Equilibrium analysis and phase synchronization of two coupled HR neurons with gap junction

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Abstract The properties of equilibria and phase synchronization involving burst synchronization and spike synchronization of two electrically coupled HR neurons are studied in this paper. The findings reveal that in the non-delayed system the existence of equilibria can be turned into intersection of two odd functions, and two types of equilibria with symmetry and non-symmetry can be found. With the stability and bifurcation analysis, the bifurcations of equilibria are investigated. For the delayed system, the equilibria remain unchanged. However, the Hopf bifurcation point is drastically affected by time delay. For the phase synchronization, we focus on the synchronization transition from burst synchronization to spike synchronization in the non-delayed system and the effect of coupling strength and time delay on spike synchronization in delayed system. In addition, corresponding firing rhythms and spike synchronized regions are obtained in the two parameters plane. The results allow us to better understand the properties of equilibria, multi-time-scale properties of synchronization and temporal encoding scheme in neuronal systems.

Keywords Equilibrium · Bifurcation · Gap junction · Time delay · Synchronization

Introduction

Stability and bifurcation are two basic dynamical properties in dynamical systems (Kuznetsov 1995; Lu et al. 2010), so from the standpoint of dynamics, analysis of equilibria is very important. Since Gray and Singer (1989) discovered the stimulation-induced γ synchronous oscillation on the cat's primary visual cortex, the synchronous oscillation of the coupled neurons has attracted more and more attention in the neuroscience. Synchronization, especially phase synchronization (PS), as a collective behavior in coupled systems, has been suggested as a mechanism for information binding (Fries 2009), neural information processing and transmission (Nowotny et al. 2008; Suykens and Osipov 2008), neurological diseases like epilepsy or Parkinson's disease (Levy et al. 2000). In experiments, it has been pointed out that synchronous oscillation in nervous activity is closely related to the cognitive function (Vaadia 1995).

A number of studies have investigated stability and bifurcations of equilibria of two coupled oscillators (Fan et al. 2010; Burić and Ranković 2007; Sterpu and Rocsoreanu 2005; Ranković 2011; Kobelevskiy 2008). Fan et al. (2010) presented the stability and Hopf bifurcation of a synaptically coupled nonidentical HR model with two time delays. Burić and Ranković (2007) studied bursting behavior induced by coupling delays and analyzed stability of the stationary solution of two electrically coupled HR neurons, and Hopf bifurcation curves in the (c, τ) plane were given. Sterpu and Rocsoreanu (2005) investigated Hopf bifurcation in a system of two coupled advertising oscillators, and the symmetric and nonsymmetric equilibria were found. Ranković (2011) performed an analysis of bifurcations of the stationary solution in a two coupled Fitzhugh-Nagumo excitable system with chemical delayed

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coupling. Koblelevskiy (2008) presented a thesis on bifurcation and asymptotic analysis of two coupled Morris-Lecar neuronal model with gap-junctional coupling in the non-delayed and delayed cases.

PS occurs if the phase difference between two sub-systems becomes bounded, while the amplitudes can be quite different. In order to state about the existence of PS, a suitable phase $\phi(t)$ function is often introduced. For the system with one time scale, such as Lorenz system, three straightforward definitions of phase are given (Rosenblum et al. 1996; Boccaletti et al. 2002). One is the analytical signal approach, one is the projection method, another is the Poincaré section method. But for the multi-time-scale neuronal systems with bursting/spiking behaviors, we must modify the definition and introduce the burst phase and spike phase (Wang et al. 2010). Correspondingly, study of PS should involve synchrony of individual spike, i.e. spike synchronization (SS) and synchrony of bursts, i.e. burst synchronization (BS). Sometimes SS and BS are also called rhythm synchronization (Shi and Lu 2007), which are closely related to the temporal encoding scheme. Since bursting is considered to enhance the reliability of communications between neurons by facilitating transmitter release (Izhikevich 2005), so study of burst synchronization can help us better understand the temporal encoding scheme than the rate coding scheme for encoding information.

Neurons can exchange signals each other via two different mechanisms: electrical coupling realized by gap junction connections and chemical coupling provided by neurotransmitters (Hao et al. 2011; Shi and Lu 2009). Electrical coupling frequently occurs between neurons of the same type or sometimes different types. Although communications between two neurons through electrical couplings is fast, a synaptic transmission time-delay is unavoidable. An important question in studying synchronization in time-delayed systems is the dependence of synchronization on time delay. For example, Dhamala et al. (2004) pointed out that neural synchrony can be enhanced by time delay in the electrically coupled HR neurons, while Burić et al. (2008) showed synchronized bursting domains in the two parameters plane for the fast threshold modulation model. Wang et al. (2005) revealed that time delay can suppress chaos and enhance complete synchronization in certain coupling strength ranges. Ma et al. (2010) studied synchrony and lag synchronization affected by time delay. Phase synchronization and ordered patterns influenced by time delay and the coupling strength were given by Shen et al. (2008).

