Stochastic Networks with Subthreshold Oscillations and Spiking Activity

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Abstract. Subthreshold oscillations actively participate in information coding and processing of living neural systems. In this paper we present a new model of stochastic neural networks in which the neurons display subthreshold oscillations and spiking activity. The network is built with diffusive coupling among close neighbors. We show that these stochastic networks are able to generate a wide variety of coherent spatio-temporal patterns. Emerging phenomena in this networks can be of great interest in applications related to the coding and control of rhythms.

1 Introduction

Several neural systems of living animals exhibit subthreshold oscillations in addition to spiking activity. One example is the ampullae of Lorenzini of the dogfish where the subthreshold oscillations determine the basic rhythm of the impulse generation [1]. Another example is the inferior olive (IO) of mammals which is composed of networks of electrically coupled neurons. The IO cells generate subthreshold oscillations and spiking activity [2]. *In vitro* experimental recordings using slices of IO neurons have shown the presence of characteristic spatio-temporal patterns of activity [3, 4]. The cerebellum and the IO have been studied extensively, but the role of this system remains unclear. Several hypothesis relate the IO to the control and learning of motor rhythm coordination [5, 6, 2, 7]. Computer models of the IO can provide useful information to disclose its function. In [8] the authors studied the characteristic spatio-temporal patterns generated by a network of Hodgkin-Huxley type neurons showing that these patterns of network activity can easily encode several coexisting rhythms.

In this paper we propose a stochastic model to study the generality of emerging properties of systems with electrically coupled neurons displaying subthreshold oscillations and spiking activity. Several interesting phenomena related to this particular behavior have been observed in living neural systems and in conductance-based models. The stochastic model can reproduce qualitatively these phenomena but considerably reducing the time of computation needed to implement large networks with more realistic approaches [9, 8]. The model can

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be useful not only to test hypothesis about the role of the IO and other neural systems, but also to investigate the computational abilities of such networks. The activity of the isolated neuron is implemented using a random walk with absorbent barriers [10, 11]. The interaction between single units is introduced through a diffusive coupling among close neighbors. We show that networks of stochastic neurons with subthreshold oscillations can exhibit coherent spatio-temporal patterns which are similar to those obtained with detailed conductance-based models [8].

2 The Stochastic Model

We have built a stochastic neural model with subthreshold oscillations and spiking activity. The spontaneous evolution of the activity of an isolated neuron follows a random walk. The neuron activity is considered as a discrete variable and characterized in time by $a(t)$. The stochastic dynamics of a single unit i is given by:

$$a_i(t+1) \;=\; \begin{cases} a_i(t) + C & \text{with probability } p \\ a_i(t) & \text{otherwise,} \end{cases} \tag{1}$$

where p is the transit probability of its internal state per time step. Therefore $1-p$ is the probability of remaining in the current state. C is a parameter that depends on the temporal evolution of the unit activity. This parameter can have three different values. The neuron starts to increase its activity from an initial state, with probability p, using $C = 1$. If the neuron reaches its activation threshold, L, it produces a spike according to a firing probability p_f. The activity is incremented in $3L$ in order to model the spike event. After the spike, the neuron activity begins to decrease to the initial state following equation 1 with $C = -L$ until it reaches the lower activity. When the unit reaches the threshold and it does not fire, with probability $1-p_f$, its activation begins to decrease again, but now $C = -L/5$. A schematic representation of this model is shown in Figure 1. The evolution of an isolated neuron is shown in Figure 2 for different values of p_f. For all simulations, the initial activity of each neuron is chosen randomly in the $[1, L]$ interval.

To construct the networks we use difussive coupling among neighbor units. We build bidimensional networks with periodic boundary conditions to avoid border effects. The neurons are connected emulating electrical coupling, and the interchange rule between unit i and its neighbors j is defined by:

$$a_i(t) = a_i(t) + g \sum_{j=neighbors} [a_j(t-1) - a_i(t-1)], \tag{2}$$

where g is the electrical coupling conductance and $a_j(t)$ is the activity of its neighbors. The value of the conductance g is the same in every connection. The electrical coupling induces a local synchronization in the network as a function of g.

