Multistable Phase Locking Patterns in a Bursting Neural System

Seon-Hee Park, Young-Sup Hwang, Jae-Hun Choi
Bioinformatics research team, ETRI
Daejeon, 305-350, Korea

***Abstract* - We quantitatively analyze the multistability of dynamic patterns of a busting 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.**

1. INTRODUCTION

Multistability has been introduced to provide mechanisms for information processing in biological neural systems. In 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]. 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. 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.

2. EFFECTIVE COUPLING METHOD IN A BURSTING NEURAL SYSTEM

In this paper we study a system of Hindarsh-Rose (HR) neurons [9,10]. Even though this model is not based on physiology, it simulates some features observed in neuronal bursting. The electrically coupled HR model with two neuron is described by the following 3 coupled equations

$$dX_i/dt = Y_i - aX_i^3 + bX_i^2 - Z_i + I - K(X_i - X_j) \quad (1a)$$

$$dYi/dt = c - dXi2 - YI \quad (1b)$$

$$dZi/dt = r[s(Xi - \alpha) - Zi], \quad (1c)$$

where i, j = 1,2, which labels the two neurons. Variable X is thought of as the membrane voltage of a 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. We refer to Ref. [9] for a detailed bursting 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,

$$D\phi/dt = (d\phi/dV)\,(dV/dt) = 1. \qquad (2)$$

When there is a small perturbation P(V),

$$D\phi/dt = 1 + \mathrm{grad}_V\phi P(V). \qquad (3)$$

Then the small coupling in Eq. (1), where only the variable X is involved, gives

$$D\phi_i/dt = 1 + \mathrm{grad}_{Xj}\phi_j P(X_i,X_j), \qquad (4)$$

where $P(X_i,X_j)$ is the coupling term in Eq. (1).

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

$$D\psi/dt = \Gamma(\psi) = (1/2\pi)\ \Sigma d\phi Z(\phi)\ P(\phi,\psi), \qquad (5)$$

where ψ is the difference between the phase of the two neurons, $\phi_i - \phi_j$, and ZP is the phase shift defined as $Z(\phi)\ P(\phi,\psi) = (\mathrm{grad}_V\phi)\ P(\phi,\psi)$, where $(\mathrm{grad}_V\phi)$ is evaluated at $V=V_0(\phi)$ and V_0 is the point on the limit cycle at phase ϕ. Σ is the integration and it ranges from 0 to 2π. 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. (1) expressed as a function of the phases, which is considered a small perturbation. The sensitivity function $Z(\phi) = \mathrm{grad}_V\phi$ evaluated at $V=V_0(\phi)$ 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.

3. MULTISTABILITY ANALYSIS

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.

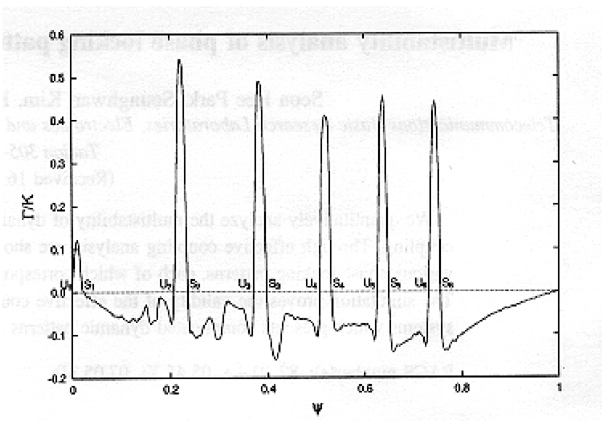

Fig. 1 : The antisymmetric part of the effective coupling normalized by the coupling strength vs the phase difference (units in π). U1-U6 are unstable fixed points, and S1-S6 are stable fixed points. The locations of S1-S6 are at ψ=0.017π, 0.23π, 0.39π, 0.52π, 0.64π, and 0.75π, respectively.

In Fig.1, we plot the asymmetric part of 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.1, S1,S2,…,S6, correspond to the stable fixed points, and the ones with positive slope values, U1,U2,…,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 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.

Six phase locking patterns when K=0.001 are explicitly presented in Fig. 2; each corresponds to one of the stable fixed points in Fig.1. To check the validity of the effective coupling method, we simulated the changing rate of phase difference, which 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.

4. 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.

The rhythmic activities of oscillatory networks, such as the swimming and heartbeat of invertebrates, have been widely understood via the post-inhibitory rebound mechanism [12]. Here an alternating patterns 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. (1), we observed various patterns both on the spiking and on the bursting levels. Our results, therefore, suggest another route to generating the rhythmic patterns, which, however, should be supported by the physiological facts.

