

Multistability analysis of phase locking patterns in an excitatory coupled neural system

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We quantitatively analyze the multistability of dynamic patterns of a bursting neural system with diffusive coupling. Through effective coupling analysis, we show that the system is not in-phase locking but exhibits various phase locking patterns, each of which corresponds to the stable fixed points of the effective coupling. The simulation proves the validity of the effective coupling method in analyzing the multistability of neural systems which presents complicated dynamic patterns such as bursting. [S1063-651X(99)13008-3]

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I. INTRODUCTION

Multistability has been introduced to provide mechanisms for information processing in biological neural systems. In the perception of ambiguous or reversible figures, it has been proposed that different interpretations of a figure correspond to switching among dynamic patterns with different collective frequencies in a switching time course [1]. The multistability of dynamic patterns can also be used to explain activity changes of theoretical neural systems occurring due to the transient input changes. This corresponds to a parameter-independent mode-switching mechanism with fixed parameter values, which is distinguished from a parameter-dependent mechanism based on changing parameter values such as synaptic coupling [2].

Various parameters or concepts such as time delay [1], stochastic resonance [3], etc., based on physiology have been introduced to explain the multistability in neural systems. A quantitative analysis of multistable dynamic patterns, however, remains the focus of research. In this paper we show that various phase locking patterns coexist in a neural system with diffusive coupling. In other words, the system is ultimately stabilized in one of those phase locking patterns. We analyze multistable phase locking patterns using the effective coupling method [4,5]. In Ref. [5], the same method was applied to the Hodgkin-Huxley neuron model with synaptic coupling to find the multistability at the weak coupling regime. We focus on limit cycle oscillators with diffusive coupling which model the electrical activities of gap junctional neural system [6].

It has been recently shown that diffusive coupling may induce dephasing of limit cycle oscillators [7,8]. Using effective coupling analysis for the weak coupling case, we show that at some parameter values the system is out of phase, and even exhibits multistable out-of-phase locking dynamic patterns. We choose a limit cycle oscillator system which presents not only the firing behavior of neurons but sequences of bursts [8–12] to show the wide applicability of the effective coupling method. The multistability analysis of bursting neural systems has not yet been tried, to our knowledge. For fixed parameter values, we find all of the dynamic patterns, each of which corresponds to one of the fixed points of the asymmetric part of the effective coupling. By changing the initial conditions, which corresponds to changing the

transient inputs, the system is switched from a locking mode to another with fixed parameters. In Sec. II, the one-neuron system is explained. The effective coupling method is explained in Sec. III. The results of this paper are presented in Sec. IV, where the dephasing of the system is explained with the phase shift plot and the multistable phase locking patterns corresponding to the stable fixed points of the effective coupling are explicitly presented. The summary and discussions are contained in Sec. V.

II. A BURSTING NEURONAL MODEL

In this paper we study a system of Hindmarsh-Rose (HR) neurons [9,10]. Even though this model is not based on

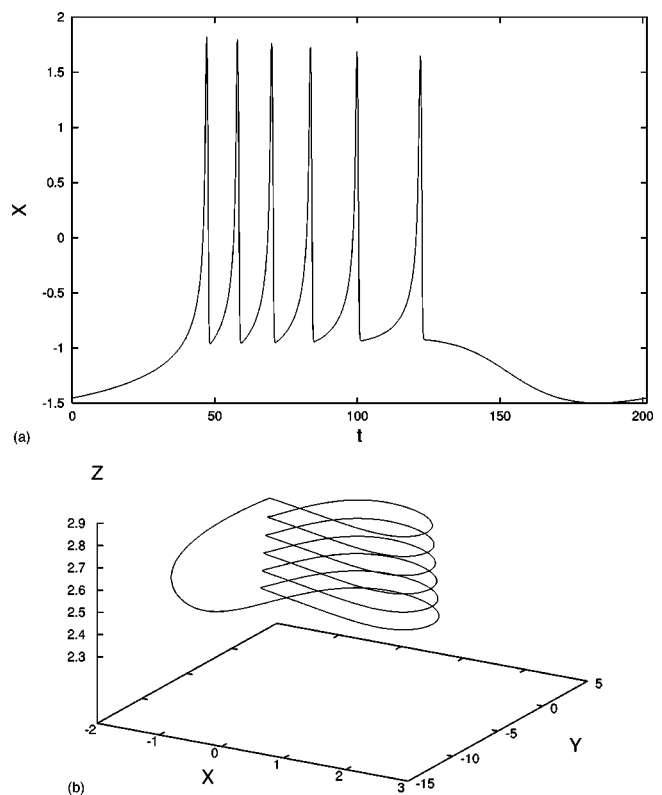


FIG. 1. (a) Time evolution of the membrane voltage X , (b) 3 (X , Y , Z)-dimensional contour plot of Eq. (1).

