

Synchronization in Pulse-Coupled Networks of Bursting Neurons

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Abstract—We study the influence of coupling strength and network topology on synchronization behavior in pulse-coupled networks of bursting neurons. We find that the stability of the completely synchronous state in networks of coupled Hindmarsh-Rose neurons only depends on the number of signals each neuron receives, independent from all other details of the network topology. This is in contrast with linearly coupled bursting neurons where complete synchrony strongly depends on the network structure and number of cells. Through analysis and numerics, we show that the onset of synchrony in a network with *any* coupling topology admitting complete synchronization is ensured by one single condition.

1. Introduction

Model studies of neuronal synchronization can be separated in those where threshold models of the integrate-and-fire type are used [1, 2] and those where conductance-based spiking and bursting models are employed [3]. Bursting occurs when neuron activity alternates, on a slow time scale, between a quiescent state and fast repetitive spiking. There has been much work on mechanisms that produce such bursting [6]. In contrast to coupled spiking neurons, whose synchronous dynamics is relatively simple, interacting bursting neurons may exhibit different forms of synchrony; including synchronization of individual spikes, burst synchronization when only the envelopes of the spikes synchronize, and complete synchrony [9]. Typically, burst synchronization arises at a low coupling strength whereas complete synchrony, which involves both burst and spike synchronization regimes, requires a stronger coupling. Models of interacting bursting neurons often use one of two different forms of coupling depending on whether the synapse is electrical or chemical. In the first case, the coupling through gap junctions is linear and directly dependent on the difference of the membrane potentials. In the second case, the coupling is pulsatile and often modeled as a static sigmoidal nonlinear input-output function with a threshold and saturation [10]. One important question about interacting bursting neurons with such linear and pulsatile couplings is that of complete synchronization: What are the conditions for the stability of the completely synchronous state, especially with respect to coupling strengths and coupling configurations of the net-

work? This problem was intensively studied for linearly coupled networks of bursting neurons [11, 12], and more generally, of limit-cycle and chaotic oscillators [13, 14]. In particular, it has been shown that synchrony in such networks strongly depends on the structure and size of the network.

In this paper we present a surprising find regarding the synchronization of synaptically coupled networks of bursting neurons [15]. Studying a network of pulse-coupled Hindmarsh-Rose (HR) neurons [16], we discovered that all that matters for the onset of complete synchrony is the number of signals, k , received by each neuron. This is independent of all other details of the network structure. More precisely, the synchronization threshold is inversely proportional to the number of incoming signals k . This criterion applies to a neuronal network with *any* coupling topology admitting complete synchrony. For this property to be true, each neuron must receive signals from k others, where k is uniform for all neurons. The synchronization condition we present below is not restricted to the HR neuron, but is directly applicable to many other bursting Hodgkin-Huxley-type neurons as well; including the 3D Morris-Lecar [8], Sherman [11], and Wilson [17] models.

2. Network considered

In this work, we shall concentrate on networks of HR neurons exhibiting square-wave bursting, which is very resistant to synchronization. The single HR model [16] reads

$$\begin{aligned}\dot{x} &= y + ax^2 - x^3 - z + I, \\ \dot{y} &= 1 - dx^2 - y, \\ \dot{z} &= \mu(b(x - x_0) - z),\end{aligned}$$

where x represents the membrane potential, and y and z are associated with fast and slow currents, respectively. a, d, b, I, x_0, μ are parameters, and μ is small. For the sake of simplicity, the HR model with the above set of parameters can be transformed, using the substitution $(y, z) \rightarrow (1 - y, 1 + I + z)$, $d = a + \alpha$, $c = -1 - I - bx_0$, into the form

$$\begin{aligned}\dot{x} &= ax^2 - x^3 - y - z, \\ \dot{y} &= (a + \alpha)x^2 - y, \\ \dot{z} &= \mu(bx + c - z).\end{aligned}$$

Consider now a network of n pulse-coupled HR models. The equations of motion are the following:

$$\begin{aligned}\dot{x}_i &= ax_i^2 - x_i^3 - y_i - z_i - g_s(x_i - V_s) \sum_{j=1}^n c_{ij} \Gamma(x_j), \\ \dot{y}_i &= (a + \alpha)x_i^2 - y_i, \quad \dot{z}_i = \mu(bx_i + c - z_i), \quad i, j = \overline{1, n}.\end{aligned}\quad (1)$$