As is known that phase synchronization and synchronization transitions have become more and more important because of their physiological and pathological significance. With the help of conditional Lyapunov expo-

nents, Dhamala et al. (2004) presented that the coupling strength can increase incoherent first and then induces two different transitions to synchronized states, one associated with burst and the other with spikes, moreover, there is an order of synchrony onsets: first, synchrony on the slow time-scale oscillations (burst synchrony), and then synchrony on the fast time-scale oscillations (spike synchrony). Phase synchronization in two electrically coupled chaotic HR neurons was investigated by Shuai and Durand (1999), different synchronization transitions for the one-time-scale system-Lorenz system and HR neuronal system are given. Jalili (2011) investigated phase synchronization in the delayed chemically coupled HR neural network. Stochastic phase dynamics in cognitive neurodynamics is used to study collective activities in neural oscillator population (Wang and Zhang 2003; Wang and Jiao 2006). Phase synchronization and coding in a neural networks are investigated by means of the theory of stochastic phase dynamics (Liu et al. 2010; Zhang et al. 2010). Wang et al. (2010), Shi and Lu (2007) investigated the transitions from burst synchronization to spike synchronization using different neuronal models and measurements. Synchronization transition in gap-junction-coupled leech neurons with co-existing attractors of spiking and bursting firings were investigated by means of the bifurcation diagram of interspike intervals and the correlation coefficient (Wang et al. 2008). It was shown that transitions of neuronal spiking and bursting synchronization are closely related and sensitive to initial conditions of the coupled neurons. Due to the importance of bursting rhythm, burst synchronization in neural networks has attracted more and more interest in recent years. Shi et al. (2012) studied in-phase burst synchronization of a map-based neuronal network, the burst phase order parameter was given to characterize the phenomenon. The transition from spatiotemporal chaos to burst synchronization in a diffusively coupled network of bursting neurons were studied by Shen et al. (2008). Front propagation and synchronization transitions in dependence on time delay, coupling strength and average degree in scale-free neuronal networks were considered by Wang et al. (2009). Spatiotemporal patterns and chaotic burst synchronization in a small-world neuronal network with noise were investigated by Zheng and Lu (2008).

Here we study dynamics of two electrically coupled HR neurons. We mainly focus on how the coupling strength and time delay affect the properties of equilibria and phase synchronization. Detailed analysis on stability and bifurcations of equilibria is performed. Phase synchronization transition and spike synchronized regions in two parameters region will be given. The paper is organized as follows: in section “[Model description](#)” we

outline the neuronal model. Section “[Equilibrium analysis](#)” deals with stability and bifurcations of equilibria in two identically coupled neurons. In section “[Phase synchronization](#)” we investigate phase synchronization transitions and synchronized regions of two coupled neurons with parameters mismatch. Our conclusions are left to the last Section.

Model description

It is well known that the Hindmarsh-Rose (HR) neuronal model (Hindmarsh and Rose 1984) is an alternative candidate for studying dynamics of neuronal systems since it has a relatively simple mathematical form and can exhibit various spiking/bursting firing rhythm patterns and synchronization phenomena. The single HR neuronal model read as:

$$\begin{aligned}\dot{x} &= y - ax^3 + bx^2 - z + I, \\ \dot{y} &= c - dx^2 - y, \\ \dot{z} &= r[s(x + \chi_0) - z].\end{aligned}\quad (1)$$

where x is the fast variable which describes the membrane potential, y describes the exchange of ions across the neuron membrane through fast ionic channels and z the exchange of ions through slow ionic channels. Parameters a, b, c, d, s, r shall always be fixed to the values $a = 1, b = 3, c = 1, d = 5, s = 4, r = 0.006$, I is the external input current and here we choose $I = 3$.

The two coupled HR neurons with gap junction can be described as:

$$\begin{aligned}\dot{x}_{1,2} &= y_{1,2} - ax_{1,2}^3 + bx_{1,2}^2 - z_{1,2} + I + g_s[x_{2,1}(t - \tau) - x_{1,2}(t)], \\ \dot{y}_{1,2} &= c - dx_{1,2}^2 - y_{1,2}, \\ \dot{z}_{1,2} &= r[s(x_{1,2} + \chi_{01,02}) - z_{1,2}].\end{aligned}\quad (2)$$

where g_s is the synaptic coupling strength, $\tau \geq 0$ represents time delay. $\chi_{01,02}$ describe the parameters mismatch between two neurons. First, we consider two identical neurons with $\chi_{01} = \chi_{02} = 1.56$, so the two neurons exhibit chaotic bursting behavior and have a unique equilibrium $e_0(-0.7288, -1.6557, 3.3248)$.

Equilibrium analysis

In the present section, we study the dynamics of equilibrium of (2), and we will analyze the existence, types,

number, stability and bifurcations of equilibria with respect to g_s and τ in the cases of $\tau = 0$ and $\tau > 0$.