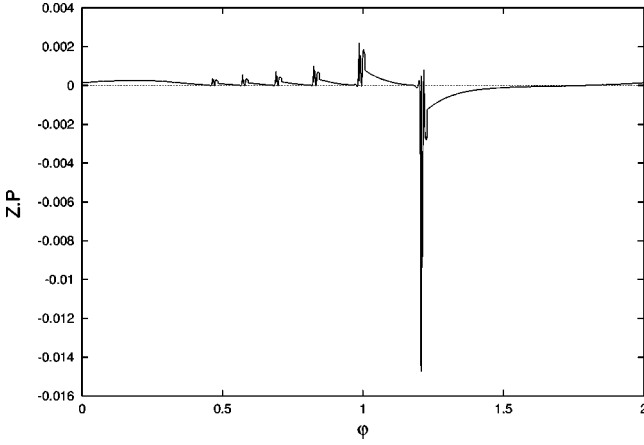


FIG. 2. Phase shift ZP vs ϕ (units in π) for $\psi=0.01\pi$.

physiology, it simulates some features observed in neuronal bursting. The HR model was originally introduced to give a long interspike interval and burst typical of real neurons. The three-variable HR model is given by

$$\begin{aligned} \frac{dX}{dt} &= Y - aX^3 + bX^2 - Z + I, \\ \frac{dY}{dt} &= c - dX^2 - Y, \\ \frac{dZ}{dt} &= r[s(X - \alpha) - Z]. \end{aligned} \quad (1)$$

X is thought of as the membrane voltage of the neuron, Y as the recovery variable, and Z as a slow adaptation current. I is the uniform external current. α is the membrane voltage when the neuron is at a stable fixed point of the null clines $dX/dt=0$ and $dY/dt=0$ for $I=0$. We will fix the parameters to the values $a=1.0$, $b=3.0$, $c=1.0$, $d=5.0$, $s=4.0$, $r=0.003$, and $I=2.7$.

A bursting time course for a single neuron is shown in Fig. 1(a) for one period of bursting. The bursting mechanism in the mathematical neuronal systems was extensively studied in Refs. [9,11]. We refer to Ref. [9] for a detailed bursting mechanism of the HR model. A brief explanation on the bursting mechanism of HR model is as follows. As in Fig. 1(a), each burst contains six spikes followed by a quiescent state. The spikes are generated when the neuron is on the limit cycle which surrounds an unstable fixed point. As can be seen in Fig. 1(a), the spike interval becomes longer in a burst as the limit cycle trajectory draws closer to the saddle point separatrix, and eventually a saddle-loop bifurcation occurs. Then the firing ceases and the neuron stays at the stable fixed point until a stable limit cycle appears through a homoclinic connection so that another burst starts. The three-dimensional (X , Y , and Z) contour plot is shown in Fig. 1(b).

The bursting oscillation originates from the evolution of the slow variable Z which switches the dynamics of the system between the steady state and the oscillatory state on the limit cycle by changing the geometry of the stable fixed point, the saddle point, and the unstable fixed point. The

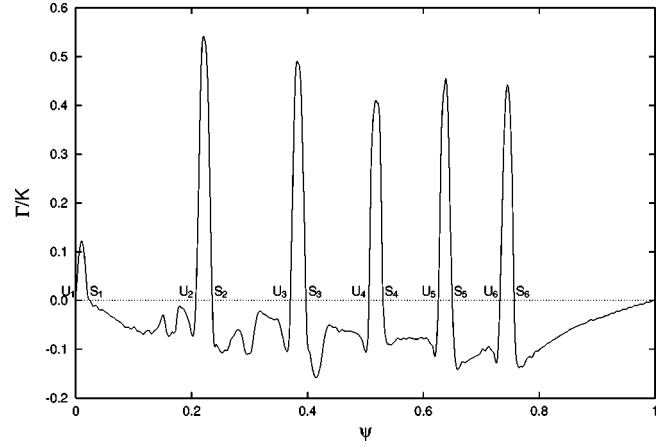


FIG. 3. The antisymmetric part of the effective coupling normalized by the coupling strength vs the phase difference (units in π). $U1-U6$ are unstable fixed points, and $S1-S6$ are stable fixed points. The locations of $S1-S6$ are at $\psi=0.017\pi$, 0.23π , 0.39π , 0.52π , 0.64π , and 0.75π , respectively.

parameter r determines the bursting duration and the number of spikes in one burst. For smaller values of r , the slow variable Z leads to a longer period of bursting with more spikes. According to the detailed role of the slow and fast variables, a classification scheme for the bursting oscillation was proposed by Bertram *et al.* [12].