Here, the neurons are identical and the synapses are fast and instantaneous, i.e. time delays and internal synaptic variables are ignored. The parameter g_s is the synaptic coupling strength. The reversal potential V_s is assumed to be greater than $x_i(t)$ for all x_i and all times t , i.e. the synapse is excitatory. The synaptic coupling function is modeled by the sigmoidal function $\Gamma(x_j) = 1/[1 + \exp\{-\lambda(x_j - \Theta_s)\}]$ (a limiting version of $\Gamma(x_j)$ is the Heaviside function). This oft-used coupling form was called fast threshold modulation (FTM) by Somers and Kopell [10]. The threshold Θ_s is chosen such that every spike in the single neuron burst can reach the threshold (see Fig. 1). Hereafter, the individual neuronal parameters, Θ_s and V_s are chosen and fixed as follows: $a = 2.8$, $\alpha = 1.6$, $c = 5$, $b = 9$, $\mu = 0.001$, $\Theta_s = -0.25$, $V_s = 2$.

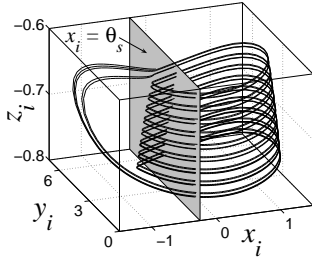


Figure 1: The synaptic threshold Θ_s and square-wave bursting of the HR model.

$\mathbf{C} = (c_{ij})$ is the $n \times n$ connectivity matrix: $c_{ij} = 1$ if neuron i is connected to neuron j , $c_{ij} = 0$ otherwise, and $c_{ii} = 0$. Matrix \mathbf{C} can be asymmetric such that both mutual and unidirectional couplings are allowed. We require equal row-sums $k = \sum_{j=1}^n c_{ij} = k$, $i = 1, \dots, n$. This requirement is a necessary condition for the existence of the synchronous solution, namely the invariance of hyperplane $D = \{\xi_1(t) = \xi_2(t) = \dots = \xi_n(t)\}$, $\xi_i = (x_i, y_i, z_i)$, $i = 1, n$. In fact, the equal row-sum property implies a network where each cell has the same number k of inputs from other neurons. Synchronous behavior on the manifold D is generated by the system:

$$\begin{aligned}\dot{x} &= ax^2 - x^3 - y - z - kg_s(x - V_s)\Gamma(x), \\ \dot{y} &= (a + \alpha)x^2 - y, \quad \dot{z} = \mu(bx + c - z).\end{aligned}\quad (2)$$

3. Stability equations for the synchronous solution

Adding and subtracting an additional term $g_s(x_i - V_s) \sum_{h=1}^n c_{ih} \Gamma(x_i) = kg_s(x_i - V_s)\Gamma(x_i)$ from the x -equation of system (1), and introducing the differences between the neural oscillator coordinates $\xi_{ij} = x_j - x_i$, $\eta_{ij} = y_j - y_i$, $\zeta_{ij} = z_j - z_i$, $i, j = 1, \dots, n$ in the limit when these differences are infinitesimal, we derive the stability equations for the transverse perturbations to the synchronization manifold D :

$$\begin{aligned}\dot{\xi}_{ij} &= (2ax - 3x^2)\xi_{ij} - \eta_{ij} - \zeta_{ij} - kg_s\Gamma(x)\xi_{ij} + \\ &\quad + g_s(V_s - x)\Gamma'_x(x) \left(k\xi_{ij} + \sum_{h=1}^n \{c_{jh}\xi_{jh} - c_{ih}\xi_{ih}\} \right), \\ \dot{\eta}_{ij} &= 2(a + \alpha)x\xi_{ij} - \eta_{ij}, \quad \dot{\zeta}_{ij} = \mu(b\xi_{ij} - \zeta_{ij}).\end{aligned}\quad (3)$$