As is known that for $\tau = 0$, when complete synchronization occurs, the coupled terms in system (2) are zero, and the two coupled subsystems become decoupled, thus the stability of solutions is independent of g_s and τ . Due to the symmetry of (2), if $(\tilde{x}, \tilde{y}, \tilde{z})$ is a solution of system (1), then $(\tilde{x}, \tilde{y}, \tilde{z}, \tilde{x}, \tilde{y}, \tilde{z})$ will be a solution of system (2) as well, we call it symmetric solution. It is easy to know that the single neuronal model (1) has a unique unstable saddle $e_0(-0.7288, -1.6557, 3.3248)$, so system (2) has a symmetric equilibrium $E_0(-0.7288, -1.6557, 3.3248, -0.7288, -1.6557, 3.3248) \triangleq (x_0, y_0, z_0, x_0, y_0, z_0)$, whose existence is independent of g_s and τ , but the stability depends on the variation of g_s and τ .

It is noticed that system (2) is invariant with respect to interchanging indexes 1 and 2, so if $(x_1, y_1, z_1, x_2, y_2, z_2)$ is a solution of system (2), then $(x_2, y_2, z_2, x_1, y_1, z_1)$ will be a solution of system (2) as well, we call this solution the non-symmetric solution. All the non-symmetric equilibria appear in pairs in (2). Because the equilibrium of (2) is the solution where all state variables are constant in time, hence, equilibria are the same for all values of $\tau \in \mathbb{R}$.

Stability and bifurcation with $\tau = 0$

Firstly, we deal with the symmetric equilibrium. To determine the stability of E_0 , we linearize (2) near E_0 , and the corresponding Jacobian matrix can be written as

$$\begin{aligned}B &= \begin{pmatrix} -3x_1^2 + 6x_1 - g_s & 1 & -1 & g_s & 0 & 0 \\ -10x_1 & -1 & 0 & 0 & 0 & 0 \\ 4r & 0 & -r & 0 & 0 & 0 \\ g_s & 0 & 0 & -3x_2^2 + 6x_2 - g_s & 1 & -1 \\ 0 & 0 & 0 & -10x_2 & -1 & 0 \\ 0 & 0 & 0 & 4r & 0 & -r \end{pmatrix} \Big|_{E_0} \\ &= \begin{pmatrix} -3x_0^2 + 6x_0 - g_s & 1 & -1 & g_s & 0 & 0 \\ -10x_0 & -1 & 0 & 0 & 0 & 0 \\ 4r & 0 & -r & 0 & 0 & 0 \\ g_s & 0 & 0 & -3x_0^2 + 6x_0 - g_s & 1 & -1 \\ 0 & 0 & 0 & -10x_0 & -1 & 0 \\ 0 & 0 & 0 & 4r & 0 & -r \end{pmatrix}.\end{aligned}\quad (3)$$

The characteristic polynomial is given by where

$$f_B(\lambda) = |\lambda I - B|$$

$$= \begin{vmatrix} \lambda + 3x_0^2 - 6x_0 + g_s & -1 & 1 & -g_s & 0 & 0 \\ 10x_0 & \lambda + 1 & 0 & 0 & 0 & 0 \\ -4r & 0 & \lambda + r & 0 & 0 & 0 \\ -g_s & 0 & 0 & \lambda + 3x_0^2 - 6x_0 + g_s & -1 & 1 \\ 0 & 0 & 0 & 10x_0 & \lambda + 1 & 0 \\ 0 & 0 & 0 & -4r & 0 & \lambda + r \end{vmatrix} \triangleq \begin{vmatrix} A_3 & -g_s \Gamma \\ -g_s \Gamma & A_3 \end{vmatrix}, \quad (4)$$

$$A_3 = \begin{pmatrix} \lambda + 3x_0^2 - 6x_0 + g_s & -1 & 1 \\ 10x_0 & \lambda + 1 & 0 \\ -4r & 0 & \lambda + r \end{pmatrix}, \Gamma$$

$$= \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

According to the theory of blocked determination, we get

$$f_B(\lambda) = |A_3^2 - g_s^2 \Gamma|$$

$$= |A_3 + g_s \Gamma| \cdot |A_3 - g_s \Gamma| \triangleq \Delta_1(\lambda) \cdot \Delta_2(\lambda)$$

where

$$\Delta_{1,2}(\lambda) = (\lambda + 3x_0^2 - 6x_0 + g_s)(\lambda + 1)(\lambda + r) + 4r(\lambda + 1) + 10x_0(\lambda + r) \pm g_s(\lambda + 1)(\lambda + r),$$

Obviously, $\Delta_1(\lambda)$ depends on g_s , while $\Delta_2(\lambda)$ is independent of g_s , substitute $x_0 = -0.7288$ and $r = 0.006$ into $\Delta_2(\lambda) = 0$, we obtain a triple equation of λ with the solution $\lambda_1 = -7.1483$, $\lambda_2 = 0.1622$, $\lambda_3 = 0.0139$, thus E_0 is always an unstable symmetric equilibrium regardless of g_s .

Assume that E_0 experiences fold bifurcation, i.e. the corresponding eigenvalue $\lambda = 0$, we solve $\Delta_1(0) = 0$, i.e.

$$3x_0^2 + 4x_0 + 2g_s + 4 = 0,$$

and deduce that $g_s = -1.3391$, so we say that when $g_s = -1.3391$, fold bifurcation occurs in the symmetric equilibrium E_0 . Substitute $i\omega$ ($\omega \in \mathbb{R}$) into $\Delta_1(\lambda) = 0$, we get that when $g_s = 0.62568$, E_0 experiences the Hopf bifurcation with a pair of pure imaginary eigenvalues $\pm 0.05358i$.