III. EFFECTIVE COUPLING METHOD

We now introduce the effective coupling method to the electrically coupled HR model which is described by Eq. (1) with an additional coupling term, which is given by

$$\begin{aligned} \frac{dX_i}{dt} &= Y_i - aX_i^3 + bX_i^2 - Z_i + I - K(X_i - X_j), \\ \frac{dY_i}{dt} &= c - dX_i^2 - Y_i, \end{aligned} \quad (2)$$

$$\frac{dZ_i}{dt} = r[s(X_i - \alpha) - Z_i],$$

where $i, j=1,2$, and K denotes the coupling strength.

In order to describe the phase dynamics of the coupling, we calculate the effective interactions. Assuming the weak coupling, the system may be approximated as a phase model [4], where the phase ϕ of a limit cycle oscillator is defined as $d\phi(V)/dt=1$ and $V=(X, Y, Z)$ in this paper.

For the limit cycle without perturbation,

$$\frac{d\phi}{dt} = \frac{d\phi}{dV} \frac{dV}{dt} = 1. \quad (3)$$

When there is a small perturbation $P(V)$,

$$\frac{d\phi}{dt} = 1 + \text{gra}_{dV} \phi P(V). \quad (4)$$

Then the small coupling in Eq. (2) gives

$$\frac{d\phi_i}{dt} = 1 + gra d_{X_j} \phi_j P(X_i, X_j), \quad (5)$$

where $P(X_i, X_j)$ is the coupling term in Eq. (2).

The effective coupling $\Gamma(\psi)$ is then defined as

$$\frac{d\psi}{dt} = \Gamma(\psi) = \frac{1}{2\pi} \int_0^{2\pi} d\phi Z(\phi) P(\phi, \psi), \quad (6)$$

where ψ is the difference between the phase of the two neurons, $\phi_i - \phi_j$, and ZP is the phase shift defined as $Z(\phi)P(\phi, \psi) = (gra d_V \phi)_{V=V_0(\phi)} P(\phi, \psi)$, where V_0 is the point on the limit cycle at phase ϕ . Here we adapted the extended notion of phase using the concept of isochrons which are defined as a subset of domain converging to a point on the limit cycle. $P(\phi, \psi) = P(V_0(\phi), V_0(\phi + \psi))$ describes the rate of change of the state vector V of an oscillator due to the interaction with the other at phase difference ψ . $P(\phi, \psi)$ is the coupling term in Eq. (2) expressed as a function of the phases, which is considered a small perturba-

