; Kishimoto & Amari, 1979; Hansel & Sompolinsky, 1998; Ermentrout, 1998) except that the gain function we have derived is a result of the intrinsic neuronal dynamics of our model (Gerstner, 1995). Combining (13) and (16) we obtain the condition for a stationary asynchronous solution

$$u_i^0 = \sum_j \frac{J_{ij}}{N} G[u_j^0], \quad (18)$$

For a finite sized system, the time averaged firing rate of the neurons follows a profile given by $A_j^0 = G[u_j^0]$.

We first consider mean-field solutions to (18). We assume that $u_i^0 = u^0$, $I_i = I$ and $\sum J_{ij}/N = J$ yielding

$$u^0 = JG[u^0] \quad (19)$$

If $I > 1$ (oscillatory neurons), then there are no solutions if J is too large and one solution if J is small enough. For $I < 1$ (excitatory neurons), (19) has one solution at $u_0 = 0$ if J is too small and two solutions if J is large enough (See Fig. 2, which shows the case $J = 2$). These two states correspond to an ‘all-off’ state and an ‘all-on’ state respectively.

3.1 Bump State

In order for a bump to exist, a solution to (18) for u_i^0 must be found such that $u_i^0 + I_i$ is above threshold ($u_i^0 + I_i > 1$) in a localized region of space. We show example figures of such solutions in Figs. 3 and 4. Amari (1977) and Kishimoto & Amari (1979) proved that such a solution can exist for a class of gain functions $G[z]$. Similar to the mean field solution, we find that for subthreshold input ($I_i < 1$), the all-off state always exists and the bump state can exist if the weight function has enough excitation. We will discuss stability of the bump in Sec. 4. Stability will be affected by the synaptic time scale, the weight function, the amount of applied current and the size of the network. For a finite sized system, we show in Appendix A that the individual neurons in a bump do not fire with a fixed spatially dependent period. These finite sized fluctuations act as a source of noise.

As noted by Gerstner (1995, 1998), the spike response model can be connected to classical neural network or population rate models (Wilson and Cowan, 1972; Amari, 1977; Hopfield, 1984). If we choose $\epsilon(s) = e^{-s}$, which is true for $\alpha(t) = \delta(t)$, and assume near synchronous firing so that $A_i(t) \simeq G[u_i(t)]$, then by differentiating (10) with respect to time we obtain:

$$\frac{d}{dt}u_i(t) = -u_i(t) + \sum_j J_{ij}G[u_j(t)] \quad (20)$$

This is the classical neural network or population rate model. Amit and Tsodyks (1991), Gerstner (1995) and Shriki *et al.* (

bump, this computation is quite involved. Instead, we infer the conditions for stability of the bump from a stability analysis of the homogeneous asynchronous state of the spike response model and confirm our conjectures with numerical simulations.

Stability of the bump state has previously been examined in a first order rate model. Amari (1977) and Kishimoto & Amari (1979) found for saturating gain functions, that the stability of the bump in the rate model depended on a relationship between the gain function and the applied current. Hansel & Sompolinsky (1998) find the stability constraints for a model with a simplifi

of neurons can be activated by noise, but they cannot persist if β is too large.

We conjecture that the loss of stability in the bump for large β is due to a loss of stability of the asynchronous bump state due to the synchronizing tendency of the neurons with fast excitatory coupling as is seen in the homogeneous network. Integrate-and-fire neurons belong to what is known as Type I or Class I neurons (Hansel *et al.*, 1995; Ermentrout, 1996). It is known that for Type I neurons, fast excitation has a synchronizing tendency whereas slow excitation has a desynchronizing tendency (Van Vreeswijk *et al.*, 1994; Gerstner, 1995; Hansel *et al.*, 1995). Chou (

of the fluctuations in the input due to the finite number of neurons and the synchronizing dynamical effect. The termination of the bump as β is increased is not due to this overall decrease in

by a corresponding population rate model. However, when the synapses occur on a fast time scale, bumps can no longer be sustained in the network. They either lose stability to traveling waves or completely switch off. We also find that heterogeneity or disorder can pin the bumps to a single location and keep them from wandering. We conjecture that the loss of stability of the bump is due to partial synchronization between the neurons. It is known for homogeneous networks of Type 1 neurons that fast excitatory synapses have a synchronizing tendency. We use this instability to turn off bumps with a brief excitatory stimulus to partially synchronize the neurons.

