Vol 14 No 1, January 2005
1009-1963/2005/14(01)/0077-09

Chinese Physics

© 2005 Chin. Phys. Soc.
and IOP Publishing Ltd

Firing patterns and complete synchronization of coupled Hindmarsh–Rose neurons*

Shi Xia(石 霞) and Lu Qi-Shao(陆启韶)†

School of Science, Beijing University of Aeronautics and Astronautics, Beijing 100083, *China*

(Received 21 April 2004; revised manuscript received 2 September 2004)

The firing activities of Hindmarsh–Rose (HR) neurons are studied by means of numerical simulation and bifurcation analysis. A single HR neuron exhibits various firing patterns, such as quiescent state, periodic spiking, periodic bursting and chaos, when the external current input is changed. The fast/slow dynamical analysis is applied to explore the dynamical behaviour of the HR model. The complete synchronization of two coupled identical HR neurons with electrical coupling mimicking gap junctions can be realized in certain ranges of the coupling strength, whenever each individual neuron shows quiescency, periodic firing and chaos. The criteria for complete synchronization are analysed theoretically, and the corresponding numerical simulation is presented as well. The persistence of the interspike intervals bifurcation structure of the coupled HR neuronal system under electrical coupling is also discussed.

Keywords: Hindmarsh–Rose neuron, synchronization, coupling, gap junction
PACC: 0545, 0547, 8725

1. Introduction

Systems of coupled oscillators have been extensively studied in past decades, which appear in physical, chemical and biological systems. Especially, the synchronization problems of coupled chaotic oscillators have attracted a great deal of attention in recent years,[1−7] and can be further applied to the field of neuroscience using either numerical simulations or analytical methods. Synchronized chaos in a network model of bursting neurons responding to an inhomogeneous stimulus was investigated in Ref.[8], and three types of phases for the network were found: that is, asynchronous stationary state, synchronized oscillations, and synchronized chaos. Reference [9] explored the dynamical properties of the time interval sequences and the spatio-temporal patterns of firings in a coupled neuronal system, which presented a complex dynamical behaviour of neural activity.

A variety of mathematical neuronal models, such as those of Hodgkin–Huxley, FitzHugh–Nagumo, Morris–Lecar, Hindmarsh–Rose (HR), and Chay *et al*, have been investigated in terms of bifurcation analysis to explore the firing mechanism. The HR model was constructed from voltage clamp data to provide a simple description of the patterned activity observed in molluscan neurons. Even though this model is not wholly based on physiology, it can simulate some features observed in neuronal bursting.

An individual neuron may show various firing behaviour, while an ensemble of coupled neurons may synchronize in order to process biological information. Which factors are responsible for such synchronization? This question can be answered in terms of the theories of phase-locking and chaos synchronization. A main part of information transmission between neurons is through synapses, which include electrical synapses and chemical ones. For electrical synapses, impulses can be electrically transferred from one neuron to another, and the transmission is more rapid than for chemical synapses. In this article, the complete synchronization of two identical coupled neurons with electrical synapse coupling is explored.

An outline of this paper is given as follows. The differential equations corresponding to a single HR neuron are introduced in Section 2, and the numerical results of firing patterns are also presented. In Section 3, the criteria for estimating complete synchronization

*Project supported by the National Natural Science Foundation of China (Grant No 10432010) and the Doctoral Research Foundation of Beijing University of Aeronautics and Astronautics.

†Corresponding author, E-mail address: qishaolu@hotmail.com, liming03@iscas.cn

of two identical HR neurons through electrical coupling are analysed theoretically, and the corresponding numerical simulation is presented. The influence of coupling on the interspike intervals (ISIs) bifurcation structures of electrically coupled HR neurons is also discussed. Finally, a conclusion is presented in Section 4.

2. Model description

2.1. Single HR neuron model

The three-variable HR model of action potential[10] was proposed as a mathematical representation of the firing behaviour of neurons, and it was originally introduced to give a bursting type with long ISIs of real neurons. It can be used to simulate spiking/bursting and chaos phenomena in real neurons. The equations of the HR model are given as follows:

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

where x represents membrane action potential, y is a recovery variable and z is a slow adaptation current; a, b, c, d, r, s and χ are constants; I is the external direct current. In the following numerical simulations, let a=1.0, b=3.0, c=1.0, d=5.0, r=0.006, s=4.0 and $\chi = -1.6$ and treat I as a control parameter to produce various firing patterns.

The time evolution course of the action potential x with different external currents I is plotted in Fig.1. From Fig.1, it can be seen that for different external currents, a single HR neuron experiences different dynamical processes, such as quiescent state, periodic firing and chaos.

