# Phase synchronization and its transition in two coupled bursting neurons: theoretical and numerical analysis*

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(Received 15 January 2010; revised manuscript received 17 March 2010)

It is crucially important to study different synchronous regimes in coupled neurons because different regimes may correspond to different cognitive and pathological states. In this paper, phase synchronization and its transitions are discussed by means of theoretical and numerical analyses. In two coupled modified Morris–Lecar neurons with a gap junction, we show that the occurrence of phase synchronization can be investigated from the dynamics of phase equation, and the analytical synchronization condition is derived. By defining the phase of spike and burst, the transitions from burst synchronization to spike synchronization and then toward nearly complete synchronization can be identified by bifurcation diagrams, the mean frequency difference and time series of neurons. The simulation results suggest that the synchronization of bursting activity is a multi-time-scale phenomenon and the phase synchronization deduced by the phase equation is actually spike synchronization.

**Keywords:** phase synchronization, synchronization transition, bifurcation diagram
**PACC:** 0545, 0547, 8725

## 1. Introduction

Nowadays synchronization is playing an increasingly crucial role at the macroscopic as well as cellular level in information processing, cognitive functions and neural coding.[1−4] It is reported that synchronization is ubiquitous in the brain, which may cause many physiological mechanisms of normal as well as pathological brain functioning, and some neurological diseases such as epilepsy, essential tremor and Parkinson's disease.[5]

Bursting, as a unit of information, is characteristic of fast/slow dynamical systems, in which neural activity presents two timescales, a fast one related to the spike process and a slow timescale related to the burst process. Correspondingly, there are two rhythmic processes associated with interacting bursting neurons: burst synchronization or synchronization of bursts, where the bursts start at approximately the same time for all coupled neurons, even though their spikes are nonsynchronous in each burst; and spike synchronization or synchronization of individual spikes, which means that two neurons always generate spikes almost simultaneously. Of the two types of synchronization, one does not imply the other, but there exists an additional regime when both synchronization types may occur simultaneously.[6−10]

Recently, a modified Morris–Lecar (ML) neuronal model[6] which is derived from the two-dimensional ML model was put forward. This model can exhibit a variety of bursting types involving regular bursting or irregular ones and complex bifurcation structures.[11,12] According to the neural coding theory, a neuron can encode information by bursting behaviour and some special interspike interval (ISI) bifurcation structures may provide us with a clue to the understanding of the coding mechanism.[13] Different coupled bursters process information differently.[6] Different synchronous regimes may correspond to different cognitive and pathological states.[2] Hence, the investigation of different synchronous regimes and synchronization transitions of coupled bursting neurons is particularly important.

So far, most studies of synchronization dynamics and synchronization transition depend mainly on numerical simulations (e.g., Refs. [7]–[10], [14] and [15]). In Ref. [7] the phase synchronization of two coupled HR neurons was studied by means of phase function and cross-correlation. It was shown that phase synchronization was in fact spike synchroniza-

*Project supported by the National Natural Science Foundation of China (Grant Nos. 10872014 and 10802012), the Development Foundation of Science of Nanjing University of Science and Technology (Grant No. XKF09036).

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tion and Hindmarsh–Rose neurons followed a different transition route from that of Rössler oscillators. The rhythm synchronization of two coupled HR neurons was investigated with the help of spike phase and the similarity function, and the critical coupling strengths for spike and burst synchronization with different oscillatory regimes were found.[8] The phase synchronization of two electrically coupled HR neurons with large parameter mismatch and different firing modes was considered in Ref. [9]; it was shown that phase synchronization and complex firing patterns may occur with proper coupling strength. Transition from burst synchrony to spike synchrony in coupled bursting neurons was obtained with the help of the transverse Lyapunov exponents.[10] Various regimes of phase synchronization in neuronal ensembles in a chain of nonidentical neurons with different oscillatory behaviours coupled by electrical and chemical synapses were studied in Ref. [14], and rich synchronous modes such as in-phase or antiphase synchronization with different firing patterns were discovered. The synchronization transition in gap-junction-coupled leech neurons was also investigated with an ISI bifurcation diagram in Ref. [15].