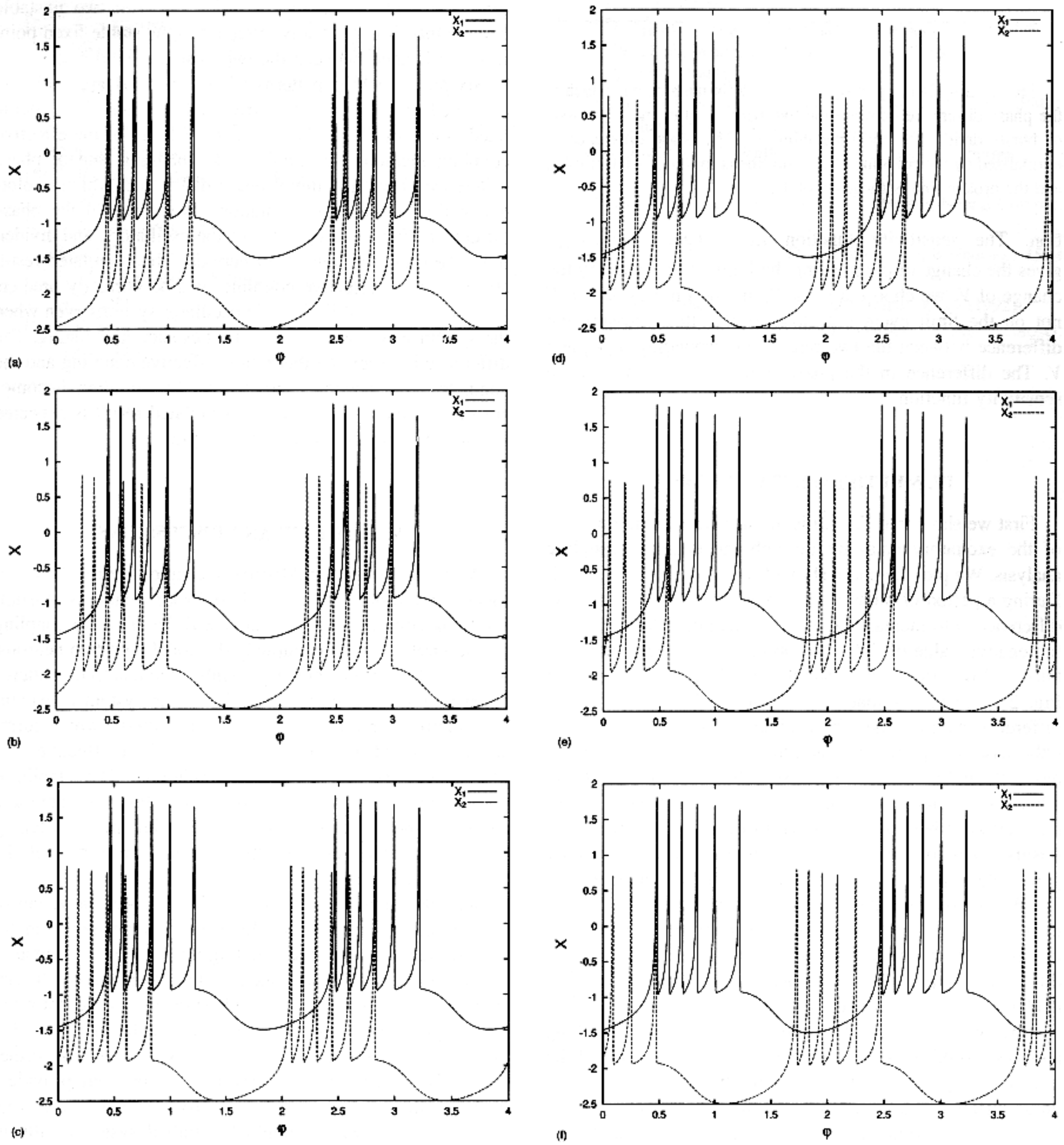

Fig. 2(a)-(f) Phase locking patterns of Eq. (1) when K=0.001. The membrane voltages of the two neurons, X_1 and X_2 are plotted vs ϕ (units in π). Each pattern corresponds to one of the stable fixed points, S1-S6 in Fig.1, which is equal to $(2\pi/T)t$, where T and t are the duration of one period of bursting and time, respectively.

ACKNOWLEDGEMENT

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