Secondly, we consider the non-symmetric equilibria of (2) denoted by $E_1(x_1, y_1, z_1, x_2, y_2, z_2)$ satisfying:

$$\begin{aligned} y_1 - x_1^3 + 3x_1^2 - z_1 + 3 + g_s(x_2 - x_1) &= 0, \\ y_1 &= 1 - 5x_1^2, \\ z_1 &= 4(x_1 + \chi_0), \\ y_2 - x_2^3 + 3x_2^2 - z_2 + 3 + g_s(x_1 - x_2) &= 0, \\ y_2 &= 1 - 5x_2^2, \\ z_2 &= 4(x_2 + \chi_0), \end{aligned} \quad (5)$$

Substitute the second, the third, the fifth and the sixth equations into the first and the fourth equations, we obtain two equations that completely determine all possible equilibria of (2):

$$\begin{aligned} x_1^3 + 2x_1^2 + 4x_1 + 4\chi_0 - 4 + g_s(x_1 - x_2) &= 0, \\ x_2^3 + 2x_2^2 + 4x_2 + 4\chi_0 - 4 + g_s(x_2 - x_1) &= 0. \end{aligned} \quad (6)$$

We might as well rewrite (6) as:

$$\begin{aligned} f(x_1) + g_s(x_1 - x_2) &= 0, \\ f(x_2) + g_s(x_2 - x_1) &= 0. \end{aligned} \quad (7)$$

where $f(x) = x^3 + 2x^2 + 4x + 4\chi_0 - 4$. (7) is a nonlinear system involving two equations and three unknown variables x_1, x_2, g_s . Enlightened by Kobelevskiy (2008), to determine how many solutions (2) has for each value of g_s , we introduce a new variable $u = x_2 - x_1$, thus (7) has the following form:

$$\begin{aligned} f(x_1) - g_s u &= 0, \\ f(x_2) + g_s u &= 0. \end{aligned} \quad (8)$$

By taking the sum and difference of the two equations in (8), we may rewrite it in the form:

$$\begin{aligned} f(x_1) + f(x_1 + u) &= 0, \\ f(x_1 + u) - f(x_1) + 2g_s u &= 0. \end{aligned} \quad (9)$$

Obviously, the first equation of (9) is independent of g_s , and it can define x_1 implicitly as a function of u , i.e. $x = x_1(u)$. Take $x = x_1(u)$ into the second equation of (9), we obtain

$$f(x_1(u)) - f(x_1(u) + u) = 2g_s u. \quad (10)$$

The left side of (10) is independent of g_s , we might as well denote it as $Y_1(u) = f(x_1(u)) - f(x_1(u) + u)$, which is an odd function of the variable u due to the symmetry of the coupled HR equations. To see this, note that changing the sign of the variable u is equivalent to interchanging x_1 and x_2 since $u = x_2 - x_1$, so we have $Y_1(-u) = -Y_1(u)$. The right side of (10) is a linear function of u passing

Fig. 1 Graphs of Y_1 , Y_2 with respect to u for some values of g_s

through the origin with a slope $2g_s$, we might as well denote it as $Y_2(u) = 2g_s u$, oddness of which is obvious. The number of solutions of (10), equivalently, the number of different equilibria of system (2), could be computed by plotting curves of Y_1 and Y_2 together, so we can determine the equilibria by seeing the intersections of the curves for each value of g_s . The graphs of Y_1 and Y_2 are given in Fig. 1 with some special values of g_s .

In Fig. 1, the curve represents Y_1 , while the lines from top to bottom correspond to graphs of Y_2 for $g_s = -5$, $g_s = -3$, $g_s = -1.3391$ and $g_s = 0.45$. It follows from the figure that when $g_s > 0$, Y_1 and Y_2 intersect only at $u = 0$, this corresponds to the symmetric equilibrium. It is easy to explain. Note that for $u = 0$, i.e. $x_1 = x_2$, the coupling terms in system (2) are equal to zero, so (2) is equivalent to two identical decoupled HR neurons, as is shown above, system (1) has a unique equilibrium $(\tilde{x}, \tilde{y}, \tilde{z})$, thus system (2) has a symmetric equilibrium $(\tilde{x}, \tilde{y}, \tilde{z}, \tilde{x}, \tilde{y}, \tilde{z})$. In fact, the symmetric equilibrium E_0 exists for all values of $g_s \in R$.

