

Pattern formation and encoding rhythms analysis on a spiking/bursting neuronal network

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Abstract. In this work we study the formation of patterns of neuronal activity when some input are presented to the network. For this task a recently developed model of neuron is utilized. This model requires a very low computational effort but presents many characteristics of more complex models such as, spiking, bursting and sub-threshold oscillations, and therefore the realistic study of the behavior of big ensembles of neurons can be aborbed, even under real time conditions. New results of the application of the wavelet transform technique to the analysis of pattern formation and the possible encoding of rhythms are presented; they show that this simple, low-computational, neuron model behaves much like more complex ones.

1 Introduction

There is currently a very active line of work trying to reproduce numerically the observed behavior in real ensembles of neurons, like sub-threshold oscillations, spiking, bursting and spatio-temporal patterns, which seem to play an important role in the function of these ensembles [1–3]. One of the most followed approaches for the numerical simulation of the collective behavior of these ensembles is the use of some differential equations models for the neurons and their interactions. Some of the most widely used models of this kind are the Hodgkin–Huxley (HH) model [4], the Hindmarsh–Rose (HR) model [5] and the FitzHugh–Nagumo model (FN) [3, 6, 7]; but these models have a high computational cost, as they require a lot of floating point operations to be carried out: 1200 operations in the case of the HH model and 70 operations in the HR model, just to simulate a single neuron in the network for 1 ms. So, the simulation of relatively large neural networks for long periods of time may take too much time.

Another approach that has been recently taken is to build simpler models on a phenomenological basis [8, 9]. The aim of these models is to mimic the observed phenomena on real neural networks, though some of them [8] have some biophysical interpretation that simplify the tuning of the parameters to obtain neuron behavior such as, spiking, tonic spiking, bursting, etc. These models are implemented as iterative two-dimensional maps, and have a much lower computational effort than the ones based on differential equations, so they are good candidates for the simulation of large networks over long periods of time.

We present here one of these phenomenological models [10, 11], based on a two-dimensional continuous piecewise linear map, which is able to model sub-threshold oscillations, spiking and bursting. This model has a very low computational cost: just around two floating point

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operations for each iteration. We also show how this model can reproduce the synchronization in the activity of a coupled pair of neurons.

These kind of simulations may be applied to the study of the spatio-temporal patterns of real neural networks like the inferior olive (IO) [12]. The structure of the inferior olive and the cerebellar circuits of mammals has been deeply studied, but their functional role is not yet very clear. It has been argued that the internal oscillations of the IO neurons, along with their coupling, may control some rhythms in the organism. Numerical simulations have showed the relevance of sub-threshold oscillations and spiking in the generation of spatio-temporal patterns which may encode several coexisting rhythms. We use here the above phenomenological model to study the behavior of a network of such neurons, with coupling and stimuli, and show how the discrete wavelet transform may be used to analyze the network activity and give a quantitative characterization of the spatio-temporal patterns that arise.

2 The neuron model

Two-dimensional maps have been used recently to model neural behavior, avoiding the high computational cost of standard differential equations models [8,13]. These models are based in the interplay of a slow and a fast dynamic, accounting for the rapid bursting of spikes on a substrate of slow oscillations. However, these two dynamics are correlated, so that spiking in the fast variable occurs for high values of the slow variable, while low values of the slow variable are associated with the resting periods of the fast variable.

We will use here a simplified model based on these ideas [10,11]. This model consists of a two-dimensional map (y, s) , where y represents the membrane potential, while s indicates if the value of the membrane potential y is de-polarizing ($s = 1$) or re-polarizing ($s = 0$). The variable y takes its values along two continuous piecewise linear function (see figure 1, one corresponding to re-polarizing state ($s = 0$), where the value of y goes down, and the other one corresponding to the de-polarizing state ($s = 1$), with y values going up. The different segments of these piecewise linear functions correspond to different behavior of the neuron: resting and sub-threshold oscillations for the $(0, C)$ segment in figure 1, and spiking and bursting for the (C, D) segment. The neuron changes its state from de-polarizing to re-polarizing when the value of y is too high, and from re-polarizing to de-polarizing when y is too small, or when it lies near the bottle in C .