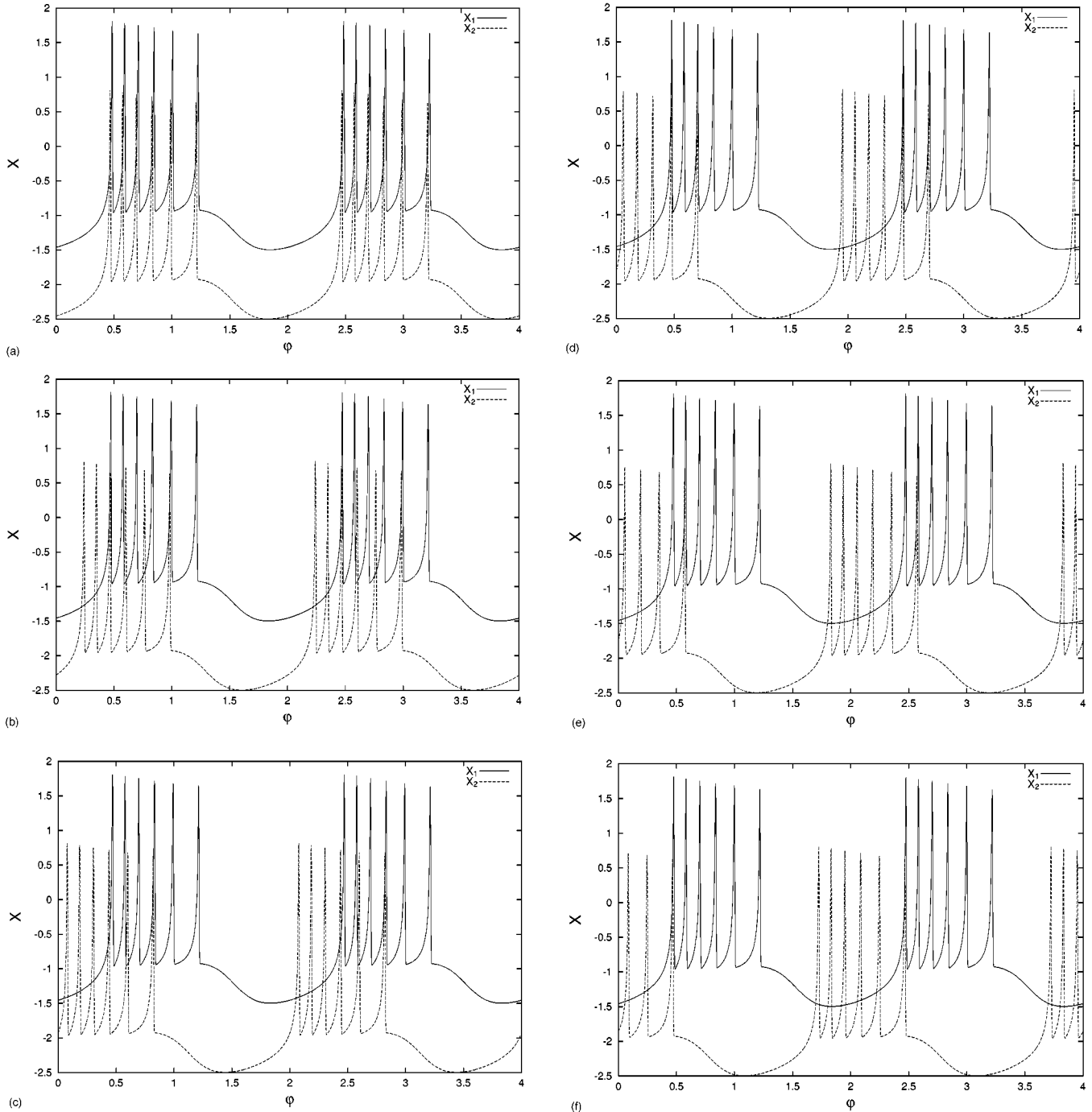


FIG. 4. (a)–(f) Phase locking patterns of Eq. (2) when $K=0.001$. The membrane voltages X_1 and X_2 are plotted vs ϕ (units in π). Each pattern corresponds to one of the stable fixed points, $S1$ – $S6$ in Fig. 3, which is equal to $(2\pi/T)t$, where T and t are the duration of one period of bursting and time, respectively.

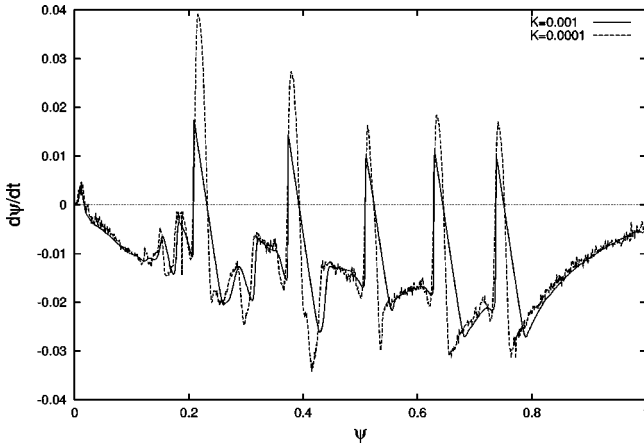


FIG. 5. Simulation plot of $d\psi/dt$ vs ψ (in units of π), which is the phase difference between the two neurons after the 20 periods of bursts divided by the time duration. The phase difference is normalized by the coupling. The solid line is for the $K=0.001$ case, and the broken line is for $K=0.0001$.

tion. The sensitivity function $Z(\phi) = (grad_{\psi}\phi)_{V=V_0(\phi)}$ gives the change of phase along the limit cycle caused by the change of V : we choose a point V_0 on the limit cycle and V not on the limit cycle but close to V_0 , then measure the difference between the two phases corresponding to V_0 and V . The difference in the phase divided by $|V - V_0|$ is the sensitivity function.