When g_s decreases to -1.3391 , the graph of Y_2 is tangent to the graph of Y_1 at the point $u = 0$, the symmetric equilibrium is the knee of the curve Y_1 , according to the former theoretical analysis, it implies the occurrence of fold bifurcation when $g_s = -1.3391$. With the further decrease of g_s , the number of intersection points are dependent on g_s , for example, we take $g_s = -3$, there are three intersection points between Y_1 and Y_2 , which correspond to a symmetric equilibrium E_0 and two non-symmetric equilibria in pairs denoted by $B(1.1458, -5.5647, 10.8233, -2.5054, -30.3844, -3.7815)$ and $B'(-2.5054, -30.3844, -3.7815, 1.1458, -5.5647, 10.8233)$ with the same eigenvalues being $\lambda_1 = -31.9088$, $\lambda_2 = 3.8911$, $\lambda_3 = 1.2472$, $\lambda_4 = -0.1445$, $\lambda_5 = -0.0154$, $\lambda_6 = -0.0088$. If we take $g_s = -5$, there are also three intersections involving a symmetric equilibrium E_0 and two non-symmetric equilibria in pairs denoted by $A(2.0346, -19.6979, 14.3784, -3.3814, -56.1687, -7.2855)$ and $A'(-3.3814, -56.1687, -7.2855,$

$2.0346, -19.6979, 14.3784)$ with the same eigenvalues $\lambda_1 = -50.7168$, $\lambda_{2,3} = 2.1084 \pm 3.1803i$, $\lambda_4 = -0.2979$, $\lambda_5 = -0.0072$, $\lambda_6 = -0.0083$.

To test the valid of the above method and clearly study the influence of the coupling strength g_s on equilibria numerically, we show the bifurcation diagram with respect to g_s in Fig. 2.

It is shown that whatever the value of g_s , there always exists an unstable symmetric equilibrium. With the variation of g_s changing from positive to negative, when one of the eigenvalue of Jacobian matrix in system (2) becomes zero, the branch of symmetric equilibrium gives birth to two new branches of unstable non-symmetric equilibria through a fold bifurcation denoted by the point BP at $g_s = -1.3391$. As g_s decreases further, there exists three equilibria involving one symmetric equilibrium and two non-symmetric equilibria in pairs. Moreover, when $g_s = -1.5496$, the non-symmetric equilibria experience Hopf bifurcations with the bifurcation points being $H_2(-0.055, 0.9849, 6.0199, -1.3623, -8.2794, 0.7908)$ and $H_2'(-1.3623, -8.2794, 0.7908, -0.055, 0.9849, 6.0199)$. The corresponding Jacobian matrix of system (2) has the eigenvalue $\lambda_1 = -13.45$, $\lambda_2 = -1.22$, $\lambda_{3,4} = \pm 0.052i$, $\lambda_5 = 0.0016$, $\lambda_6 = 1.67$. Another two Hopf bifurcations occur at $g_s = -2.2818$ when the eigenvalue of the Jacobian matrix is $\lambda_1 = -23.95$, $\lambda_2 = -0.012$, $\lambda_{3,4} = \pm 0.06i$, $\lambda_5 = 0.29$, $\lambda_6 = 3.78$ with the Hopf bifurcation points denoted by $H_1(0.6903, -1.3828, 9.0013, -2.0634, -20.2877, -2.0135)$ and $H_1'(-2.0634, -20.2877, -2.0135, 0.6903, -1.3828, 9.0013)$. From above analysis, we can clearly see the influence of g_s on stability and bifurcations with no time delay.

Stability and bifurcation with $\tau > 0$

The above result is for two coupled neurons without coupling delay. However, in reality, there are usually some time delays in transmitting the neural information.

Fig. 2 Bifurcation diagram of the first membrane potential x_1 versus the coupling strength g_s

Therefore, time delays should be taken into account. In the present section, we start the analysis of the delayed neuronal model by investigate how the variation of τ and g_s affect the stability and bifurcation of equilibria. As has been shown in section “Stability and bifurcation with $\tau = 0$ ”, the structure of equilibria is independent of τ , but the stability and bifurcation depend on τ and g_s .

Consider the symmetric equilibrium E_0 , we set

$$\begin{aligned}\tilde{x}_1 &= x_1 - x_0, \\ \tilde{y}_1 &= y_1 - y_0, \\ \tilde{z}_1 &= z_1 - z_0, \\ \tilde{x}_2 &= x_2 - x_0, \\ \tilde{y}_2 &= y_2 - y_0, \\ \tilde{z}_2 &= z_2 - z_0.\end{aligned}\quad (11)$$

substituting (11) into (2), and rewriting $\tilde{x}_1, \tilde{y}_1, \tilde{z}_1, \tilde{x}_2, \tilde{y}_2, \tilde{z}_2$ as $x_1, y_1, z_1, x_2, y_2, z_2$, gives

$$\begin{aligned}\dot{x}_1 &= y_1 - ax_1^3 - 3ax_0x_1^2 - 3ax_0^2x_1 + bx_1^2 + 2bx_0x_1 - z_1 + y_0 \\ &\quad - ax_0^3 + bx_0^2 - z_0 + I + g_s[x_2(t - \tau) - x_1], \\ \dot{y}_1 &= -dx_1^2 - 2dx_0x_1 - y_1 + c - dx_0^2 - y_0, \\ \dot{z}_1 &= r[sx_1 - z_1 + sx_0 + s\chi_0 - z_0], \\ \dot{x}_2 &= y_2 - ax_2^3 - 3ax_0x_2^2 - 3ax_0^2x_2 + bx_2^2 + 2bx_0x_2 - z_2 + y_0 \\ &\quad - ax_0^3 + bx_0^2 - z_0 + I + g_s[x_1(t - \tau) - x_2], \\ \dot{y}_2 &= -dx_2^2 - 2dx_0x_2 - y_2 + c - dx_0^2 - y_0, \\ \dot{z}_2 &= r[sx_2 - z_2 + sx_0 + s\chi_0 - z_0].\end{aligned}\quad (12)$$