In the present paper, we are concerned with phase synchronization from the point of view of theoretical analysis and its transition route. We use the interspike intervals and IBI bifurcation diagrams, spike and burst mean frequency differences based on the definitions of spike phase and burst phase, and time series to illustrate the occurrence of burst and spike synchronization, then the corresponding critical coupling strengths will be obtained. As a numerical confirmation of our phase synchronization theory, we will show time evolutions of phase difference with several coupling strengths. Although our results are obtained for two coupled neurons, the theoretical method can be generalized to neuron networks, and the method of ISI and IBI bifurcation may help us better understand the multi-time-scale synchronization and neural coding mechanisms.

The rest of the present paper is organized as follows: model descriptions and definitions of phase are introduced in Section 2. Section 3 outlines the theoretical deduction of phase synchronization. In Section 4 we investigate the synchronization transitions via different synchronization regimes of two coupled bursting neurons. Section 5 gives the numerical confirmation of Section 3. Some conclusions are given in the last section.

## 2. Model description and definition of phase

We consider the neuronal model modified by Izhikevich,[6] by changing the external current $I$ in the two-dimensional ML model to a slow linear feedback $u$ which is governed by a linear differential equation. The single neuronal model is written with three variables $V, w$ and $u$ as

$$\begin{aligned} \dot{V} &= -g_{\rm ca} m_\infty (V - V_{\rm ca}) - g_{\rm k} w (V - V_{\rm k}) \\ &\quad - g_{\rm l}(V - V_{\rm l}) - u, \\ \dot{w} &= \frac{1}{3}(w_\infty - w)\tau, \\ \dot{u} &= 0.005(V + 0.2), \end{aligned} \tag{1}$$

where

$$\begin{aligned} m_\infty &= \frac{1}{2}\left(1 + \tanh\frac{V - v_1}{v_2}\right), \\ w_\infty &= \frac{1}{2}\left(1 + \tanh\frac{V - v_3}{v_4}\right), \\ \tau &= \cosh\frac{V - v_3}{2v_4}. \end{aligned}$$

The model possesses two timescales, shown in Fig. 1. In Eq. (1), each neuron is characterized by three time-dependent variables: membrane potential $V$, recovery variable $w$ and a slow adaptation current $u$. $g_{\rm ca}, g_{\rm k}$ and $g_{\rm l}$ are the maximum conductance values for $Ca^{2+}$, $K^+$, and the leak pathways, respectively, $V_{\rm ca}, V_{\rm k}, V_{\rm l}$ are the equilibrium potential corresponding to $Ca^{2+}$, $K^+$ and the leak conductances, respectively. Throughout the paper, the parameters are chosen to be $g_{\rm ca} = 1.2$ mmho/cm$^2$, $g_{\rm k} = 2$ mmho/cm$^2$, $g_{\rm l} = 0.5$ mmho/cm$^2$, $V_{\rm ca} = 1$ mV, $V_{\rm l} = -0.5$ mV, $v_1 = -0.01$ mV, $v_2 = 0.15$ mV, $v_3 = 0.1$ mV, $v_4 = 0.05$ mV, and we choose $V_{\rm k}$ as a controlled parameter to investigate the bursting dynamics. For convenience, we neglect the unit of measurement in each variable in the following.

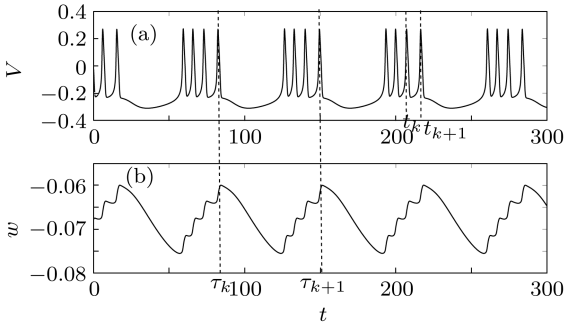



**Fig. 1.** Time evolution of fast (top) and slow (bottom) variables $V, w$ of an isolated neuron.

It is common that three definitions of phase are introduced in single-time-scale chaotic oscillators such as the Rössler system,[16] but for multiple-time-scale neuronal systems characterized by spike-burst activity, synchrony of an individual spike or burst may be included. Hence, we should modify the usual definition of phase function to hold true for neurons. We define the spike phase based on an appropriate Poincaré section.[8] If the trajectory successively crosses the chosen Poincaré section, a spike occurs, so the phase increases by a value of $2\pi$ and the phase can be computed with a linear interpolation, i.e.