The mapping algorithm is the following, and is plotted in figure 1:

$$\begin{aligned}
 y_{n+1} &= \begin{cases} \frac{H(s_n)}{B} * y_n & \text{if } 0 \leq y_n < B \\ (y_n - B) * \frac{K(s_n) - H(s_n)}{C - B} + H(s_n) & \text{if } B \leq y_n < C \\ (y_n - C) * \frac{T(s_n) - K(s_n)}{D - C} + K(s_n) & \text{Otherwise} \end{cases} \\
 s_{n+1} &= \begin{cases} 0 & \text{if } s_n = 1 \text{ and } y_{n+1} > D \\ 0 & \text{if } s_n = 1 \text{ and } C - S < y_{n+1} < C \\ 1 & \text{if } s_n = 0 \text{ and } y_{n+1} < L \\ 1 & \text{if } s_n = 0 \text{ and } C < y_{n+1} < C + E \\ s_n & \text{Otherwise} \end{cases} \quad (1)
 \end{aligned}$$

where $H(s) = H_0 + s * (H_1 + \sigma)$, $K(s) = K_0 + s * (K_1 + \sigma)$ and $T(s) = T_0 + s * (T_1 + \sigma)$ and $B, C, D, S, E, L, H_1, H_0, K_1, K_0, T_1, T_0$ are non-negative parameters verifying the following conditions: $L < B < C < D$, $H_0 \leq B$, $H_1 + H_0 \geq B$, $K_0 \leq C$, $K_1 + K_0 \geq C$, $T_0 \leq D$ and $T_1 + T_0 \geq D$; σ represents an external total input to the neuron. The parameter C is the spike threshold. The parameters L, E and D are thresholds that force the change of value of the slow variable s as the fast variable y crosses one of these thresholds, where L is the hyper-polarization

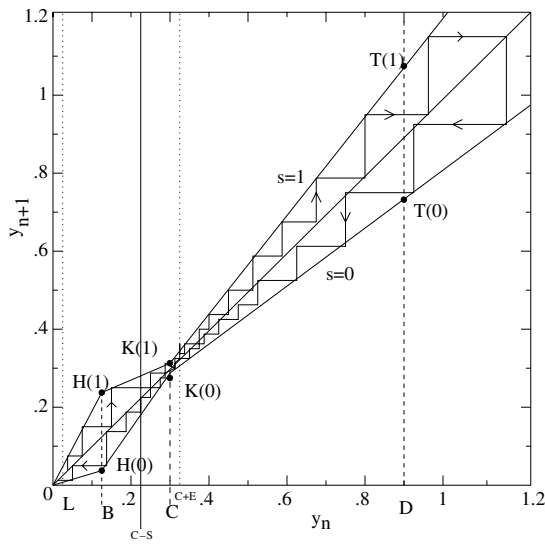


Fig. 1. Graph of the piecewise linear function y .

value and D is the depolarization value. The other parameters determine the length and the step of the segments that compound the function y .

2.1 Sub-threshold oscillations, spiking and bursting

By tuning the parameters of the model, i.e. slopes of the linear segments and thresholds, different neuron behavior can be reproduced. L and D are the hyper-polarization and depolarization values respectively; these parameters act as thresholds where the neuron change its state when the membrane potential is too low or too high. The parameter C is the spiking threshold, where the neuron passes from a rest or sub-threshold oscillation state to a spiking one. The parameters S and E control, respectively, the amount of sub-threshold oscillation and bursting in the neuron response; they do this by setting how difficult is to pass through the spiking threshold C when either coming from low or high values of the potential y .

In figure 2 an example of spiking behavior over sub-threshold oscillations is showed, while in figure 3 one can see a bursting response. Parameter values for figure 2 are: $L = 0.01$, $B = 0.15$, $C = 0.3$, $D = 0.9$, $S = 0.01$, $E = 0$, $H(0) = 0.14$, $K(0) = 0.28$, $T(0) = 0.75$, $H(1) = 0.01$, $K(1) = 0.04$, $T(1) = 0.3$ and $\sigma = 0.001$. For figure 3 parameter values are the same except for $E = 0.023$, which controls the bursting behaviour.