IV. MULTISTABILITY ANALYSIS

First we show that Eq. (2) is not in-phase locking in spite of the excitatory coupling through the effective coupling analysis. We plot the phase shift ZP with $\psi=0.01\pi$ in Fig. 2. During a period of bursting, the interaction causes the phase difference ψ to increase (a positive value of ZP) or decrease (a negative value of ZP). One observes that each spike in a burst in Fig. 1(a) corresponds to one of the six ‘‘bursts’’ in Fig. 2. This means that the coupling influences the phase difference mainly when the oscillator is on the limit cycle. Otherwise, the phase shift is almost zero, i.e., the coupling has little influence on the phase difference of the system when the oscillator is at the steady state. Averaging ZP over one period of bursting, as shown in Eq. (6), one obtains the positive value of the slope at the origin of the antisymmetric part of the effective coupling, i.e., $\Gamma'(0)$, as can be seen in Fig. 3. This shows that the diffusive coupling of Eq. (2) leads to a dephasing of the system. This unexpected dephasing originates from the deformation of the phase flow, i.e., the difference in phase velocity across the limit cycle. This dephasing mechanism was explained in detail in Ref. [8].

Now we investigate the multistability in phase locking patterns. To this end, we consider the asymmetric part of the effective coupling, and therefore only the positive part of the phase difference. In Fig. 3, we plot the antisymmetric part of the effective coupling normalized by the coupling value. The zero of the antisymmetric part of the effective coupling with negative value of the slope in Fig. 3, $S1, S2, \dots, S6$, correspond to the stable fixed points, and the ones with positive slope value, $U1, U2, \dots, U6$, correspond to the unstable

points. The system is eventually stabilized in one of the stable fixed points according to the initial conditions. In other words, the system is eventually phase locked with the phase difference given by the corresponding stable fixed point. The reasoning for this is as follows. If the phase difference of the two neurons is initially given by a value, for example, between $U2$ and $S2$, the effective coupling is positive. This implies that the phase difference becomes larger by Eq. (6) until it hits $S2$. By the same argument, the initial difference at a value between $S2$ and $U3$ is attracted to $S2$. Therefore, the unstable points play the role of a separatrix. For example, if the phase difference between the two neurons is initially given by the value between two unstable fixed points, it is gradually attracted to the stable fixed point which is located between the two unstable fixed points.

Six phase locking patterns when $K=0.001$ are explicitly presented in Fig. 4; each corresponds to one of the stable fixed points in Fig. 3. To check the validity of the effective coupling method, we simulate the changing rate of phase difference versus the initial phase difference, which is plotted in Fig. 5. For the simulations, we observed the phase difference after the 20 periods of the oscillators, and divided it by the time duration of 20 periods. This simulated result shows that the effective coupling method correctly predicts the multistability of limit cycle oscillator systems even when the system is at complicated activities such as bursting. The difference between the theoretical effective coupling and the simulated one becomes smaller as the coupling becomes smaller. At the $K \rightarrow 0$ limit, the simulated result is expected to coincide with the theoretical one [13].

V. SUMMARY AND DISCUSSIONS

We have shown that diffusively coupled neuronal oscillators exhibit various rhythmic phase locking patterns. Assuming weak coupling, we have analyzed the effective coupling on the limit cycle of a coupled HR model with two neurons. The model has been shown to exhibit stable activity patterns coexisting at fixed parameter values. The system is eventually stabilized in one of the coexisting patterns which correspond to one of the stable fixed points of the effective coupling according to the initial conditions. The stabilized pattern is reformed to another by a slight transient input at a fixed parameter. This corresponds to the mode-switching mechanism which changes the electrical properties of the system with fixed parameters.

We calculated the effective coupling for various values of the external current, I , and r . In general, as the spike number is increased, the effective coupling receives more ‘‘bursts,’’ and the number of stable fixed points is increased. It can, therefore, be suggested that dephasing due to the deformation of phase flow on the limit cycle results in multistable phase locking patterns, whose analysis is deferred for further study. The microscopic analysis in this paper may provide a clue to understanding various collective behaviors of a large network system which should be studied systematically in the future.

The rhythmic activities of oscillatory networks, such as the swimming and heartbeat of invertebrates, has been widely understood via the post-inhibitory rebound mecha-

nism [14–16]. Here an alternating pattern of activity is produced through post-inhibitory rebound between the inhibitory coupled neurons or groups of neurons. Adjusting the external current value or the coupling strength of Eq. (2), we observed various dynamic patterns: in-phase (antiphase) locking patterns both on the spiking and on the bursting levels. Our results, therefore, suggest another route to generat-

ing the rhythmic patterns, which, however, should be supported by the physiological facts.

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