

Spike-train bifurcation scaling in two coupled chaotic neurons

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We investigate the variation of the out-of-phase periodic rhythm produced by two chaotic neurons (Hindmarsh-Rose neurons [J. L. Hindmarsh and R. M. Rose, Proc. R. Soc. London B **221**, 87 (1984)]) coupled by electrical and reciprocally synaptic connections. The exploration of a two-parametric bifurcation diagram, as a function of the strength of the electrical and inhibitory coupling, reveals that the periodic rhythms associated to the limit cycles bounded by saddle-node bifurcations, undergo a strong variation as a function of small changes of electrical coupling. We found that there is a scaling law for the bifurcations of the limit cycles as a function of the strength of both couplings. From the functional point of view of this mixed typed of coupling, the small variation of electrical coupling provides a high sensitivity for period regulation inside the regime of out-of-phase synchronization. [S1063-651X(97)50603-9]

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Individual neurons often generate chaotic oscillation [2,3], but circuits of them can demonstrate periodic pulsation. In order to answer the important question of how neural assemblies get and control regular rhythm, we investigate here the simplest chaotic neural circuit. We work with two model neurons coupled electrically and synaptically. The dynamics of each neuron is chaotic and spiking bursting [1] [see Fig. 1a]. Such dynamics are typical for many neurons in cortex [4] and small neural systems like the central pattern generators (CPG) that control the rhythmic motor behavior of animals [5–8]. The most typical connection between spiking-bursting neurons in CPGs is reciprocal inhibition followed by electrical coupling (see the book [9]). On a few occasions, both inhibitory and electrical coupling appear together connecting two neurons. It is not a trivial problem to understand the nonlinear dynamics of neurons with such antagonistic types of coupling. As has been previously shown [3,10], sufficiently strong inhibitory coupling between chaotic neurons organizes regular out-of-phase rhythmic behavior. The change of the strength of the inhibitory coupling is responsible for the variations in the number of the spikes in each burst. A saddle-node bifurcation takes place to eliminate the limit cycle L_i , but another limit cycle with $i+1$ spikes in each burst is already present. How is the electrical coupling affecting the dynamics and the bifurcations of such a system? Such a connectivity pattern appears contradictory for experimentalists as electrical connections are usually present to ensure in-phase oscillations while reciprocal inhibition is expected to produce out-of-phase oscillations. A parallel goal for this work that goes along with the investigation of the nonlinear dynamics of this complex system is to provide a functional explanation for their appearance together.

We investigate two identical coupled model neurons which interact through both electrical and reciprocal, inhibitory coupling. Each model neuron is a Hindmarsh-Rose oscillator, and the differential equations of the coupled system are given by

$$\frac{dx_1}{dt} = x_2 + 3x_1^2 - x_1^3 - x_3 + I - \epsilon_i \left(\frac{x_1 + V_c}{1 + \exp \frac{x_4 - X}{\sigma}} \right) - \epsilon_e(x_1 - x_4) \quad (1)$$

$$\frac{dx_2}{dt} = 1 - 5x_1^2 - x_2, \quad (2)$$

$$\frac{dx_3}{dt} = -rx_3 + rS(x_1 + 1.6), \quad (3)$$

$$\frac{dx_4}{dt} = x_5 + 3x_4^2 - x_4^3 - x_6 + I - \epsilon_i \left(\frac{x_4 + V_c}{1 + \exp \frac{x_1 - X}{\sigma}} \right) - \epsilon_e(x_4 - x_1) \quad (4)$$

$$\frac{dx_5}{dt} = 1 - 5x_4^2 - x_5, \quad (5)$$

$$\frac{dx_6}{dt} = -rx_6 + rS(x_4 + 1.6), \quad (6)$$

where $I=3.281$, $r=0.0012$, neuron 1 is given by the variables (x_1, x_2, x_3) and neuron 2 is given by (x_4, x_5, x_6) . ϵ_i is the strength of the synaptic coupling with the reverse poten-