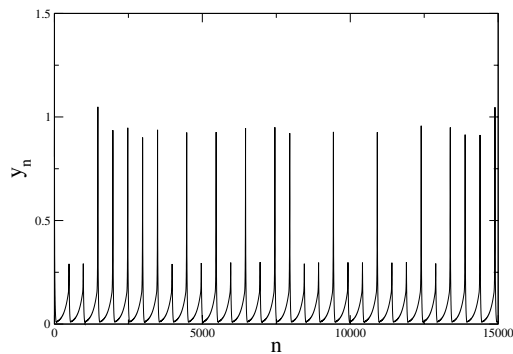


Fig. 2. Neuron behavior modeling: sub-threshold oscillation and spiking.

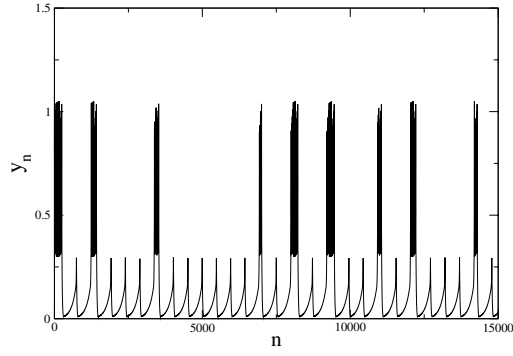


Fig. 3. Neuron behavior modeling: sub-threshold oscillation and bursting.

2.2 Synchronization in two coupled maps

These simplified maps, with low computational cost, are very well suited for the study of large ensembles of coupled neurons. In these ensembles, chemical synaptic transmission can be modeled by substituting the external, global, input σ for some specific total input to neuron i , with some coupling terms [10]:

$$\sigma_{n,i} = \sigma_i^e + \frac{1}{\Gamma_i} \sum_{j=1}^N g_{ij} s_{n-1,j} H(y_{n-1,j} - \Theta) \quad (2)$$

where σ_i^e represents both the external input to neuron i and the action of any current not explicitly captured by the model. Γ_i is the number of neighbors of neuron i , N is the number of neurons in the network, $y_{n,j}$ and $s_{n,i}$ represent respectively the value of y and s for the neuron j at time n . The parameter g_{ij} is the synaptic coupling coefficient between neuron i and neuron j and $H(x)$ is the usual Heaviside function. The threshold Θ has been chosen such that every spike in the single neuron can reach the threshold ($\Theta = C$)

Synchronous behavior of coupled neurons is thought to be of particular interest in the transmission and coding of information along neural networks. It has been studied in the olfactory system [14], the visual cortex region [15], and neurophysiology experiments [16,17] have demonstrated that it shows up in real neuron ensembles.

This synchronous behavior can be reproduced either by differential or iterative models [13], and it can also be obtained by the simplified model of equation (1). In figure 4 we show an example of synchronization of two neurons. After a transient period, we can see that the membrane potential of both neurons, $y_{n,0}$ and $y_{n,1}$, is almost the same for the rest of the simulation. This is very clear in the second plot of this figure, where the difference of these potentials is plotted. The parameters of the neuron model in this case are those used for

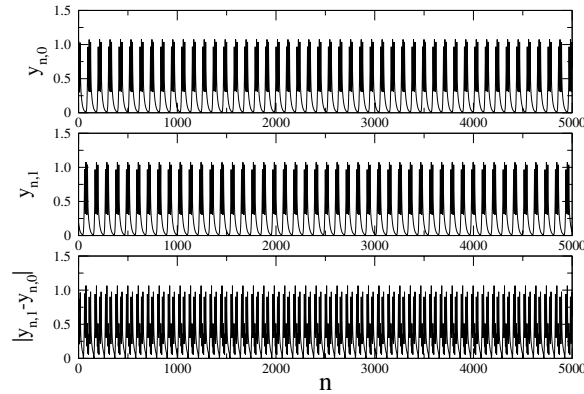


Fig. 4. Synchronization in coupled maps, $y_{n,0}$ and $y_{n,1}$, with bursting behavior.