The global dynamical behaviour of system (1) has been extensively studied by Holden and Fan in a series of articles,[11−14] in which I is fixed at some specified values and r is chosen as a control parameter. They presented the bifurcation diagrams in terms of the Poincaré return maps, and showed the bursting patterns, complex oscillatory behaviours and chaos for this model by both numerical and qualitative approaches. It is known that the neuronal information is encoded mainly based on the time intervals inside neuronal firings. Hence, in this article we study the bifurcation structures of ISIs of HR neurons, in which the external excitation I as a control parameter is varied to explore various firing patterns.

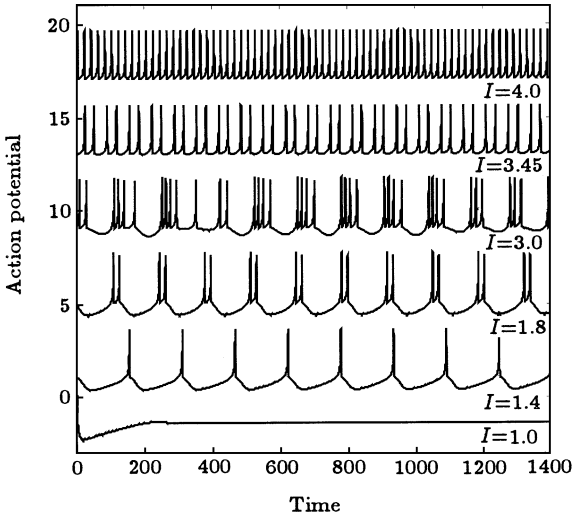


Fig.1. Time evolution of the action potential of a single HR neuron with different external direct currents.

2.2. ISI bifurcation analysis of a single HR neuron

We investigate the bifurcation structure of ISIs in terms of the single HR neuron model (1), in which ISIs are measured when the upstrokes of the voltage variable x reaching the peak $x = 0.8$. Figure 2 gives the bifurcation diagram constructed as ISIs vs the parameter I. According to Fig.2, for the additional current $I \leq 1.31$, the neuron lies in a quiescent state, which corresponds to an equilibrium point of system (1). According to Ref.[12], $I \approx 1.32$ is a Hopf bifurcation point of the HR system for r=0.006. Therefore, a period-1 firing pattern arises from this Hopf bifurcation point and lasts for $I \in [1.32, 1.55]$. When $I \geq 1.56$, periodic firings with period two, three, four, etc appear through a sequence of period-adding bifurcations. Figure 3 gives the magnification of two local areas of Fig.2, which correspond to the transitions between periodic firing and chaos. Then it is obvious that after I=2.88, the HR neuron exhibits chaos via period-doubling bifurcations. When $I \geq 3.42$, the ISI series experience reverse period-doubling bifurcations, and the HR neuron recovers to periodic firings from period four to two, and then to one.

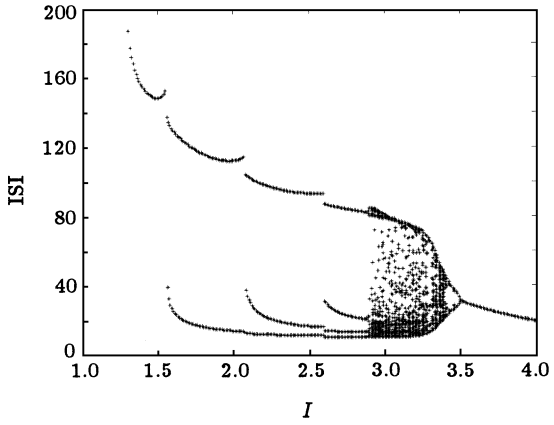


Fig.2. Bifurcation diagram of ISIs vs the additional current I in the single HR neuron model.

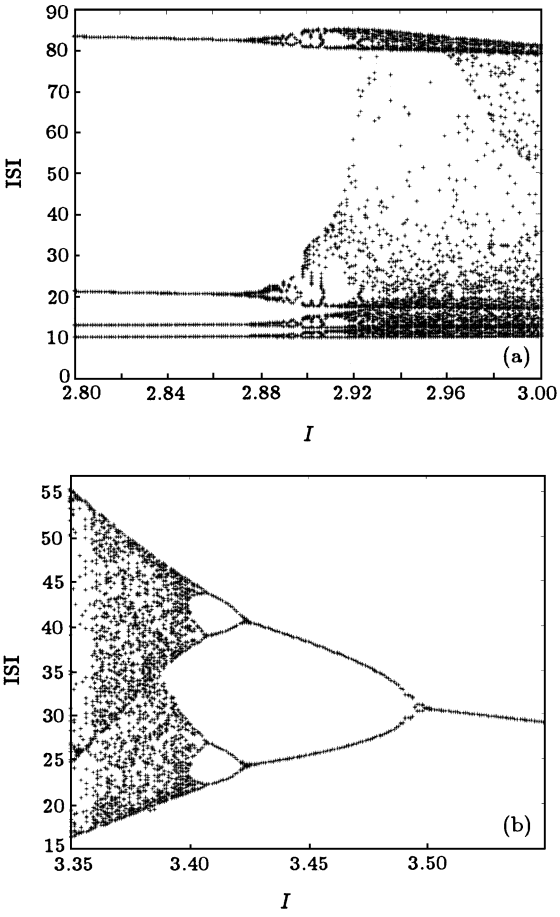


Fig.3. Two local magnifications of Fig.2: (a) a local magnification of the transition from periodic firings to chaos, (b) a local magnification of the transition from chaos to periodic firings.

