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Qualitative and quantitative aspects of synchronization in coupled CA1 pyramidal neurons

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ABSTRACT

We investigated the synchronization phenomena of two electrically coupled CA1 pyramidal neurons on the basis of the coupling strength and capacitance. By means of the distribution of phase differences and ISI-distances, synchronization could be described from the qualitative and quantitative aspects, respectively. Firstly, based on the distribution of phase differences, asynchronous and multiple synchronous states such as in-phase and out-of-phase were observed. We found that both of coupling strength and capacitance could induce the transitions of synchronization states, and the distribution of synchronization states was illustrated in a two-dimensional parameter plane. Secondly, synchronization states were quantitatively indicated by ISI-distance. These results could exhibit the level of the same synchronization states arising in different parameter ranges, complementing the deficiency of phase differences.

1. Introduction

Synchronization is acknowledged to be a fundamental neural mechanism which supports information processing and neural plasticity and is probably related to lots of cognitive process [1–6]. Hence, in modeling researches of neurons and neural circuits, synchronization phenomena have received considerable attention in recent years. Typically, coupled neurons connected via synapses (electrical or chemical) are served as the basic networks to study synchronization phenomena [7–11]. One key question about such interacting neurons is: What factors have an effect on the synchronization states between spike trains? In a number of studies, the role of coupling strength was emphasized because coupling strength could induce the variation of synchronization states [12–14]. In particular, some results have shown that complete synchronization can be achieved at strong coupling strength [15–18]. In addition, time delay was another important factor and was taken into account in some models for the propagation of the excitement in realistic neuron is not instantaneous [12,19,20]. Noise has also been confirmed to be a cause of synchronization. Once the strength of noise exceeds a threshold, complete synchronization of coupled neurons would occur [21–23]. In some coupled networks, synchronization even strongly depends on the topology structure and size of the network [24].

Recent research advances in synchronization have shown that phase synchronization plays a pivotal role in memory processes [1,25,26]. Some long-term memory-related activities, such as recalling dreams, are relevant to enhancements of phase synchronization between intra-hippocampus neurons [4,27,28]. Based on these facts, we couple two CA1 pyramidal neuron models and try to study the synchronization between them in two methods. In the first case, phase differences will be applied to divide synchronization phenomena into three states: in-phase synchronization, out-of-phase synchronization and asynchronization [29,30]. By perturbing some parameters, the transition of synchronization states can be indicated. However, phase differences are incapable to distinguish the level of the same synchronization states arising in different parameter ranges. Thus, in the second case, we will use ISI-distance to quantitatively depict the synchronization level, complementing the deficiency of phase differences [31,32].

This paper is organized as follows. We describe the neuronal model in Section 2. Section 3 presents the numerical simulation methods (the phase difference and ISI-distance). Section 4 demonstrates the numerical results. Finally, a brief conclusion is given in the last section.

2. Model description

In our present work, we research the model of CA1 pyramidal neuron model proposed by Golomb et al. [33] which contains the following currents: the transient sodium current (I_{Na}), the delayed

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rectifier potassium current (I_{Kdr}), the muscarinic-sensitive potassium current (I_M), the persistent sodium current (I_{NaP}), the A-type potassium current (I_A) and the leak current (I_L). The two coupled CA1 pyramidal neurons with gap junction can be described as:

$$CdV_i/dt = -I_L - I_{Na} - I_{NaP} - I_{Kdr} - I_A - I_M - I_{couple} + I_{app}, \quad (1)$$

$$dh_i/dt = \phi(h_\infty(V_i) - h_i)/\tau_h(V_i), \quad (2)$$

$$dn_i/dt = \phi(n_\infty(V_i) - n_i)/\tau_n(V_i), \quad (3)$$

$$db_i/dt = (b_\infty(V_i) - b_i)/\tau_b, \quad (4)$$

$$dz_i/dt = (z_\infty(V_i) - z_i)/\tau_z, \quad (5)$$

where V_i $(i = 1, 2)$ represent the membrane potential, and other variables h_i, n_i, b_i, z_i $(i = 1, 2)$ represent the activation or inactivation of ionic channels. The subscript 1 (or 2) is used to indicate neuron 1 (or 2). Each ionic current is expressed in the form:

$$I_L = g_L(V_i - V_L), \quad (6)$$

$$I_{Na} = g_{Na} m_\infty^3(V_i) h_i (V_i - V_{Na}), \quad (7)$$

$$I_{NaP} = p_\infty(V_i)(V_i - V_{Na}), \quad (8)$$

$$I_{Kdr} = g_{Kdr} n_i^4 (V_i - V_K), \quad (9)$$

$$I_A = g_A a_\infty^3(V_i) b_i (V_i - V_K), \quad (10)$$

$$I_M = g_M z_i (V_i - V_K), \quad (11)$$

$$x_\infty(V_i) = 1/(1 + exp(-(V_i - \theta_x)/\sigma_x)), x = m, h, n, a, b, z, p, \quad (12)$$

$$\tau_h(V_i) = 0.1 + 0.75/(1 + exp(-(V_i - \theta_{ht})/\sigma_{ht})), \quad (13)$$

$$\tau_n(V_i) = 0.1 + 0.5/(1 + exp(-(V_i - \theta_{nt})/\sigma_{nt})). \quad (14)$$

The bidirectional coupling of two neurons I_{couple} has the form:

$$I_{couple} = g_c(V_i - V_j), i, j = 1, 2, i \neq j, \quad (15)$$

where g_c is the coupling strength between neuron 1 and 2.