Obviously, $O(0, 0, 0, 0, 0, 0)$ is the equilibrium of (12). Linearizing (12) gives

$$\begin{aligned}\dot{x}_1 &= y_1 - 3ax_0^2x_1 + 2bx_0x_1 - z_1 + g_s[x_2(t - \tau) - x_1], \\ \dot{y}_1 &= -2dx_0x_1 - y_1, \\ \dot{z}_1 &= r[sx_1 - z_1], \\ \dot{x}_2 &= y_2 - 3ax_0^2x_2 + 2bx_0x_2 - z_2 + g_s[x_1(t - \tau) - x_2], \\ \dot{y}_2 &= -2dx_0x_2 - y_2, \\ \dot{z}_2 &= r[sx_2 - z_2].\end{aligned}\quad (13)$$

Introduce $X = (x_1, y_1, z_1, x_2, y_2, z_2)^T$, (13) can be rewritten as the following vector form

$$X(\dot{t}) = CX(t) + DX(t - \tau) \quad (14)$$

where

$$C = \begin{pmatrix} -3x_0^2 + 6x_0 - g_s & 1 & -1 & 0 & 0 & 0 \\ -10x_0 & -1 & 0 & 0 & 0 & 0 \\ 4r & 0 & -r & 0 & 0 & 0 \\ 0 & 0 & 0 & -3x_0^2 + 6x_0 - g_s & 1 & -1 \\ 0 & 0 & 0 & -10x_0 & -1 & 0 \\ 0 & 0 & 0 & 4r & 0 & -r \end{pmatrix},$$

and

$$D = \begin{pmatrix} 0 & 0 & 0 & g_s & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ g_s & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}.$$

According to stability theory of the delay differential equations with constant delay, stability of the zero equilibrium O is determined by roots of the characteristic equation $h(\lambda) = \lambda I - C - D e^{-\lambda\tau} = 0$. O is asymptotically stable provided all roots of $h(\lambda) = 0$ have negative real part, O is unstable if there exists a root with positive real part. Due to the summand of $D e^{-\lambda\tau}$, the characteristic equation has an infinite number of roots $\lambda \in \mathbb{C}$, among which there always exists a root with the largest real part and the stability can be determined by a finite number of roots (Campbell 2007). Bifurcation occurs whenever roots pass through the imaginary axis, furthermore, if the root is real, then fold bifurcation occurs; if the roots are complex conjugate, then Hopf bifurcation occurs.

By calculating, the characteristic polynomial can be expressed as,

$$\begin{aligned}h(\lambda) &= \begin{vmatrix} \lambda + 3x_0^2 - 6x_0 + g_s & -1 & 1 & -g_s e^{-\lambda\tau} & 0 & 0 \\ 10x_0 & \lambda + 1 & 0 & 0 & 0 & 0 \\ -4r & 0 & \lambda + r & 0 & 0 & 0 \\ -g_s e^{-\lambda\tau} & 0 & 0 & \lambda + 3x_0^2 - 6x_0 + g_s & -1 & 1 \\ 0 & 0 & 0 & 10x_0 & \lambda + 1 & 0 \\ 0 & 0 & 0 & -4r & 0 & \lambda + r \end{vmatrix} \\ &\triangleq \begin{vmatrix} A_3 & -g_s e^{-\lambda\tau} \Gamma \\ -g_s e^{-\lambda\tau} \Gamma & A_3 \end{vmatrix}, = |A_3^2 - g_s^2 e^{-2\lambda\tau} \Gamma| \triangleq \Delta_1(\lambda) \cdot \Delta_2(\lambda)\end{aligned}\quad (15)$$

where A_3, Γ are defined in section “Stability and bifurcation with $\tau = 0$ ”, and

$$\begin{aligned}\Delta_1(\lambda) &= (\lambda + 3x_0^2 - 6x_0 + g_s + g_s e^{-\lambda\tau})(\lambda + 1)(\lambda + r) \\ &\quad + 4r(\lambda + 1) + 10x_0(\lambda + r), \\ \Delta_2(\lambda) &= (\lambda + 3x_0^2 - 6x_0 + g_s - g_s e^{-\lambda\tau})(\lambda + 1)(\lambda + r) \\ &\quad + 4r(\lambda + 1) + 10x_0(\lambda + r).\end{aligned}$$

It is known that $\Delta_{1,2}$ depend on g_s and τ .