The evolution of each neuron activity in the network is given by two contributions: the spontantaneous random walk described by equation 1 and the

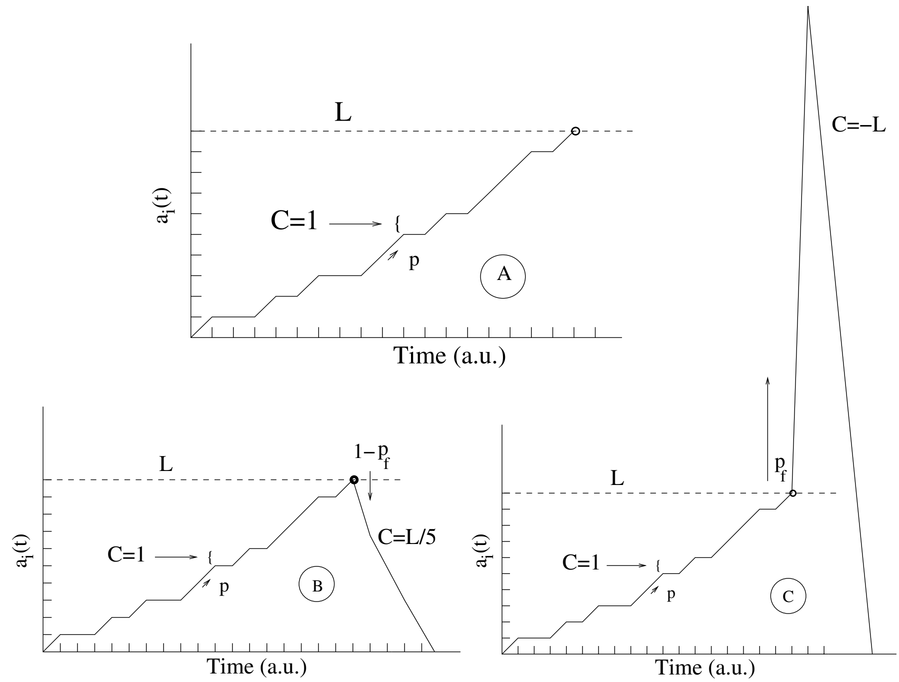

Fig. 1. Schematic representation of the stochastic single neuron model. (A) Spontaneous evolution of the subthreshold activity as determined by the parameters of the model. (B) Subthreshold oscillation after failure to produce a spike. (C) Emission of a spike after reaching the threshold.

interaction among neighbor neurons (diffusive electrical coupling described by equation 2).

3 Results

We have studied the generation of coherent spatio-temporal patterns of subthreshold and spiking activity in bidimensional networks of 50 × 50 identical stochastic neurons. In all networks described in this paper, each neuron was connected to its four nearest neighbors through the diffusive coupling described in the previous section. The appearance of spatio-temporal patterns of activity in these networks strongly depends on g, the value of the electrical coupling conductance.

We first tested the model in two extreme cases. For very small coupling, $g = 0.001$, the neurons behave similarly to the non-coupled case (see time series at the top of Figure 3 and the temporal sequence at the top of Figure 4). In Figure 4 dark dots correspond to neurons with subthreshold activity, while white dots mean spiking activity. Neurons with the same color have the same value of

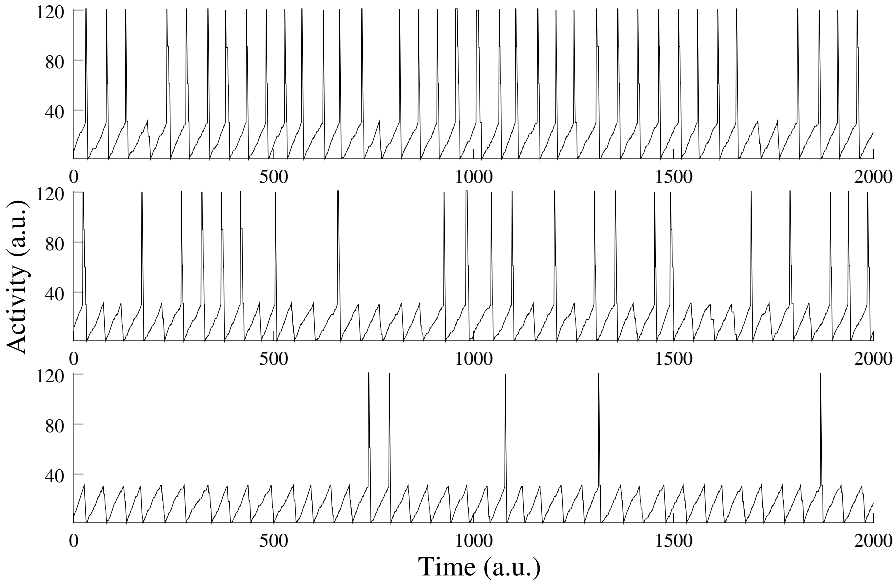

Fig. 2. Activity of an isolated neuron for three different values of p_f. From top to bottom: $p_f = 0.9,\ 0.5,\ 0.1$ (p=0.7 and L=30 in all simulations).

the activity. Neighbor neurons are not synchronized due to the different initial activities and the stochastic nature of their evolution including the spike generation. Conversely, for strong coupling $g = 0.17$ the neuronal activity is nearly synchronized as we can observe in the third row of Figure 3 and Figure 4. Coherent spatio-temporal patterns with well-defined wave fronts can not be found in the activity of the network for these two extreme values of the coupling.