The derivatives are calculated at the point $\xi = 0, \eta = 0, \zeta = 0$, and $\{x(t), y(t), z(t)\}$ corresponds to the synchronous bursting solution defined via system (2). The first coupling term $S_1 = -kg_s\Gamma(x)\xi_{ij}$ accounts for the number of inputs k . At the same time, the contribution of the second coupling term $S_2 = g_s(V_s - x)\Gamma'_x(x) \cdot (\cdot)$ depends on the coupling configuration. Note that the term $\sum_{h=1}^n \{c_{jh}\xi_{jh} - c_{ih}\xi_{ih}\}$ is the same as for linear coupling [13]. In terms of the original variables x_i , the corresponding coupling matrix $\mathbf{G} = \mathbf{C} - k\mathbf{I}$ is the Laplacian of the connected graph, except for a sign change. It is well known that \mathbf{G} has one zero eigenvalue γ_1 and all other eigenvalues have non-positive real parts [?]. The eigenvalue γ_2 with the largest real part is crucial for the stability analysis of the synchronized solution. If the coupling is mutual, \mathbf{G} is symmetric and all eigenvalues are real. For simplicity, suppose that γ_2 is simple. Then, applying the linear transformation that diagonalizes \mathbf{G} to Eq. (3), we obtain the stability equation for the most unstable transverse mode:

$$\begin{aligned}\dot{\xi} &= (2ax - 3x^2)\xi - \eta - \zeta - \Omega(x)\xi, \\ \dot{\eta} &= 2(a + \alpha)x\xi - \eta, \quad \dot{\zeta} = \mu(b\xi - \zeta),\end{aligned}\quad (4)$$

where $\Omega(x) = kg_s\Gamma(x) - g_s(V_s - x)\Gamma'_x(x)(k + \gamma_2)$. System (4) is an analog of the Master Stability function [13] for pulse-coupled networks (1). If γ_2 is not simple, then we can write similar equations to system (4) for the vectors spanning the corresponding blocks in the Jordan normal form of \mathbf{G} . The stability discussion, however, is essentially the same.

4. Complete synchrony: what matters in the network topology?

Applying the stability equation (4) to basic network configurations (for the details of the proof, see [15]), we come to the following assertion.

Statement [15]. *The coupling threshold for complete synchronization in the network (1) is estimated as follows:*

$$g_s^* = g_s^{(n=2)}/k, \quad (5)$$

where k is the number of signals each neuron receives, and $g_s^{(n=2)}$ is a constant corresponding to the synchronization coupling threshold between two mutually coupled HR neurons ($k = 1$). The estimate (5) is valid for the networks (1) with any coupling configuration (whether global or local, regular or random, mutual or unidirectional) under the constraint that the number of inputs k is uniform for all neurons.

The constant $g_s^{(n=2)}$ comes from the application of the Lyapunov function method to the system (4) with $n = 2$ and gives an overestimate for the real coupling strength that leads to complete synchronization of two HR neurons: 2.94 (theoretically predicted) versus 1.285 actual for the above mentioned parameters and $\lambda = 10$. However, using the numerically obtained $g_s^{(n=2)}$, we can predict the threshold g_s^* , for any k from Eq. (5), as shown in the numerical examples below.

In support of this claim, we determine numerically the threshold for complete synchronization as a function of k for various coupling configurations (local, intermediate and global), and compare it to the value predicted by Eq. (5). For $g_s^{(n=2)}$, the value from simulation of two mutually coupled HR neurons was used. This value is $g_s^{(n=2)} = 1.285$ for $\lambda = 10$ and $g_s^{(n=2)} = 1.139$ for $\lambda = 50$. From the results shown in Fig. 2 it can be seen that the prediction is nearly perfect. Note that even for large λ , when the synaptic function $\Gamma(x_i)$ approaches the Heaviside function, the estimate (5) gives an excellent numerical prediction.

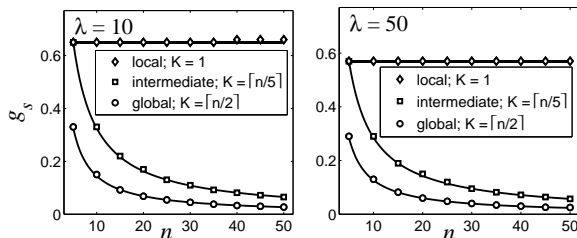


Figure 2: Synchronization thresholds g_s^* in a ring of $2K$ -nearest neighbor coupled HR neurons as functions of n for various coupling configurations (different K). Markers: Simulation results. Solid line: Prediction of Eq. (5).