It can be seen from Fig.2 that the periods of periodic firing patterns before and after chaos lie in different ranges, and the period of periodic firing before chaos is longer than that after chaos. The waveforms of these two periodic firings are also different: for example, the period-1 firing patterns for I=1.4 and I=4.0 and the period-2 firing patterns for I = 1.8 and I=3.45 (see Fig.1).

r is usually a small quantity, and then z varies much slower than the other variables. Therefore, the fast/slow dynamical analysis can be applied as follows to explore the dynamical behaviour of the HR model. The fast subsystem (abbreviated as FS) of the HR model consists of the first two equations of Eq.(1), and the slow variable z is now considered as a control parameter governed by the last equation of Eq.(1).

Without loss of generality, only the period-1 firings for the parameter I=1.4 and 4.0 will be discussed here. The equilibrium points of FS with respect to z (that is, the bifurcation parameter of FS) form the Z-shaped curves in the (z, x)-phase plane (see Fig.4(a)). The upper, middle, and lower branches of each Z-shaped curve are composed of unstable focuses, saddles and stable nodes, respectively. Hence, there is a bistable regime, in which a stable limit cycle around the unstable focus and a stable node (i.e. rest state) coexist. Moreover, the trajectories of the periodic firings shown as closed orbits are plotted in Fig.4(a) along with the corresponding Z-shaped bifurcation curves of FS.

For the additional current I=1.4, it can be seen from Fig.4(a) that the corresponding rest state of FS disappears at LP (a limit point) and makes a transition to spiking state via a fold bifurcation, and finally hits the middle branch. The homoclinic point (HCP) is just the point where the stable periodic orbit of spiking intersects with the saddle branch, and the spiking terminates as soon as it passes the point HCP. Hence, the spiking state disappears via a saddle homoclinic bifurcation, and the trajectory returns to the rest state on the lower branch. Therefore, the period-1 firing takes place through two bifurcations of FS associated with bursting (that is, the fold bifurcation of a rest state that leads to repetitive spiking and the saddle homoclinic bifurcation of repetitive spiking that leads to a rest state), and it should be a period-1 bursting.

When the additional current I=4.0, it can be seen from the magnification of the dotted rectangular frame in Fig.4(a) (see Fig.4(b)) that the closed orbit has no intersection point with the corresponding Z-shaped bifurcation curve of FS. Since there do not exist the above two bifurcations of FS associated with bursting and the closed orbit just corresponds to a limit cycle, the periodic-1 firing for I=4.0 is actually a period-1 spiking.

The same analysis can be applied to other situations, and it can be concluded that the periodic firing patterns before and after chaos are periodic bursting and periodic spiking, respectively.

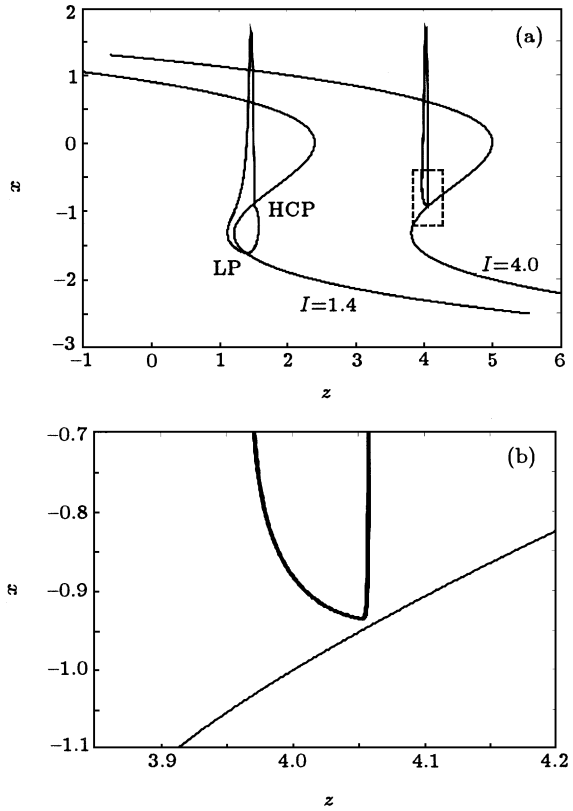


Fig.4. (a) Fast/slow dynamics of period-1 firing for $I = 1.4$ and $I = 4.0$ in the (z, x)-phase plane of the HR model. (b) The local magnification of the dotted rectangular area in (a).