The spatio-temporal patterns emerge for a moderate value of the electrical conductance. When a neuron fires, it increases the probability of spiking in its neighbors. Close neighbors tend to fire with a small phase shift. This generates a propagating wave front in the network that creates the pattern. An example of intermediate electrical coupling, $g = 0.06$, is shown in the second row of Figures 3 and 4. Note that the spike width depends on the value of the electrical coupling. An example can be seen in Figure 3 by comparing the activity for $g = 0.001$ and $g = 0.17$. We must recall that the stochastic model makes $C = -L$ (see equation 1) to simulate the activity decay after firing. When the electrical coupling is high, the activity of neighbor units accelerate the descent, and as a consequence, there is an appreciable spike focusing phenomenon in the network.

We are interested in the study of the ability of these networks to encode different rhythms that can coexist in the network. Thus, we introduced stimuli in two separate clusters within the 2D network. Each cluster is formed by a matrix of 6×6 neighbor neurons. We show the exact position of the stimulus clusters $S1$ and $S2$ in the network at the right panels of Figure 3 together with

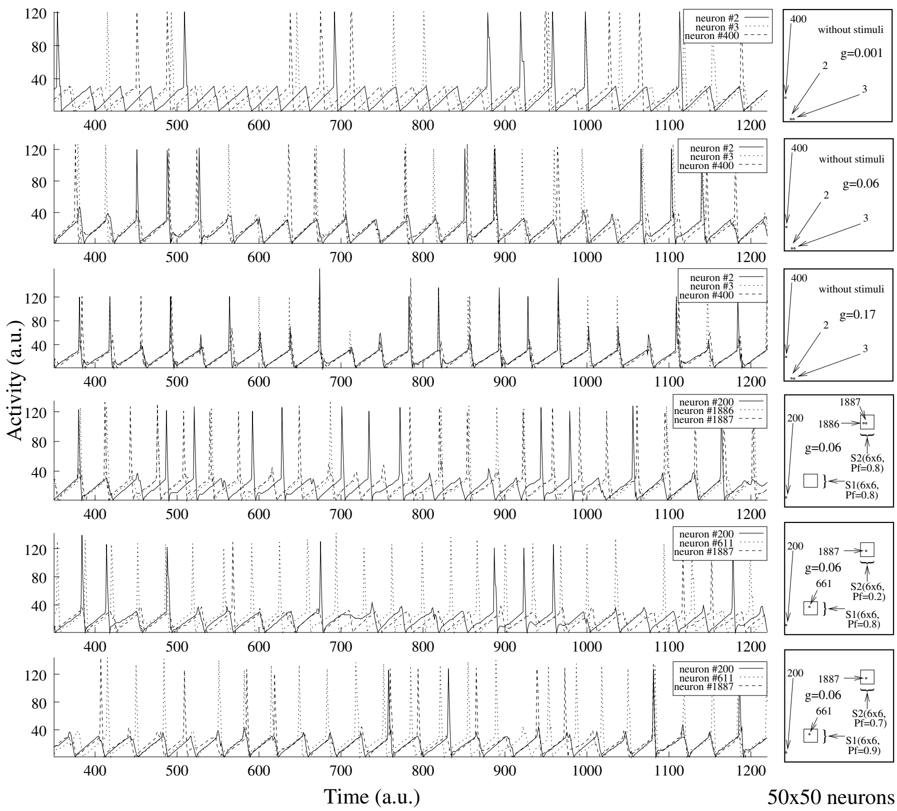

Fig. 3. Subthreshold oscillation and spiking activity for three neurons in a population of 50×50 units. In all simulations $L = 30$, $p = 0.9$ and $p_f = 0.4$. The first three rows show time series for three different values of the conductance $g = 0.001,\ 0.06,\ 0.17$. The last three rows show time series in networks with two 6×6 stimulus clusters, $S1$ and $S2$, in which the neurons had a different p_f than the value used in the rest of the neurons in the ensemble. The firing probability of the neurons not belonging to the stimulus cluster was $p_f = 0.4$. In 4th plot the firing probability for stimulus clusters $S1$ and $S2$ is the same, $p_f = 0.8$. In 5th plot the firing probability for stimulus clusters $S1$ and $S2$ are respectively $p_f = 0.8,\ 0.2$. Lastly, in 6th plot the firing probability for stimulus clusters are $p_f = 0.9$ for $S1$ and $p_f = 0.7$ for $S2$.

the unit number in which we measure the activity (see 4th, 5th and 6th time series in Figure 3).