For the network sizes that we have probed, we have found that bumps can be sustained by synapses with decay rates as fast as three to four times the firing rate of the fastest neurons in the bump. If we consider neurons in the cortex to be firing at approximately 40 Hz this would correspond to synaptic decay times of the order of 5 to 10 ms which is not unreasonable. Results with conductance-based neurons have found that the synaptic time scale can be sped up to well within the AMPA range and still sustain a bump state (Gutkin *et al.*, 2000). We also find that as the network size increases, the bump may tolerate faster synapses. While the stability of the bump depends crucially on the synaptic time scale, the activity profile of the bump depends only on the connection weights and the gain function. Thus, it may be possible to make predictions on the connectivity patterns of experimental cortical systems from the firing rates of the neurons within the bump and the firing rate (F-I) curve of individual neurons.

If these recurrent bumps are involved in working memory tasks then our results lead to some experimental predictions. For example if it is possible to pharmacologically speed up the excitatory excitations in the cortex, bump formation and hence working memory may be perturbed. A brief applied stimulus applied to the cortical area where the working memory is thought to be held may also disrupt a working memory task.

Among other authors who have produced similar work are Hansel & Sompolinsky (1998), Bressloff *et al.* (1999) and Compte *et al.* (1999). Hansel & Sompolinsky (1998) consider a rate model similar to that studied by Amari (1977) and Kishimoto & Amari (1979), using a piecewise linear gain function (our $G[z]$) and retaining only the first two Fourier components of the weight function J , which allows them to make analytic predictions about the transitions between different types of behavior. They also show the existence of a bump in a network of conductance-based model neurons and show that bumps can follow moving spatially-localized current stimulations, a feature that may be relevant for head-direction systems such as those studied by Redish *et al.* (1996) and Zhang (1996).

Bressloff & Coombes (1998) and Bressloff *et al.* (1999) study pattern formation in a network of coupled integrate-and-fire neurons, but their systems consider suprathreshold input ($I_i > 1$) so that the all-off state is not a solution. They find that by increasing the coupling weight between neurons the spatially-uniform synchronized state (all neurons behave identically) becomes unstable through a Turing-Hopf bifurcation, leading to spatial patterns similar to those shown in Fig. 4. They find bistability between a bump and a spatially-uniform synchronized state, whereas we find bistability between a bump and the all-off state. This difference is crucial if the system is to be thought of as modeling working memory as investigated by, among others, Colby *et al.* (1995) and Funahashi *et al.* (1989).

Compte *et al.* (1999), have demonstrated the existence of a bump attractor in a two-layer network of excitatory and inhibitory integrate-and-fire neurons. Their network involves

strong excitation and inhibition in a balanced state. It is possible that a corresponding rate model could be found for this network to obtain the shape of the profile. They were also able to switch the bump off and on with an excitatory stimulus. However, it is believed that their switching off mechanism is due to the inhib