Detailed bifurcation analysis confirms that with the increase of the additional current I, the firing pattern of an isolated HR neuron may undergo quiescency, periodic bursting, chaos and then to periodic spiking. In the next section, we investigate the complete synchronization of two coupled identical HR neurons when each individual neuron experiences all these firing patterns, and explore how the ISI bifurcation structure persists with respect to the coupling strength.

3. Complete synchronization of two coupled identical HR neurons

The neuronal rhythm of a single neuron is exhibited by firing patterns from periodic spiking/bursting to chaos, while the biological information is transmitted through coupling from one neuron to another in an ensemble of neurons. In order to study this process of information transfer, it is important to investigate the synchronization of coupled neurons.

Two types of transmission occur in nervous systems: that is, electrical and chemical transmissions. Electrical transmission is mediated by electrical synapses: that is, gap junctions between adjacent neurons. By electrically coupled neurons, gap junctions allow action potentials to spread between cells. Key features of electrical transmission are extreme rapidity, high fidelity and working in both directions.

In what follows, we only consider the electrical gap junction between two identical HR neurons with bidirectional coupling, where both neurons influence each other and all the parameters of them are equal. In this section we will also consider the bifurcation structures of these two electrically coupled neurons under different coupling strengths.

3.1. A network model for two electrically coupled HR neurons

Consider a network of two electrically coupled identical HR neurons. It is denoted as $\mathrm{N}_1 \longleftrightarrow \mathrm{N}_2$, in which N_1 and N_2 represent two identical neurons, and the arrow denotes the electrical synaptic transfer direction. The model is described by the following equations:

$$\begin{aligned}
\dot{x_1} &= y_1 - ax_1^3 + bx_1^2 - z_1 + I_1 + C(x_2 - x_1),\\
\dot{y_1} &= c - dx_1^2 - y_1,\\
\dot{z_1} &= r(s(x_1 - \chi) - z_1),\\
\dot{x_2} &= y_1 - ax_2^3 + bx_2^2 - z_2 + I_2 + C(x_1 - x_2),\\
\dot{y_2} &= c - dx_2^2 - y_2,\\
\dot{z_2} &= r(s(x_2 - \chi) - z_2),
\end{aligned} \tag{2}$$

in which $I_1 = I_2 = I$ is chosen as a control parameter, the term $C(x_1 - x_2)$ (or $C(x_2 - x_1)$) represents the coupling term from N_1 to N_2 (or from N_2 to N_1), and C is the coupling strength.

3.2. Theoretical analysis on complete synchronization of electrically coupled HR neurons

In the previous work about complete synchronization of two coupled identical chaotic oscillators, unidirectional coupling is mainly discussed. For bidirectional coupled identical chaotic systems, Ref.[1] gave a criterion for complete synchronization: that is, when the coupling matrix $H = kE$ (E is the unit matrix, and k is the coupling strength), both systems synchronize completely for $k > \frac{1}{2}\lambda_L$, where λ_L is the largest

Lyapunov exponent of the uncoupled chaotic systems. In this article, due to the characteristic of electrical coupling of two neurons, in which the coupling term is only added to the action potential of neurons, the former criterion no longer works here.

Let us begin with a general system with temporal evolution governed by the following equation:

$$\dot{\boldsymbol{w}} = f(\boldsymbol{w}).$$

Here $\boldsymbol{w} = (w_1, w_3, ..., w_n)$ is an n-dimensional state vector, $f : R^n \to R^n$ is a vector function. Through a bidirectional coupling, we obtain a coupled system as follows:

$$\begin{aligned} \dot{\boldsymbol{w}} &= f(\boldsymbol{w}) + K(w_1' - w_1), \\ \dot{\boldsymbol{w}}' &= f(\boldsymbol{w}') + K(w_1 - w_1'), \end{aligned} \tag{3}$$

in which $K \geq 0$ is the coupling strength. In this framework, complete synchronization is defined as the identity between the trajectories of two systems. Then the existence of complete synchronization requires that the synchronization manifold $\boldsymbol{w} \equiv \boldsymbol{w}'$ is asymptotically stable, or equivalently, $\lim_{t\to\infty} \boldsymbol{e}(t) = 0$ ($\boldsymbol{e}(t)$ is the synchronization error defined by $\boldsymbol{e}(t) \equiv \| \boldsymbol{w} - \boldsymbol{w}' \|$). This property can be justified by using the stability analysis of the following linearized system for small $\boldsymbol{e}$:

$$\begin{aligned} \dot{\boldsymbol{e}} =& f(\boldsymbol{w}') - f(\boldsymbol{w}) + K(w_1 - w_1') \\ & - K(w_1' - w_1) \\ =& (\mathrm{D}f(\boldsymbol{w}) - H)\boldsymbol{e}, \end{aligned} \tag{4}$$

where $Df(\boldsymbol{w})$ is the Jacobian of the vector field f evaluated onto the trajectory of any one of the coupled systems, and the coupling matrix H is a constant $n \times n$ matrix, in which the element $H_{11} = 2K$ and all the others are equal to zero.