Below the detailed set of model parameters are listed. Reversal potentials: $V_{Na} = 55$, $V_K = -90$, $V_L = -70$ mV. Ionic conductances: $g_{Na} = 35$, $g_{Kdr} = 6$, $g_L = 0.05$, $g_A = 1.4$, $g_{NaP} = 0.2$, $g_M = 1$ mS/cm^2. Membrane capacitance: $C = 0.9$ μF. The applied current: $I_{app} = 0.9$ nA. Activation time constants: $\tau_b = 15$, $\tau_z = 75$ ms. Other kinetics parameters: $\theta_m = -30$, $\sigma_m = 10.5$, $\theta_h = -45$, $\sigma_h = -7$, $\theta_{ht} = -40.5$, $\sigma_{ht} = -6$, $\theta_p = -47$, $\sigma_p = 3$, $\theta_n = -35$, $\sigma_n = 10$, $\theta_{nt} = -27$, $\sigma_{nt} = -15$, $\theta_a = -50$, $\sigma_a = 20$, $\theta_b = -80$, $\sigma_b = -6$, $\theta_z = -39$, $\sigma_z = 5$ mV; $\phi = 1$.

3. Methods

3.1. Phase difference

In order to study the different states of synchronization, we have analyzed the distribution of phase differences between the spiking times of the two coupled neurons. The phase difference is defined as:

$$\Delta\varphi = 2\pi \frac{\tau - t_1}{t_2 - t_1}, t_1 < \tau \le t_2, \quad (16)$$

where t_1 and t_2 represent the times of subsequent spikes of neuron 1 and τ is the spiking time of neuron 2 [18,29,30].

3.2. ISI-distance

Firstly, the most critical step to compute the ISI-distance is to extract the spiking times from the time series by means of a spike detection algorithm. In this study, the threshold (−20 mV) is chosen as the arithmetic average value of the minimum and maximum action potentials, so that the continuous time series is converted into a discrete series of spikes. The specific spike detection algorithm is implemented as follows: A series of functions are used to express each spike train. The specific expression is

$$S(t) = \sum_{i=1}^{M} \delta(t - t_i), \quad (17)$$

where t_1,..., t_M denotes the series of spiking times and M is the number of spikes.

Secondly, we define the distance between two spike trains as following procedure: In a first step, the value of the current interspike interval is detected at each time instant

$$x_{isi}(t) = min\{t_i^x | t_i^x > t\} - max\{t_i^x | t_i^x < t\}, t_1^x < t < t_M^x, \quad (18)$$

where t_i^x are the spiking times of the spike train $x_{isi}(t)$. Accordingly we can obtain the second spike train t_i^y. Next, in a second step, we adopt a suitable normalization to calculate the ratio between x_{isi} and y_{isi} as:

$$I(t) = \frac{x_{isi}(t) - y_{isi}(t)}{max(x_{isi}(t), y_{isi}(t))}. \quad (19)$$

The measure becomes zero if two spike trains have the same frequencies, and approaches −1 or 1 if the average firing rate of the one (or another) train is unlimited high and the other is unlimited low, respectively.

Finally, the absolute ISI-distance is integrated in the time-weighted variant as:

$$D_I = \int_{t=0}^{Time} dt |I(t)|, \quad (20)$$

where *Time* is the overall length of the spike trains, namely, the duration of the recording in our simulations.

The model is programed in Python by using a fourth-order Runge–Kutta algorithm with time step of 0.01 ms. All diagrams are drawn by an open source library in Python named Matplotlib.

4. Simulation results

4.1. Different synchronization states in coupled neurons model

In this section, synchronization phenomena of coupled neurons are researched by using the phase differences. We first conclude different synchronization states between neurons. The phase diagrams of V_1 versus V_2, the corresponding phase differences on the unit circle and firing patterns of each neuron for different coupled strengths are plotted as shown in Fig. 1. It can be observed that the coupled neurons are in different synchronization states as the coupling strength g_c changes. When $g_c = 0.0036$ nS, neurons present out-of-phase synchronization state (Fig. 1a). The firing patterns of two neurons are the same in shape, but they do not occur at the same time. One neuron starts to firing while another one is in resting state. Asynchronous state appears while $g_c = 0.0096$ nS (Fig. 1b). In this case, neurons produce irregular bursting modes, and the corresponding phase diagrams are chaotic. As g_c increases to 0.12 nS, the coupled neurons exhibit almost in-phase chaotic synchronization state (Fig. 1c). Strong coupling could induce in-phase synchronous state (Fig. 1d). For understanding the effect of coupling strength on synchronization of coupled neurons, we compute the phase differences $\Delta\varphi$ to make a clear