$$\phi_{\rm s}(t) = 2\pi k + 2\pi \frac{t - t_k}{t_{k+1} - t_k}, \quad (t_k < t < t_{k+1}),$$

where $t_k$ is the $k$-th time crossing the Poincaré section. As shown in Fig. 1(a), the successive maxima of the time series correspond to a particular Poincaré section, and the corresponding times are just $t_k$ and $t_{k+1}$, and $t_{k+1} - t_k$ is the interspike interval. Thus spike synchronization occurs if the coupled neurons always generate spikes almost at the same time, i.e. the spike phase difference is less than $2\pi$.

In order to describe burst synchronization, we introduce the definition of burst phase[17−19] as

$$\phi_{\rm b}(t) = 2\pi k + 2\pi \frac{t - \tau_k}{\tau_{k+1} - \tau_k}, \quad (\tau_k < t < \tau_{k+1}),$$

where $\tau_k$ is denoted as the moment when the $k$-th burst starts as shown in Fig. 1(b), and $\tau_{k+1} - \tau_k$ is the interburst interval. Thus, when a burst occurs, the burst phase increases $2\pi$. So burst synchronization can be identified when the burst phase difference is bounded with the value of $2\pi$.

With the knowledge of phase $\phi(t)$, the frequency $\omega(t) = \dot{\phi}(t)$ and the mean frequency $\Omega(t) = \langle \dot{\phi}(t) \rangle$ can be defined. Then the mean spike frequency $\Omega_{\rm s}(t)$ and mean burst frequency $\Omega_{\rm b}(t)$ respectively have the following forms:

$$\Omega_{\rm s}(t) = \frac{2\pi}{\langle {\rm ISIs} \rangle}, \quad \Omega_{\rm b}(t) = \frac{2\pi}{\langle {\rm IBIs} \rangle},$$

where ISIs and IBIs are the interspike intervals and the interburst intervals of the membrane potential, respectively. Thus, weak phase synchronization appears if the mean frequency difference $\Delta\Omega = \Omega_1 - \Omega_2 \to 0$.

## 3. Theoretical analysis for phase synchronization

Phase synchronization has been widely studied in recent years,[1,20−24] but it is still lacking in theoretical augmentation. In order to well understand various aspects of interaction in large ensembles of neurons, we firstly deal with two neurons, and we take two coupled modified ML neurons with electrical synapses (see Eq. (2)) as example to look for the theoretical condition for the occurrence of phase synchronization. The coupled dynamics is governed by

$$\begin{aligned} \dot{V}_{1,2} &= -g_{\rm ca} m_{1\infty,2\infty}(V_{1,2} - V_{\rm ca}) \\ &\quad - g_{\rm k} w_{1,2}(V_{1,2} - V_{\rm k1,k2}) \\ &\quad - g_{\rm l}(V_{1,2} - V_{\rm l}) - u_{1,2} + C(V_{2,1} - V_{1,2}), \\ \dot{w}_{1,2} &= \frac{1}{3}(w_{1\infty,2\infty} - w_{1,2})\tau_{1,2}, \\ \dot{u}_{1,2} &= 0.005(V_{1,2} + 0.2), \end{aligned} \tag{2}$$

where

$$\begin{aligned} m_{1\infty,2\infty} &= \frac{1}{2}\left(1 + \tanh \frac{V_{1,2} - v_1}{v_2}\right), \\ w_{1\infty,2\infty} &= \frac{1}{2}\left(1 + \tanh \frac{V_{1,2} - v_3}{v_4}\right), \\ \tau_{1,2} &= \cosh \frac{V_{1,2} - v_3}{2v_4} \end{aligned}$$

with $C > 0$ being the coupling strength; $V_{\rm k1}, V_{\rm k2}$ represents a small parameter mismatch between two neurons. It is supposed that when the attractor in the phase plane has only one rotation centre, the instantaneous phase can be defined as an angle in polar coordinates on the projection plane.[16,20] Hence, phase $\phi(t)$ of the single modified ML neuron can be defined in a more intuitive and straightforward way as