Let $J = Df(\boldsymbol{w}) - H$. Three types of complete synchronization will be considered theoretically as follows. Firstly, if the trajectory of $\boldsymbol{w}(t)$ is a fixed point, then the study of the stability problem of Eq.(4) can be made by evaluating the eigenvalues of the matrix J. Therefore, a condition for the complete synchronization of fixed points of the coupled system (3) is that the real parts of all eigenvalues of J are smaller than zero. Secondly, when the trajectory of $\boldsymbol{w}(t)$ is periodic, system (4) is a linear ordinary differential equation with periodic coefficients. According to the Floquet theorem,[15] the stability problem of Eq.(4) can be solved through calculating the Floquet multipliers. A condition for asymptotic stability of the trivial solution of Eq.(4): that is, a condition for the complete synchronization of periodic motions of the coupled system (3) is that the modula of all characteristic multipliers are smaller than 1. Finally, if the trajectory of $\boldsymbol{w}(t)$ is chaotic, then we need to calculate the Lyapunov exponents of system (4): that is, the conditional Lyapunov exponents. A condition for the complete synchronization of chaotic motions of the coupled system (3) is that all conditional Lyapunov exponents are smaller than zero.

3.3. Numerical results of complete synchronization

In this section, we test the above criteria by using numerical simulation. According to the above theoretical analysis, we have

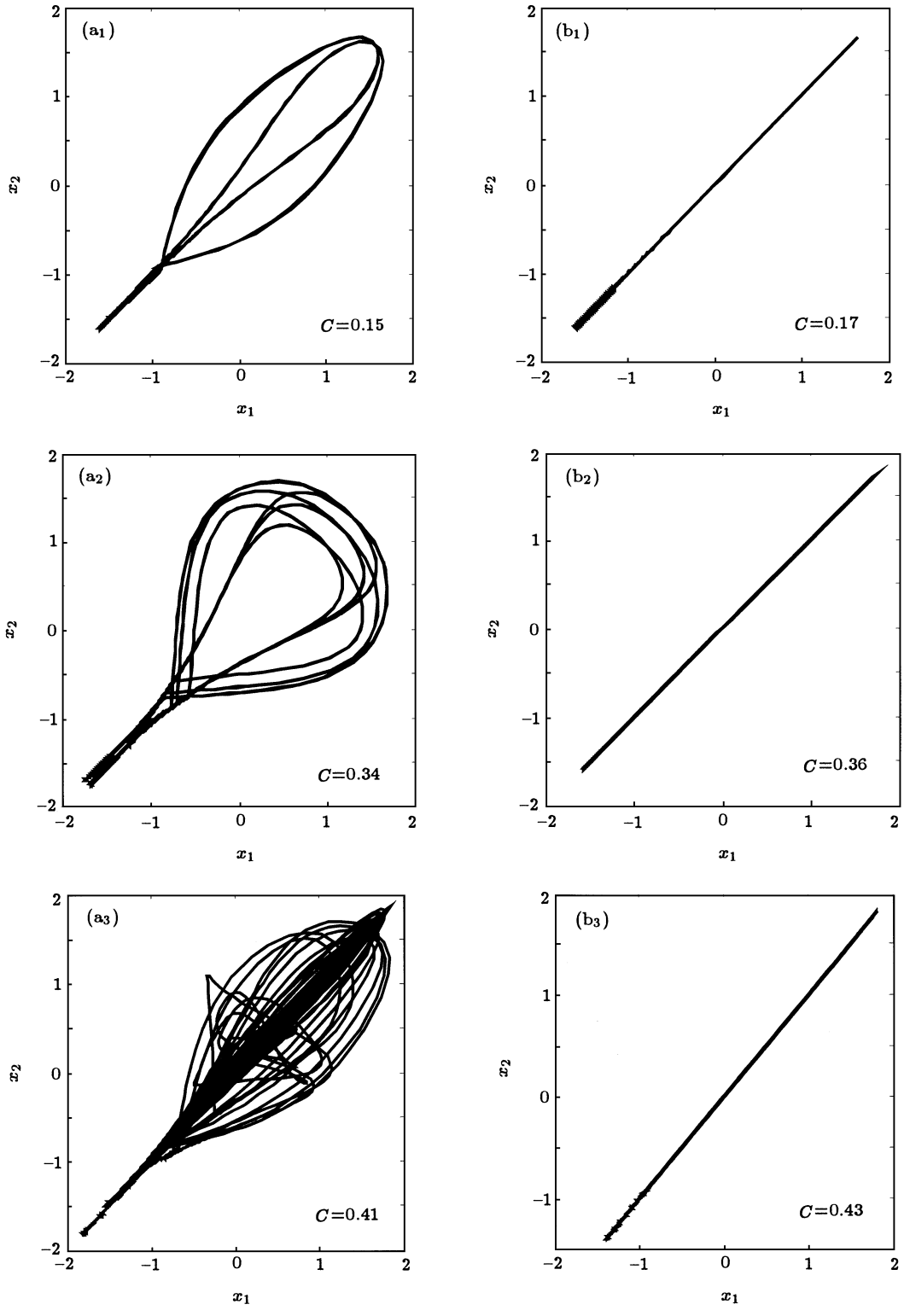
$$J = \begin{pmatrix} -3ax_1^2 + 2bx_1 - 2C & 1 & -1 \\ -2dx_1 & -1 & 0 \\ rs & 0 & -r \end{pmatrix}.$$