Note that the synchronization threshold in locally synaptically coupled networks is constant; $g_s^* = g_s^{(n=2)}/2$ for mutually nearest-neighbor coupled neurons, and does not depend on the number of neurons n . This is in sharp contrast with linearly coupled networks where the coupling required for stable synchronization has a quadratic dependence on n [14].

To illustrate the power of condition (5) even further we have simulated -in addition to the regular, mutually coupled networks from Fig. 2- a series of randomly generated *unidirectionally* coupled networks of HR neurons with uniform number of synapses as those shown in Fig. 3. For all simulated networks, numerical results are nearly identical

to the analytical predictions of Eq. (5).

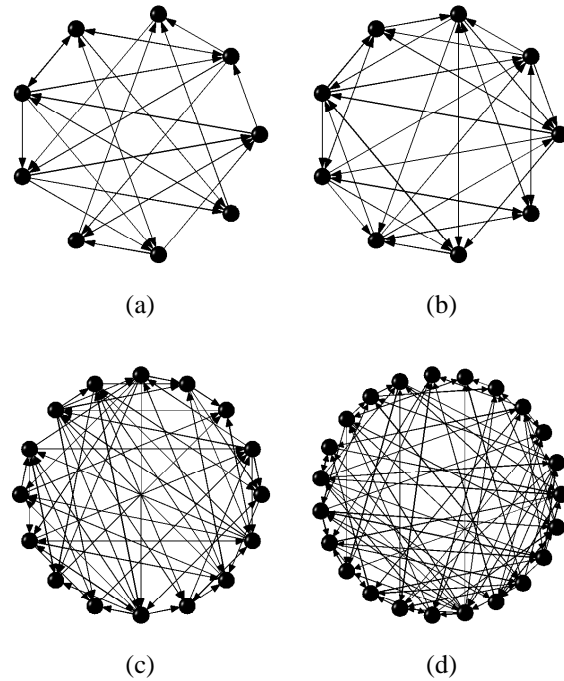


Figure 3: Examples of the unidirectional random networks simulated. Ten networks of each type, (a) $n = 9$, $k = 3$; (b) $n = 9$, $k = 4$; (c) $n = 16$, $k = 4$; (d) $n = 32$, $k = 4$ were generated randomly. The synchronization threshold for networks of type (a): $g_s^* = 0.429$ for $\lambda = 10$, and $g_s^* = 0.380$ for $\lambda = 50$; and of types (b), (c), and (d): $g_s^* = 0.322$ for $\lambda = 10$, and $g_s = 0.285$ for $\lambda = 50$. All the calculated thresholds coincide perfectly with $g_s^{(n=2)}/k$.

Finally, we have tested robustness of the synchronization with respect to a mismatch in the synaptic strengths. We have simulated networks of 20 neurons for the local, intermediate and global cases, introducing a mismatch in the synaptic strengths around the average g_s . Perfect synchronization is no longer possible in these cases, due to the absence of the synchronization manifold, and there is always an error in the synchronization. However, for a given value of g_s this error falls rapidly and then remains constant when g_s is further increased. This point can be seen as the coupling threshold for the approximate synchronization. In all simulated cases this value is nearly identical to the synchronization threshold without mismatch as shown in Fig 2. The synchronization has been verified to be robust for mismatches in g_s , of up to 5%.

In summary, the single condition (5) ensures the onset of complete synchronization in networks of synaptically coupled bursting neurons (1) with any coupling topology in which each neuron receives signals from k others. The synchronization condition depends on the number of inputs k and *not* on the connectivity matrix. The equal k constraint is often invalid for biologically relevant networks with a complex structure where the number of inputs is not nec-

essarily constant, but if k is uniform for a group of neurons, synchronization within this group of neurons can occur. The synaptic strengths can also change as a result of pre- and postsynaptic cell activity such that the inputs to the neurons become equal only for a specific interval of time. The consequence is transient synchronization [18] that is believed to be a collective mechanism for spatiotemporal neuronal integration. This work promises to allow an analytical treatment of even temporal synchrony in bursting cells.

Acknowledgments

We thank Wulfram Gerstner for his insightful involvement in this work and valuable suggestions. This research was supported by the the Swiss National Science Foundation through Grant N 2100-065268. I.B. acknowledges the INTAS grant No. 01-2061.

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