Figure 3 shows the stability along the symmetric equilibria E_0 for $\tau = 0$. For a fixed g_s . And there are six eigenvalues of the Jacobian matrix B , among which three constant eigenvalues $\lambda_1 = -7.1483$, $\lambda_2 = 0.1622$, $\lambda_3 = 0.0139$ always exist regardless of g_s . Due to the positive real part of the eigenvalues, the symmetric equilibrium E_0 keeps unstable independent of g_s . From the enlargement diagrams of the interval $[-1.8, -1]$ and $[-1, 0.8]$, we can clearly find two zero crossings, which are located at $g_s = -1.3391$ and $g_s \approx 0.63$. Furthermore, $g_s = -1.3391$ corresponds to the fold bifurcation creating the branch of non-symmetric equilibria, while $g_s \approx 0.63$ corresponds to the Hopf bifurcation, which are consistent with the theoretical results analyzed in section “Stability and bifurcation with $\tau = 0$ ”

For the case $\tau > 0$, from the characteristic equation $h(\lambda) = 0$, we can find that there is no influence of time delay on the occurrence of fold bifurcation, i.e. fold bifurcation occurs as $g_s = -1.3391$ for any value of τ . To investigate the influence of time delay on Hopf bifurcation points, we take some specific values of τ , and show the stability of the symmetric equilibria in Fig. 4.

By plotting the real parts of eigenvalues for the symmetric branch of equilibria versus the coupling strength, we see that whether τ is small (see Fig. 4a) or not (see Fig. 4c), the stability structure is unchanged as the non-delayed system, i.e. there is still one Hopf bifurcation point where

Fig. 3 Real parts of eigenvalues for the symmetric equilibria E_0 with $\tau = 0$. The right diagrams are the enlargements of the left diagram in the interval of **a** $[-1.8, -1]$ and **b** $[-1, 0.8]$

Fig. 4 Real parts of the eigenvalues for the symmetric equilibria E_0 with **a** $\tau = 0.1$, **b** $\tau = 2.1$ and **c** $\tau = 5$. **d** The enlargement of Hopf bifurcation points with $\tau = 0.1, 2.1, 3.4, 5$ from left to right, respectively

the eigenvalue crosses zero, but with the increase of time delay, the zero crossing of g_s becomes larger which can be seen from the enlargement diagram shown in Fig. 4d.

Phase synchronization

In order to investigate phase synchronization, we consider two nonidentical HR neurons with slightly parameters mismatch $\chi_{01} = 1.56$ and $\chi_{02} = 1.57$. Spike synchronization means two coupled neurons always generate spikes almost simultaneously (Izhikevich 2000; Shi and Lu 2007; Shuai and Durand 1999), and burst synchronization where bursts of two neurons start at approximately the same time, even though their spikes are nonsynchronous in each burst

Fig. 5 Illustration of t_k and τ_k in the time evolution of the fast variable x and slow variable z

(Wang et al. 2010; Izhikevich 2000; Shi and Lu 2007). So we define the spike and burst phase functions as follows (Wang et al. 2010):

$$\phi_s(t) = 2\pi k + 2\pi \frac{t - t_k}{t_{k+1} - t_k}, (t_k < t < t_{k+1}),$$

where t_k is the time when the k -th spike emits, $t_{k+1} - t_k$ is the interspike intervals abbreviated by ISIs (see Fig. 5).

Thus, when a spike occurs, the spike phase increases by a value of 2π .

$$\phi_b(t) = 2\pi k + 2\pi \frac{t - \tau_k}{\tau_{k+1} - \tau_k}, (\tau_k < t < \tau_{k+1}),$$

where τ_k is the time when the k -th burst emits, $\tau_{k+1} - \tau_k$ is the interburst intervals abbreviated by IBIs (see Fig. 5). So when a burst occurs, the burst phase increases by 2π .

We say that spike or burst synchronization takes place if the spike phase difference or burst phase difference between two neurons is bounded by a value of 2π . With the

knowledge of phase $\phi(t)$, we define the mean frequency as $\Omega(t) = \langle \dot{\phi}(t) \rangle$, so if the mean spike frequency difference $\Delta\Omega_s(t) \rightarrow 0$ or the mean burst frequency difference $\Delta\Omega_b(t) \rightarrow 0$, then spike synchronization or burst synchronization takes place.

Burst, spike synchronization and transitions with $\tau = 0$

First, we consider $\tau = 0$, and show the bifurcation diagrams of IBIs, ISIs of two neurons and the mean burst and spike frequency differences with respect to the coupling strength in Fig. 6.

It is shown from Fig. 6a, c that in the interval of $[0, 0.38]$, two neurons each exhibit chaotic bursts and keep uncorrelated state, IBIs and ISIs between them are very different. The mean spike frequency difference $\Delta\Omega_s$ and the mean burst frequency difference $\Delta\Omega_b$ shown in Fig. 6b, d fluctuate with the variation of the coupling strength, at about $g_s =$

Fig. 6 The bifurcation diagrams of **a** $IBI_{1,2}$, **c** $ISI_{1,2}$, **b** the mean burst frequency difference $\Delta\Omega_b$, **d** the mean spike frequency difference $\Delta\Omega_s$ versus the coupling strength g_s

0.38, $\Delta\Omega_b$ first descends to zero and keeps up all along, so $g_s = 0.38$ is the critical value of burst synchronization. Meanwhile, we have $IBIs_1 = IBIs_2$, i.e. two neurons generate bursts at the same time. With the increase of coupling strength, two neurons affect each other and increasingly attain to a coherent state, at about $g_s = 0.45$, $\Delta\Omega_s$ becomes zero, and $ISIs_1 = ISIs_2$, thus spike synchronization takes place. As the coupling strength increases further, nearly complete synchronization can be obtained, and the two nearly complete synchronized neurons display periodical bursting with five spikes per burst in the interval of [0.49, 0.69], then back to chaotic bursting states.