Fourth row in Figure 3 and 4 correspond to a network in which the neurons that belong to the stimulus clusters had a high spiking probability, $p_f = 0.8$. In this case, the propagating wave always emerged from the stimulus clusters (see 4th temporal sequence in Figure 4). When one cluster had a low spiking probability, $p_f = 0.2$, and the other high probability, $p_f = 0.8$, the low frequency cluster acted as a sink for the activity propagated from the other one (see fifth

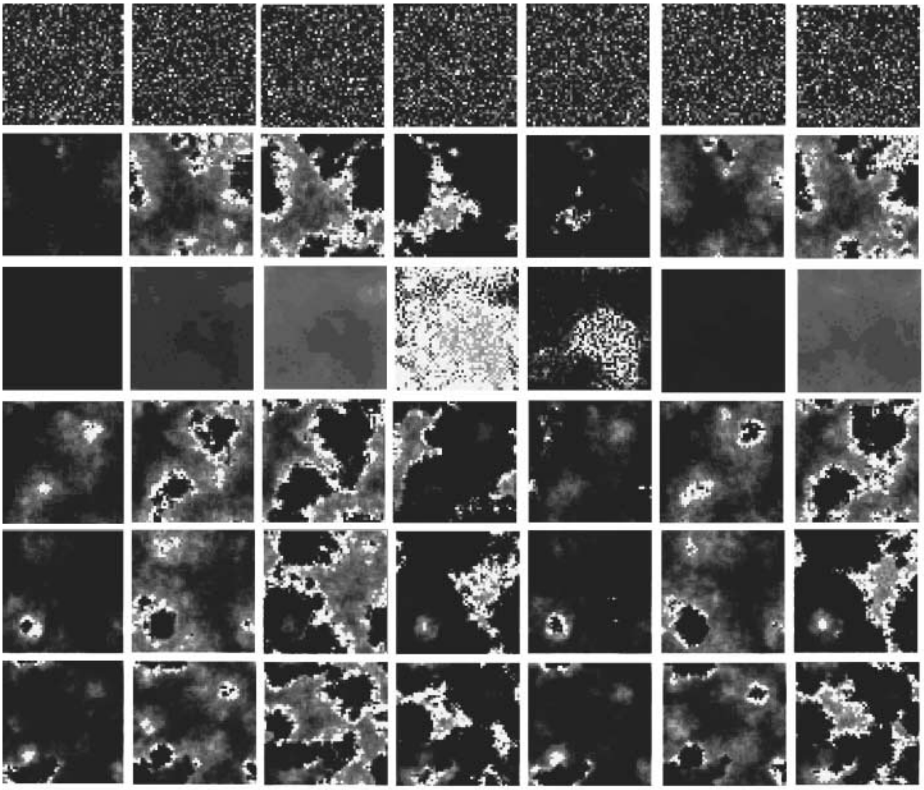

Fig. 4. Spatio-temporal patterns displayed by the networks of 50×50 neurons described in figure 2. Time sequences go from left to right. Neurons with the same color are synchronized. The first three rows correspond to networks without stimuli. In the last three rows two clusters of stimuli are introduced in the network. See detailed explanation in the text.

temporal sequence in Figure 4, and fifth plot in Figure 3). Lastly, when both stimulus clusters had a high spiking probability but different p_f (0.7 and 0.9, respectively), the propagating wave emerged from the clusters in different temporal phases. In the last two cases, there was coexistence of regions with different spiking frequencies in the network.

4 Discussion

The dynamics of spiking neurons synaptically coupled in a bidimensional array has been extensively studied [12–16]. We propose a new stochastic neural model with the ability to generate subthreshold oscillations and spiking activity. In two-dimensional networks with electrical connections, the subthreshold activity is crucial to establish an overall synchronization of under-threshold activity while keeping a high degree of independence in the spiking behavior of the population. This allows the coding of different rhythms induced by stimuli in the spiking activity under the modulation of a nearly homogeneous subthreshold oscillations. This simple model reproduces the essential phenomena found in more complex realistic networks of inferior olive neurons, showing the generality of the phenomena and also the ability of the model to be used as a tool to study hypothesis about the role of this neural system. The model does not include a refractory period in the neurons after the occurrence of a spike. In consequence, the frontiers of the spatio-temporal patterns are not as sharp and well defined as those observed with more realistic approaches. This aspect of the model will be a subject for future work.

While often neglected in the analysis of living systems and the design of artificial neural networks, subthreshold oscillations can actively participate in the coding and processing of information. In living neural systems such as the IO, the properties given by the diffusive coupling and the subthreshold oscillations could be used to encode and control different rhythms of motor behavior.

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