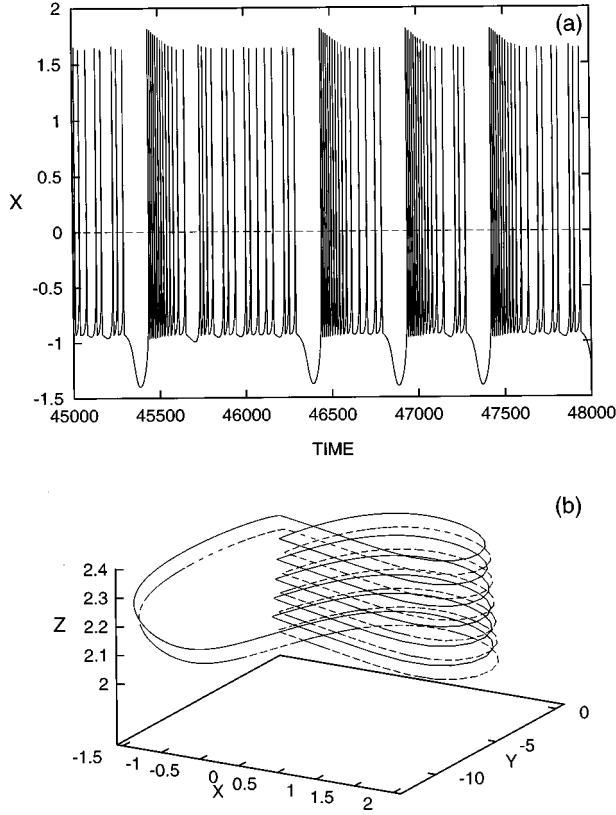


FIG. 1. (a) Typical time series generated by a chaotic Hindmarsh-Rose model. (b) Typical saddle-node bifurcation of one stable limit (solid line) and unstable limit (dashed line) cycle for two coupled Hindmarsh-Rose models, in fact, both limit cycles (stable and unstable) are very close. The distance between them has been exaggerated.

tial $V_c = 1.4$. Since each neuron must receive an input every time the other neuron produces a spike, we set $\sigma = 0.01$ and $X = 0.85$. The strength of the electrical coupling is ϵ_e . The detailed investigation of the bifurcations and crisis of one single model can be seen in [10–12].

Let us consider the local bifurcations of the limit cycles in the system (6). We will denote by L_k the periodic trajectory corresponding to the regime with k spikes per burst and we will name in $\epsilon_k^{(1,2)}$ the left and right boundaries of the region $[\epsilon_k^{(1)}(\epsilon_e) < \epsilon_i < \epsilon_k^{(2)}(\epsilon_e)]$, where the cycle L_k is stable. The pair of multipliers $(\mu_k^{(1)}, \mu_k^{(2)})$ is connected to every cycle L_k and indicates the kind of bifurcation at the points $(\epsilon_k^1, \epsilon_k^2)$. Then the condition $\mu_k^{(1,2)} = +1$ determines a saddle-node bifurcation and the condition $\mu_k^{(1,2)} = -1$ determines a flip bifurcation. As is well known the codimension one saddle-node bifurcation results when one multiplier crosses the complex unit circle at $+1$, which means that one stable L_i and unstable \hat{L}_i limit cycle merge together to annihilate, see Fig. 1(b) as an example.

The analysis of the stability of the cycles L_k for $\epsilon_e = 0$ gives the following results: $L_k(+1, +1)$ for all $k > 10$. Thus the bifurcations of the cycles L_k are saddle node. As the parameter ϵ_i increases (decreases) a sequence of bifurcations is observed. At each bifurcation point the cycle L_k with k spikes per burst disappears through a saddle-node bifurcation.

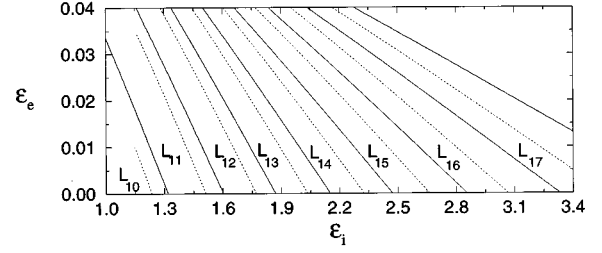


FIG. 2. Saddle-node bifurcation curves between stable limit cycles L_k . Solid lines: bifurcation curves for increasing values of ϵ_i . Dotted lines: bifurcation curves for decreasing values of ϵ_i . There is bistability in the regions between the dotted and the solid lines: L_i and L_{i+1} coexist.

The bifurcation curves $\epsilon_i = \epsilon_k^{(1)}(\epsilon_e)$ for $k = 10, \dots, 18$ are presented in Fig. 2. For sufficiently small ϵ_e $\epsilon_k^{(1,2)}(\epsilon_e)$ can be approximated by the expression $\epsilon_k^{(1,2)} = \epsilon_k^{*(1,2)} + \alpha_k^{(1,2)}\epsilon_e$, where $\epsilon_k^{*(1,2)}$ is the bifurcation point corresponding to purely inhibitory coupling ($\epsilon_e = 0$) and $\alpha_k^{(1,2)}$ defines the slope of the curves. The scaling law for the bifurcation curves is well approximated by

$$\alpha_{(k+1)}^{(1,2)} / \alpha_k^{(1,2)} = \eta [k / (k+1)]^2, \quad (7)$$

where k is the number of spikes per burst. The value of the constant is fitted from the slopes of Fig. 2, and it has a value $\eta = 1.42 \pm 0.01$. This means that Eq. (7) gives a good description of the scaling properties.