During the whole synchronization transition, we can find that the original two coupled neurons can transit from non-synchronization to burst synchronization, and then spike synchronization, finally nearly complete synchronization due to the effect of coupling. Burst synchronization usually precedes to spike synchronization, which is a general phenomenon, because the slow variables are easier to attain to synchronization than the fast variables. Both burst synchronization and spike synchronization can coexist in a certain range $[0.38, +\infty)$ of the coupling strength, spike synchronization implies burst synchronization, otherwise it is not true. In the following, we will take some values of coupling strength, and show different states and relations between two neurons before and after synchronization in Fig. 7.

In the left column, the solid and dot lines represent the membrane potentials of neuron 1 and neuron 2,

respectively. The right column represents the phase plane of two neurons. We find that when $g_s = -2$, two neurons attain to the anti-phase synchronized state with the phase difference π . The case $g_s = 0.2 < 0.38$ demonstrates the state before burst synchronization when little correlation exists between two membrane potentials, and each burst starts at the same time, but ends at different time. That $0.38 < g_s = 0.4 < 0.45$ demonstrates the state before spike synchronization and after burst synchronization when correlation is enhanced and two neurons emit burst at the same time. When $g_s = 0.5 > 0.45$, spike synchronization appears, meanwhile burst synchronization coexist. As is known that consideration of negative coupling strength has no physical meaning, but rich dynamics can be found here, which is very interesting and worth studying further.

Effect of τ and g_s on spike synchronization

As is known that neural complete synchronization can be enhanced as a result of time delay (Dhamala et al. 2004; Burić et al. 2008; Wang and Lu 2005), in this section, we will study the associated influence of time delay and the coupling strength on spike synchronization. Figure 8 shows the spike synchronized regions in the $(\tau - g_s)$ parameters plane with $\tau \in [0.1, 6]$ and $g_s \in [0.01, 0.6]$.

From the figure, we can find some spike synchronized regions characterized by $\Delta\Omega_s \rightarrow 0$ scattered on the $\tau - g_s$ plane. At low coupling strengths without time delay, such

Fig. 7 Time evolutions (*left column*) and phase portraits (*right column*) of two coupled neurons with $g_s = -2, 0.2, 0.4, 0.5$ from *top to bottom*

Fig. 8 Contour plot of $\Delta\Omega_s$ in dependence on time delay τ and the coupling strength g_s

Fig. 9 Time series and membrane potential correlation between two neurons. **a** x_1 (solid line) and x_2 (dash line) versus t at $\tau = 0$. **b** x_2 versus x_1 at $\tau = 0$. **c** x_1 (solid line) and x_2 (dash line) versus t at $\tau = 3$. **d** x_2 versus x_1 at $\tau = 3$

as $g_s = 0.1$, we have known that burst and spike synchronization can not be attained, but increase of time delay can induce spike synchronization (see Fig. 9). At high coupling strength without time delay, such as $g_s = 0.5$, spike synchronization exists, but it can be destroyed by time delay, for example we take $\tau = 1.5$ (see Fig. 8). Figure 9 shows time series and phase portraits at $\tau = 0$ and $\tau = 3$ for the same low coupling strength $g_s = 0.1$. In Fig. 9c, d, two neurons attain to spike synchronized state via time delay, each neuron emits spike almost at the same time, and the phase portrait exhibit large correlation. On the other hand, there is no synchrony when $\tau = 0$ at the same g_s shown in Fig. 9a, b, two neurons behave independently. This underscores the point that time delay can enhance or destroy spike phase synchronization. Similar results can happen to burst synchronization, and we won't consider here.

Conclusions

We have investigated equilibria and phase synchronization of two electrically coupled chaotic HR neurons in this paper. A new approach to deal with the existence of equilibria is introduced, and two types of equilibria with symmetry and non-symmetry are obtained. Based on the stability and bifurcation theories, we analyze the stability and bifurcation structures of equilibria induced by the coupling strength and time delay. It is shown that the time delayed system has the same equilibria and bifurcation mechanisms as the non-delayed system. However, for the latter, the Hopf positions shift toward the right side as time delay is increased.

In order to measure the spike and burst synchronization, we define the spike and burst phase. With the help of mean frequency difference, the transitions from burst

synchronization to spike synchronization and the corresponding firing rhythm patterns are shown in the non-delayed system. It is obtained that burst synchronization is prior to spike synchronization. For both types of phase synchronization, one does not imply another, but both can coexist in a certain range of coupling strength. For the delayed system, we have found the spike synchronized regions in the two parameters plane which can demonstrate the enhancement or destruction of spike synchronization by time delay. The results obtained can help us better understand the dynamics of coupled systems and multi-time-scale property of synchronization in neural networks.

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