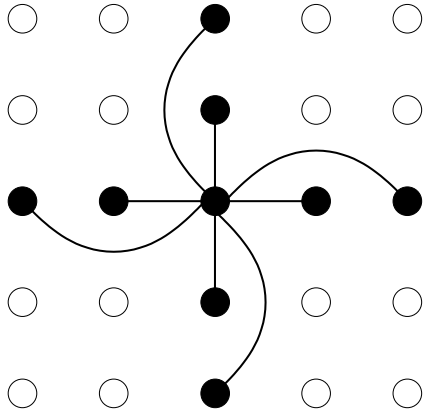


Fig. 5. Connections of a (central) node to 8 of its nearest neighbors in the rectangular grid used to model the neural network.

reproducing the bursting behavior. The parameters of the total input for each neuron are $\sigma_0^e = \sigma_1^e = 0.05$ for the external input and $g_{0,1} = g_{1,0} = 0.05$ for the coupling coefficients.

3 Neural network pattern analysis

Spatio-temporal patterns of neuron activity are of special interest nowadays. They have been observed in some in-vitro experiments in networks like the Inferior Olive (IO) [18], though the inner working of sub-cellular and network processes that give rise to this phenomena is not yet well understood. These patterns are relevant when elucidating the functional role of networks like the IO, which is not very clear. Some studies argue that the IO may act as a system controlling some intrinsic rhythms in the organism [19]. It is also known that IO cells show sub-threshold oscillations and spiking and the physical structure of the network and electrical coupling are well studied.

Some numerical simulations have been carried out trying to reproduce the observed patterns, so that they can be used to study the relevant aspects of these patterns and the neuron characteristic behavior that may originate them. In [12], an HH differential equation model is used to reproduce these patterns. In this work, it is stated the importance of sub-threshold oscillations and spiking in the generation of spatio-temporal patterns, and they also show how networks of this kind may encode different coexisting rhythms. A discrete wavelet transform (DWT) is also used to measure the complexity of the spatial patterns, and its evolution, so that, these encoding rhythms may be seen more clearly.

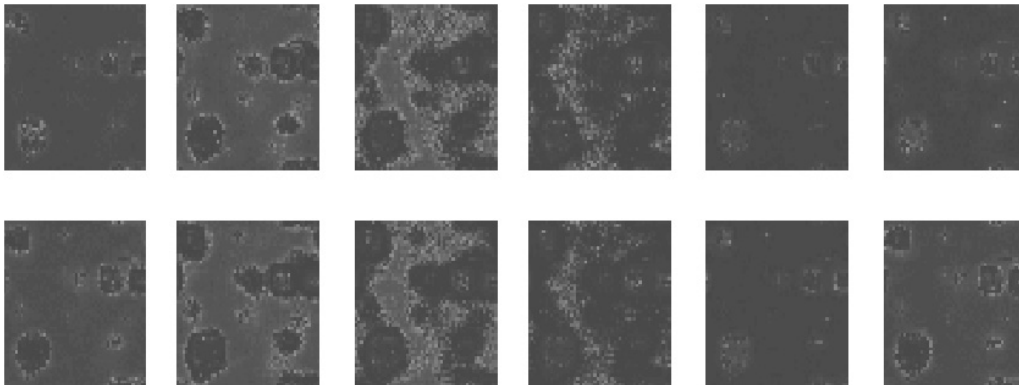


Fig. 6. Sample instantaneous patterns that arise in coupled neuron networks. Snapshots are taken every 100 iterations of the temporal evolution of the network.



Fig. 7. Spatially (apparently) uncorrelated patterns when there is no coupling between neurons. Snapshots are taken every 100 iterations of the temporal evolution of the network.

We have used the simple neuron model given by the map of equation (1) to reproduce these patterns. We have built a two dimensional network of 50×50 identical neurons, whose behavior is governed by this model, and with a synaptic coupling defined by equation (2). As shown in figure 5, each neuron is connected to 8 of its nearest neighbors in a rectangular grid, with periodic boundary conditions. Figure 6 shows the kind of patterns that arise in such a network after the injection of a uniform external current on a small area of the network; these patterns are very similar to those obtained in-vivo [18] or with more realistic, and complex, models [12]. In figure 7 we show the result of uncoupling the neurons, so that they behave independently: no patterns are observed, and every neuron fires at its own.