In order to provide an explanation for this scaling law we look for a measure of the distance between the limit cycles of close dynamical systems, i.e., for small perturbations of the parameters. This measure of the distance will be used to quantify the direction of the variation of the parameters on the plane (ϵ_e, ϵ_i) that achieves a minimal change of the limit cycle. At the same time, it provides a maximum variation that is directed towards the bifurcation boundaries. One can imagine that ‘‘minimal’’ lines must have a similar slope to the bifurcation curves. We can define a distance between the limit cycle for a particular value of ϵ_i^* with no electrical coupling and the limit cycle for any small value of ϵ_e . Let us denote by $\mathbf{x}^*(t, \epsilon_i^*, 0)$ a solution corresponding to the limit cycle for $\epsilon_e = 0$, and by $\mathbf{x}(t, \epsilon_i^* + \alpha\epsilon_e, \epsilon_e)$ a solution of the limit cycle with $\epsilon_i = \epsilon_i^* + \alpha\epsilon_e$ and electrical coupling ϵ_e , where α represents the linear dependence. The distance between these two trajectories is defined by

$$l_{\epsilon_e}(\alpha) = \int_0^{T^*} [\mathbf{x}(t, \epsilon_i^* + \alpha\epsilon_e, \epsilon_e) - \mathbf{x}^*(t, \epsilon_i^*, 0)]^2 dt, \quad (8)$$

where T^* is the period of the limit cycle $\mathbf{x}^*(t, \epsilon_i^*, 0)$ and $\mathbf{x}(0, \epsilon_i^* + \alpha\epsilon_e, \epsilon_e)$ is reset to the nearest point of $\mathbf{x}(t, \epsilon_i^* + \alpha\epsilon_e, \epsilon_e)$ to $\mathbf{x}^*(0, \epsilon_i^*, 0)$, that is, both solutions of the limit cycles in the functional (8) are set to the same phase. In fig. 3 we can see the computation of $l_{\epsilon_e}(\alpha)$ for small ϵ_e and $\epsilon_i^* = 2.0$, which corresponds to the limit cycle L_{14} . The minimum is located at $\hat{\alpha}_{14} = -11.36$, which, in fact, has a little bit larger value than the bifurcation slope ($\alpha_{14} = -18$). The value $\epsilon_i^* = 2.0$ lies far from the bifurcation curve; when ϵ_i is

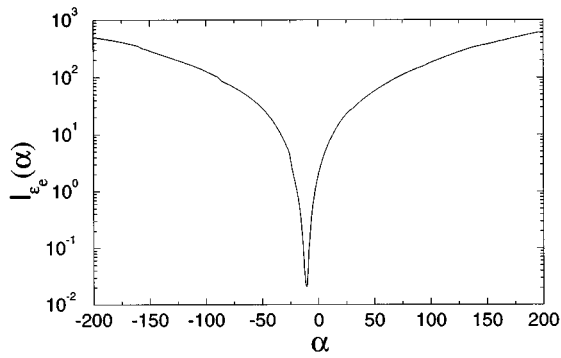


FIG. 3. Measure of the distance (8) for $\epsilon_i^* = 2.0$ and $\epsilon_e = 0.0002$, which corresponds to the region L_{14} , as function of α .

getting closer to the bifurcation point $\hat{\alpha}_{14}$ decreases its value to match the bifurcation slopes. We want to find out whether or not the values for the minima of $l_{\epsilon_e}(\alpha)$ follow a similar scaling law to the bifurcation curves given by Eq. (7). In Fig. 4 we can see the values $\hat{\alpha}$ that give the minima of the functional as a function of ϵ_e for several values of ϵ_i^* located in the middle of the area between the bifurcation curves. If we fit the values $\hat{\alpha}_k$ for several L_k given in Fig. 4 to Eq. (7) we obtain $\eta = 1.3 \pm 0.04$, which means firstly that they are well approximated and secondly that they are not far from the values obtained for the bifurcations. This shows evidence of the connection between the lines given by the minimal of the functional (8) and the bifurcation curves.

The joint activity of the reciprocal inhibitory and small electrical coupling can be useful from the neurophysiological point of view. Since these neurons with such connections

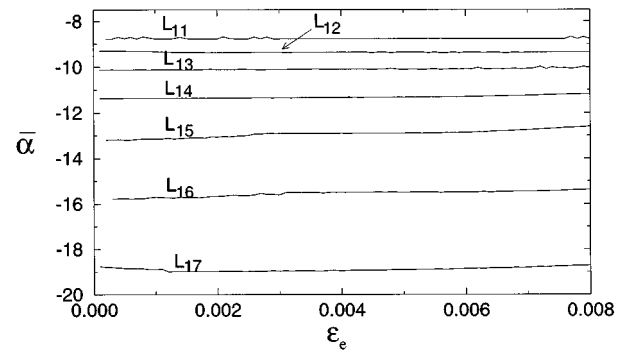


FIG. 4. α value that gives the minima of the distance $l_{\epsilon_e}(\alpha)$ as a function of the electrical coupling in some regions of the stable limit cycles L_k .

have created a frequency regulator which allows stable oscillations at selected values over a wide range of operating frequencies. The bifurcations that the model demonstrates are a welcome robustness arising from the particular coupling of these chaotic oscillators. Precise values of the chemical coupling ϵ_i need not be reached to achieve functionality associated with particular oscillation frequencies.

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