$$\phi(t) = \arctan \frac{w - b}{V - a},$$

where the rotation centre $(a, b)$ is chosen to be $(0, 0.2)$, the value of arctan function is taken so that $\phi(t)$ is continuous in time, that is to say, it varies continuously, and has no $2\pi$ jumps as $t$ varies. Aiming to better understand the mechanism of PS, we convert the coupled neuronal model (2) into the dynamics of amplitude and phase by introducing a transformation as

$$\phi_i = \arctan \frac{w_i - b}{V_i - a},$$

$$A_i = \sqrt{(V_i - a)^2 + (w_i - b)^2}, \quad i = 1, 2.$$

Thus equation (2) is rewritten in terms of $A, \phi_{1,2}, u_{1,2}$ as:

$$\dot{A}_{1,2}$$

$$
\begin{aligned}
&= \cos\phi_{1,2}[-g_{\rm ca}m_{1\infty,2\infty}(a + A_{1,2}\cos\phi_{1,2} - V_{\rm ca}) \\
&\quad - g_{\rm k}(b + A_{1,2}\sin\phi_{1,2})(a + A_{1,2}\cos\phi_{1,2} \\
&\quad - V_{\rm k1,k2}) - g_{\rm l}(a + A_{1,2}\cos\phi_{1,2} - V_{\rm l}) - u_{1,2}] \\
&\quad + \sin\phi_{1,2}(w_{1\infty,2\infty} - b - A_{1,2}\sin\phi_{1,2})\tau_{1,2}/3 \\
&\quad + C(A_{2,1}\cos\phi_{1,2}\cos\phi_{2,1} - A_{1,2}\cos^2\phi_{1,2}),
\end{aligned}
$$

$$
\begin{aligned}
&\dot{\phi}_{1,2} \\
&= \frac{\cos\phi_{1,2}}{3A_{1,2}}(w_{1\infty,2\infty} - b - A_{1,2}\sin\phi_{1,2})\tau_{1,2} \\
&\quad - \frac{\sin\phi_{1,2}}{A_{1,2}}[-g_{\rm ca}m_{1\infty,2\infty}(a + A_{1,2}\cos\phi_{1,2} - V_{\rm ca}) \\
&\quad - g_{\rm k}(b + A_{1,2}\sin\phi_{1,2})(a + A_{1,2}\cos\phi_{1,2} - V_{\rm k1,k2}) \\
&\quad - g_{\rm l}(a + A_{1,2}\cos\phi_{1,2} - V_{\rm l}) - u_{1,2}] \\
&\quad - C\left(\frac{A_{2,1}}{A_{1,2}}\sin\phi_{1,2}\cos\phi_{2,1} - \sin\phi_{1,2}\cos\phi_{1,2}\right), \\
&\dot{u}_{1,2} = 0.005(a + A_{1,2}\cos\phi_{1,2} + 0.2), \qquad (3)
\end{aligned}
$$

where

$$
\begin{aligned}
m_{1\infty,2\infty} &= \frac{1}{2}\left(1 + \tanh\frac{a + A_{1,2}\cos\phi_{1,2} - v_1}{v_2}\right), \\
w_{1\infty,2\infty} &= \frac{1}{2}\left(1 + \tanh\frac{a + A_{1,2}\cos\phi_{1,2} - v_3}{v_4}\right), \\
\tau_{1,2} &= \cosh\frac{a + A_{1,2}\cos\phi_{1,2} - v_3}{2v_4}.
\end{aligned}
$$

As found in Ref. [16], amplitudes $A_{1,2}$ vary more slowly than $\phi_{1,2}$, so we use averaging over rotations of the phases $\phi_{1,2}$, and introduce 'slow' phases $\theta_{1,2}$ according to $\phi_{1,2} = \omega_0 t + \theta_{1,2}$, where $\omega_0$ is the natural frequency of the single neuron. By averaging Eq. (3), one obtains

$$
\begin{aligned}
&\frac{\rm d}{{\rm d}t}(\theta_1 - \theta_2) \\
&= g_{\rm k}\pi(V_{\rm k1} - V_{\rm k2}) - \frac{C}{2}\left(\frac{A_1}{A_2} + \frac{A_2}{A_1}\right)\sin(\theta_1 - \theta_2). \qquad (4)
\end{aligned}
$$