For the coupled HR system (2), we need to calculate the eigenvalues, the characteristic multipliers and the conditional Lyapunov exponents with respect to the coupling strength C, when an individual neuron exhibits quiescence, periodic firings and chaos. Specifically, we choose I=1.0 for the quiescent state, I=1.4 and I=4.0 for the period-1 bursting and the period-1 spiking, I=1.8 and I=3.45 for the period-2 bursting and the period-2 spiking, and I=3.0 for the chaotic firing pattern.

Table 1 gives the critical values of the coupling strength C_{cr} for complete synchronization under these given values of I. Figure 5 gives the diagrams of the membrane potential of neuron 1 vs that of neuron 2 for I=1.4, 1.8, 3.0, 3.45, 4.0, which are just before or after certain critical values. It is obvious that complete synchronization exists when the diagrams in the $(x1, x2)$-phase plane behave as a diagonal (see Fig.5(b1)–(b5)).

Table 1. Critical values of the coupling strength C_{cr} for complete synchronization of electrically coupled HR neurons.

Parameter value	Firing pattern	C_{cr}
I=1.0	Quiescent state	0
I=1.4	Period-1 bursting	0.16
I=1.8	Period-2 bursting	0.35
I=3.0	Chaos	0.42
I=3.45	Period-2 spiking	0.53
I=4.0	Period-1 spiking	0.52