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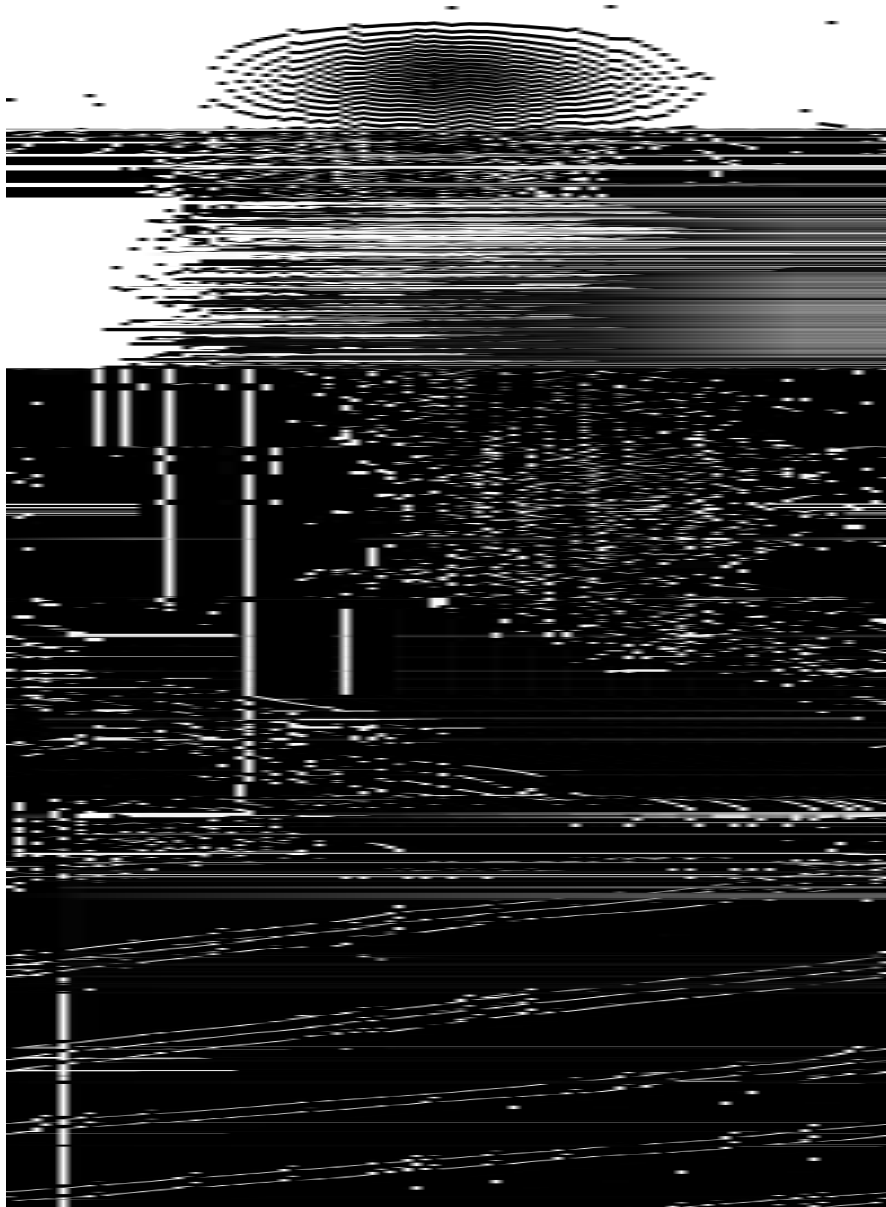
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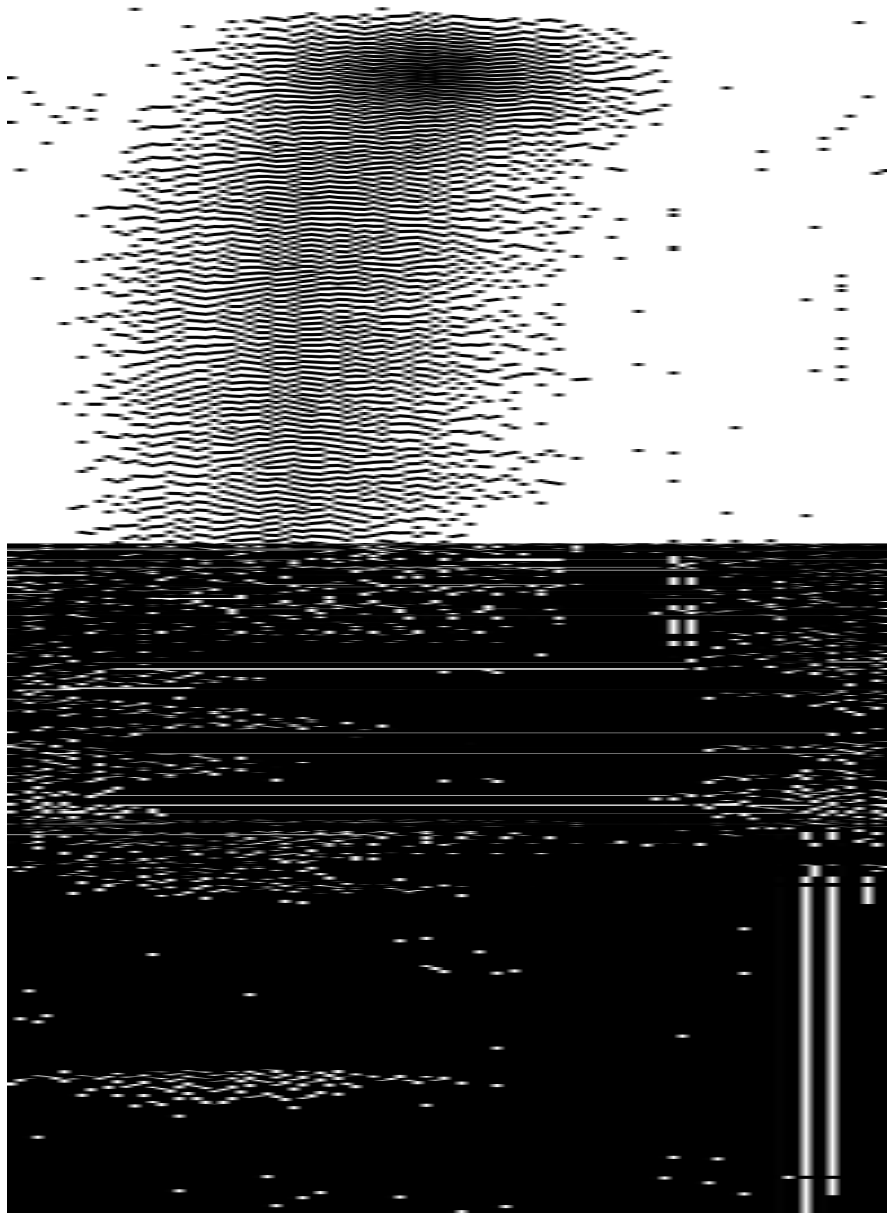
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