When we neglect the fluctuations of the amplitudes, equation (4) has an equilibrium phase difference

$$
\theta_1 - \theta_2 = \arcsin\frac{2g_{\rm k}\pi(V_{\rm k1} - V_{\rm k2})A_1A_2}{C(A_1^2 + A_2^2)}. \qquad (5)
$$

So if the coupling strength is larger than the critical value

$$
C_{\rm PS} = \frac{2g_{\rm k}\pi(V_{\rm k1} - V_{\rm k2})A_1A_2}{(A_1^2 + A_2^2)}, \qquad (6)
$$

phase synchronization occurs. This guarantees the existence of phase synchronization theoretically, and also makes it clear that the phase synchronization of two coupled neurons in Eq. (2) can be investigated from the dynamics of the phase equation (3).

## 4. Synchronization transition of two coupled bursting neurons

In this section, we will investigate synchronization transitions with different synchronous regimes of two coupled bursting neurons based on ISIs and IBIs. In our cases, we consider a coincidence of two characteristic time scales: spike synchronization and burst synchronization.

**Case 1**: two coupled periodic bursting neurons

Let $V_{\rm k1} = -0.8$ and $V_{\rm k2} = -0.7$ where the isolated neuron fires periodic bursts each with four spikes and six spikes, respectively. To analyse spike and burst synchronization between two neurons, we compare their ISIs and IBIs. If $\rm ISIs_1$=$\rm ISIs_2$ and $\rm IBIs_1$=$\rm ISIs_2$, that means two neurons generate spikes or bursts at almost the same time, so we conclude that the neurons are synchronized.

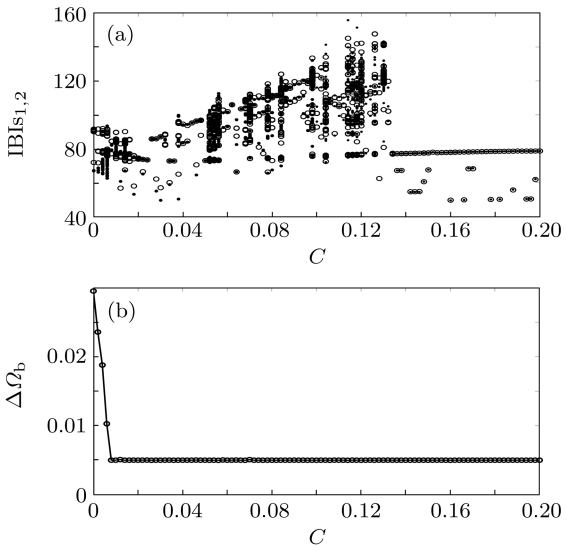



**Fig. 2.** (a) Bifurcation diagrams of IBIs of two coupled neurons versus the coupling strength $C$ and (b) mean burst frequency difference $\Delta\Omega_{\rm b}$ versus the coupling strength $C$.

Figures 2(a) and 3(a) show the IBI and ISI bifurcation diagrams of two coupled neurons dependent on the coupling strength $C$, where the circle denotes neuron 1 and the dot represents neuron 2, which will be used hereafter unless otherwise stated. We can find that when the coupling strength is small, IBIs and ISIs

between two neurons are very different, so bursts and spikes are not synchronized. With the increase of coupling strength, complex firing rhythm patterns and synchronization transition take place. The bursting behaviour is self-sustaining all the time except that the number of spikes in each burst varies, sometimes the neuron bursts periodically, sometimes it emits chaotic bursts. At a large coupling strength, the neuron is again back to the regime of periodic bursting mode but with five spikes in each burst (see Fig. 3(a)).