(a1)
C=0.15
(b1)
C=0.17
(a2)
C=0.34
(b2)
C=0.36
(a3)
C=0.41
(b3)
C=0.43
x1
x2

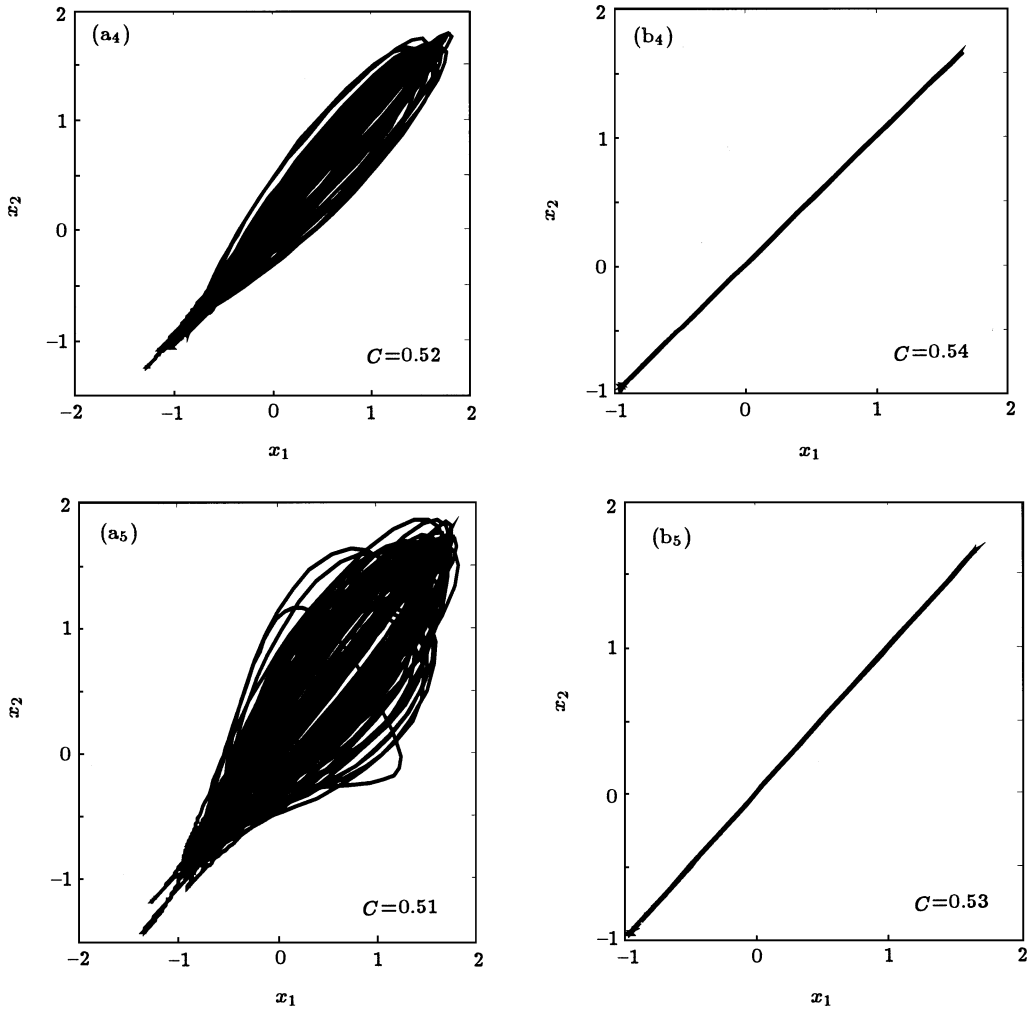


Fig.5. Membrane potentials of $N1$ vs $N2$ before and after the critical values of the coupling strength $C_{\rm cr}$ in the $(x1, x2)$-phase plane. (a1), (b1) Period-1 bursting for I=1.4; (a2), (b2) period-2 bursting for I = 1.8; (a3), (b3) chaotic firing for I = 3.0; (a4), (b4) period-2 spiking for I=3.45; (a5), (b5) period-1 spiking for I = 4.0. Complete synchronization occurs in (b1)–(b5). Here C is the coupling strength.

3.4. ISI bifurcation structure of electrically coupled HR neurons

Neuronal information is represented mainly based on the time-interval sequences of neurons. It is necessary to ask whether the ISIs bifurcation structures of coupled neurons persist by electrical coupling. This problem is analysed through the numerical results shown in Fig.6. From Table 1, the critical coupling strength $C_{\rm cr}$ for complete synchronization increases with the increase of the external direct current I. Then we choose the coupling strength C=0.1, 0.25, 0.4 and 0.6 to explore the influence of electrical coupling on the ISI bifurcation structures of electrically coupled neurons.

Numerical simulation shows that the ISI bifurcation structures of the two identical neurons are similar, whether they reach complete synchronization or not; that is, they experience the same firing pattern under the same values of parameters. This is because the two coupled neurons considered here are identical and the coupling terms between them are symmetric. For this reason, only the ISI bifurcation diagram of one neuron is available in Fig.6.

Now we consider the influence of electrical coupling. Comparing Fig.6(a) with Fig.2, we can see that if the coupling strength is larger than the maximum critical value of complete synchronization for all firing patterns with respect to the external current (such as C=0.6), the ISI bifurcation structure of the coupled neurons is the same as that of a single neuron without coupling; that is, there is no distortion caused by the coupling between neurons for neuronal information. However, if the coupling strength is lower than certain critical values for complete synchronization (such as C=0.4 and 0.25), there are some differences between the ISI bifurcation structure of the

coupled neurons and that of a single neuron; that is, the neuronal information is somewhat distorted by the coupling between neurons (see Fig.6(b) and 6(c)). If the coupling strength is lower than any critical values of complete synchronization for periodic and chaotic firing patterns (such as C=0.1), the coupled neurons undergo entirely different firing patterns from that of a single neuron under the same parameter values; that is, the neuronal information is wholly distorted by the electrical coupling between neurons (see Fig.6(d)).

From the above analysis, it is concluded that for electrically coupled HR neural network, the neurons have the same ISI bifurcation structures; however, the ISI bifurcation structures are different for different coupling strengths, and the parameter regions of complete synchronization are certainly distinct. The neuronal information persists in electrically coupled systems only when the coupling strength is large enough to exceed the critical values of complete synchronization for all firing patterns.