3.1 Wavelet analysis of the network activity

Following [12], we have also used the discrete wavelet transform (DWT) to characterize quantitatively the spatio-temporal patterns of the network. This technique gives us a better insight than a mere visual inspection of the movies of the simulations (available under request from the authors). The coefficients of the DWT represent the resolution content of the data. A two-dimensional basis was generated by direct Cartesian product of the one-dimensional Haar basis [20]. We followed a compression-like technique to characterize the spatio-temporal patterns of activity in the network. First, we calculated the two-dimensional non-standard DWT for each frame of network activity as described above. Second, we counted the number of coefficients, N , that were bigger in absolute value than a given threshold. The number of these coefficients provides a useful characterization of the patterns in which both the frequencies and the spatial extent can be discussed as shown in figure 8. Very high values of N correspond to almost random behavior of every neuron, with no patterns present; intermediate high values of N indicate the presence of complex spatial structures in the patterns, while completely synchronized networks produce a small number of coefficients.

Figure 8 shows the evolution of the number of coefficients for two different networks: a network with electrical coupling $g_{ij} = 0.0075$ and a network without coupling $g_{ij} = 0$. The average higher value of N in the latter shows a more complex spatial structure, where every neuron behaves independently, and no patterns are present. The spiky waveform in the evolution of N in the case of coupled neurons shown in figure 8 also indicates the presence of multiple

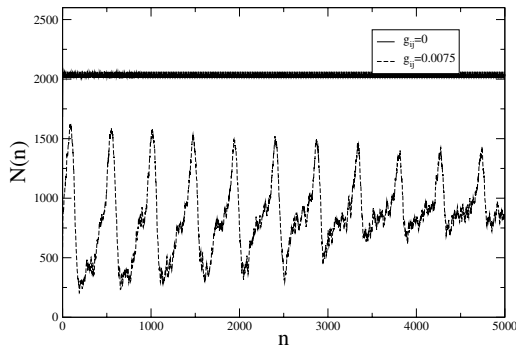


Fig. 8. Wavelet analysis of spatio-temporal patterns.

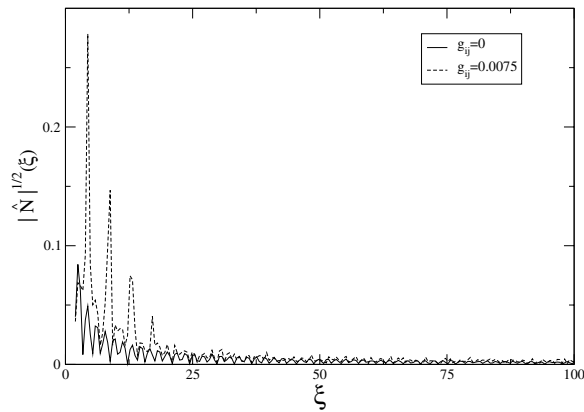


Fig. 9. Power spectrum of the wavelet analysis of spatio-temporal patterns.

spiking frequencies evoked by the stimuli in the network, and the periodic evolution of spatial patterns.

The encoding frequencies present in the network can be calculated by means of the Fourier transform of the wavelet analysis of the network activity. In figure 9 the Fourier transform of the wavelet analysis for both networks is presented. The coupled network present a clear set of dominant frequencies in the network activity that correspond with the different frequencies of the spatio-temporal patterns present in the network, on the other hand, the uncoupled network present a much less spiky distribution of the frequencies spectrum due to the absence of spatio-temporal patterns and reflecting exclusively the periodic behavior of the individual neurons in the network. These results are in-line with those obtained in [12], where a much more complex model is used.

4 Discussion

The patterns observed in the simulations were very similar to those recorded in vitro in slices of IO neurons and reported in [18] or obtained by intensive computer simulations [12]. The simple neuron model and the simulations presented here can help us to test hypotheses related to the role of network processes in the genesis of neuronal spatio-temporal patterns as well as to understand how the oscillations present in different nervous systems can encode and control several simultaneous rhythms. The discrete wavelet transform may be a useful tool when studying these encoding rhythms.

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