Figures 2(b) and 3(b) show the difference of the mean burst frequency $\Delta\Omega_{\rm b}$ and that of the mean spike frequency $\Delta\Omega_{\rm s}$ with respect to coupling strength $C$. In Fig. 2(b), as $C$ increases, $\Delta\Omega_{\rm b}$ quickly descends to zero when $C$ reaches 0.01, and then the value of zero keeps up all along. So the critical coupling strength for burst synchronization is $C = 0.01$. Thus, we consider a coincidence of slow characteristic time scale, i.e. $\mathrm{IBIs}_1 = \mathrm{IBIs}_2$. In Fig. 3(b), the coupling of neurons leads to oscillation first with a small amplitude, then $\Delta\Omega_{\rm s}$ changes into zero when $C = 0.134$, so the critical value of coupling strength for spike synchronization is $C = 0.134$. Thus we can conclude that burst synchronization often takes place before spike synchronization, which means that the slow variables reach synchronization more easily than fast variables. Meanwhile, there exists an additional regime when both spike synchronization and burst synchronization occur simultaneously.

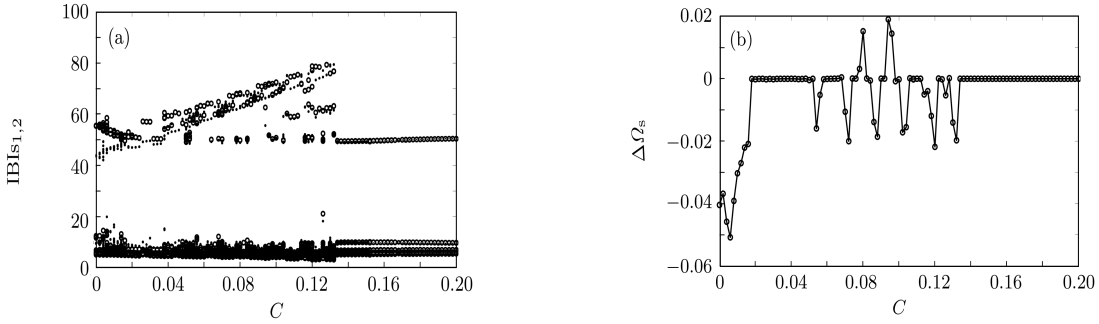



**Fig. 3.** (a) Bifurcation diagrams of ISIs of two coupled neurons versus the coupling strength $C$ and (b) mean spike frequency difference $\Delta\Omega_{\rm b}$ versus the coupling strength $C$.

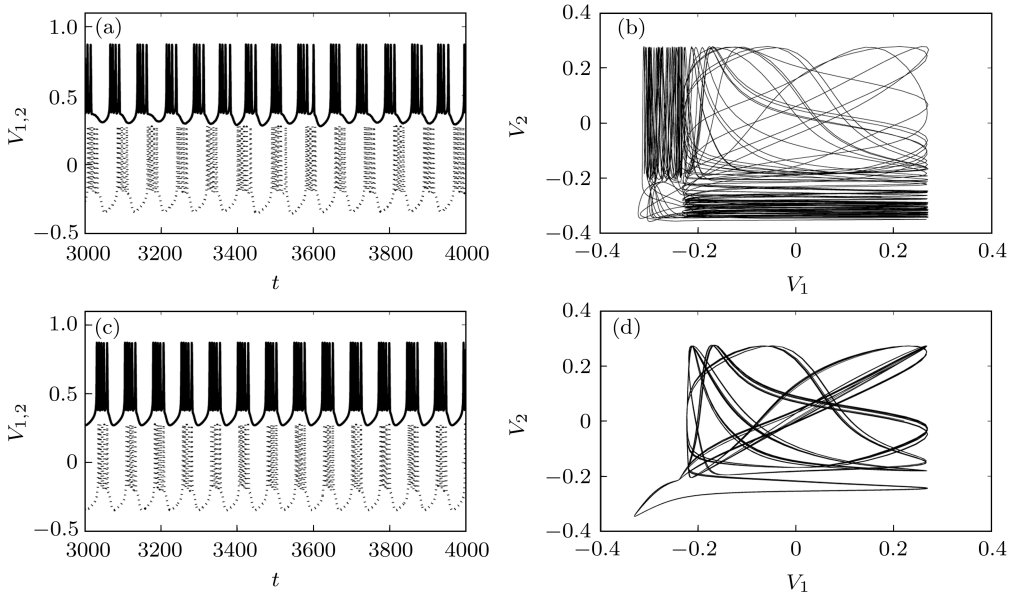



**Fig. 4.** Illustration of burst synchronization for (a), (b) $C = 0.005$, (c), (d) $C = 0.02$. Here panels (a) and (c) are the time series of two neurons before and after burst synchronization, and panels (b) and (d) display trajectories of two neurons in the $V_1$–$V_2$ plane before and after burst synchronization.