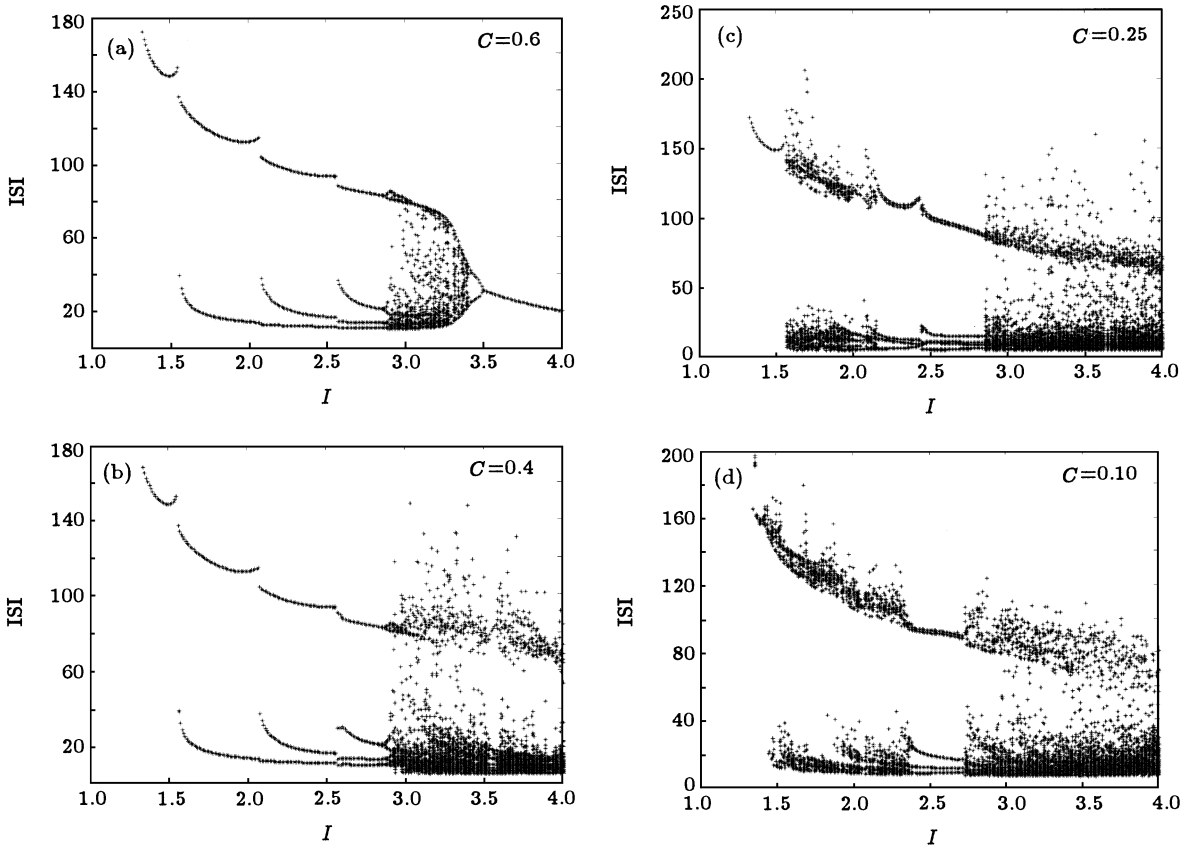


Fig.6. ISI bifurcation structures of electrically coupled HR neurons under different coupling strengths. (a) C=0.6, (b) C=0.4, (c) C=0.25, (d) C=0.1.

4. Conclusion

This paper mainly discussed the firing patterns of a HR neuron and the complete synchronization of two electrically coupled identical HR neurons. With the increase of the external direct current I, a single neuron experienced quiescence, periodic bursting, chaos and periodic spiking in series. We explored the periodic firing patterns and discerned periodic bursting from periodic spiking by the fast/slow dynamical analysis.

Some criteria for reaching complete synchronization through electrical coupling were presented theoretically and tested by numerical simulation. In this framework, we only needed to estimate the eigenvalues, the Floquet multipliers and the conditional Lyapunov exponents when a single neuron shows quiescent state, periodic firing and chaotic firing.

Through bifurcation analysis, we concluded that the ISI bifurcation structures of electrically coupled identical neurons were similar, but were strongly influenced by the coupling strength. The ISI bifurcation structure of the electrically coupled neuronal system persisted without distortion only for big enough coupling strength.

References

[1] Boccaletti S *et al* 2002 *Phys. Rep.* **366** 1

[2] Zheng Z G 2001 *Chin. Phys.* **10** 703

[3] Wang R and Shen K 2001 *Chin. Phys.* **10** 711

[4] Zhang S H and Shen K 2002 *Chin. Phys.* **11** 894

[5] Zheng Z G, Hu G, Zhou C S and Hu B B 2000 *Acta Phys. Sin.* **49** 2320 (in Chinese)

[6] Li G H, Zhou S P and Xu D M 2004 *Chin. Phys.* **13** 168

[7] Chen S H, Xie J, Lu J A and Liu J 2002 *Acta Phys. Sin.* **51** 749 (in Chinese)

[8] Hansel D and Sompolinsky H 1992 *Phys. Rev. Lett.* **68** 718

[9] Wang W, Perez G and Hilda A 1993 *Phys. Rev.* E **47** 2893

[10] Hindmarsh J L and Rose R M 1984 *Proc. R. Soc. London, Ser.* B **221** 87

[11] Holden A V and Fan Y S 1992 *Chaos, Solitons Fractals* **2** 221

[12] Holden A V and Fan Y S 1992 *Chaos, Solitons Fractals* **2** 349

[13] Holden A V and Fan Y S 1992 *Chaos, Solitons Fractals* **2** 583

[14] Holden A V and Fan Y S 1993 *Chaos, Solitons Fractals* **3** 439

[15] Verhulst F 1990 *Nonlinear Differential Equations and Dynamical Systems* (Berlin: Springer) p80