To illustrate the occurrence of burst and spike synchronizations clearly, we plot time series (see Figs. 4(a) and 4(c), Figs. 5(a) and 5(c)) and phase planes (see Figs. 4(b) and 4(d), Figs. 5(b) and 5(d)) of two coupled neurons before and after burst, spike synchronization, where the solid line and the dotted line in the time series denote neuron 1 and neuron 2, respectively. It is obvious that when burst synchronization occurs, two coupled

neurons generate bursts almost at the same time, even though some spikes are nonsynchronous in each burst, and some correlation between $V_1$ and $V_2$ can be seen in the $V_1$–$V_2$ plane as shown in Fig. 4(d). On the other hand, when spike synchronization is achieved, two neurons always generate spikes simultaneously, which means the synchronization of individual spikes. For $C = 0.14$, as shown in Fig. 5(d), the action potentials of two neurons closely approach each other; if the coupling strength continues to increase, the two neurons will reach a nearly full synchronized state.

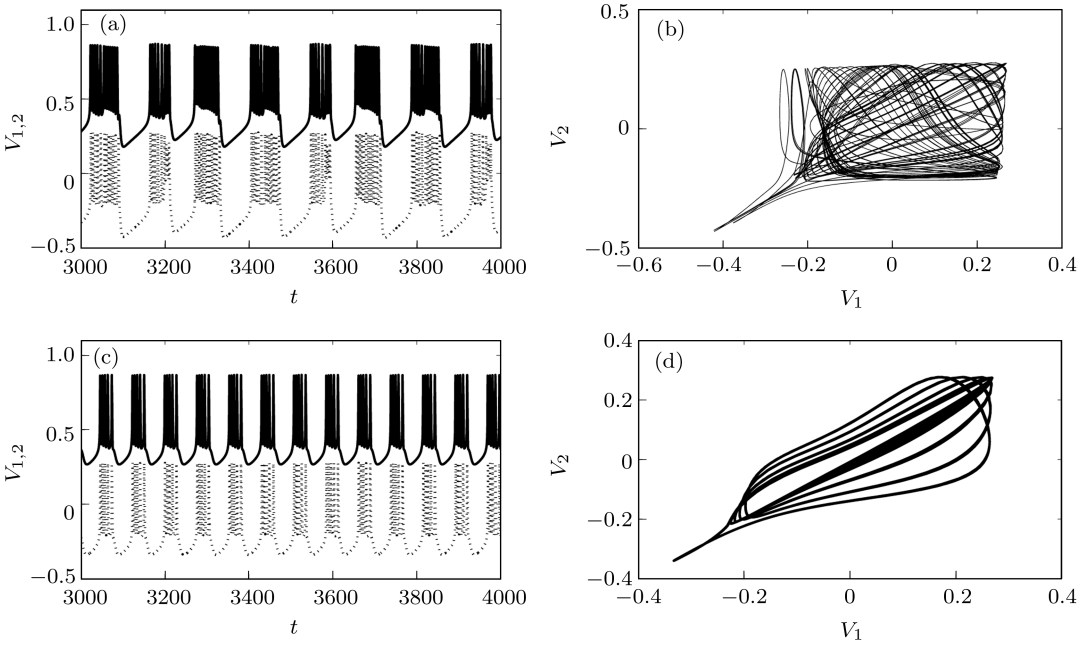



**Fig. 5.** Illustration of spike synchronization for (a), (b) $C = 0.13$, (c), (d) $C = 0.14$. Here panels (a) and (c) are the time series of two neurons before and after spike synchronization, and panels (b) and (d) display trajectories of two neurons in the $V_1$–$V_2$ plane before and after spike synchronization.

**Case 2**: two coupled chaotic bursting neurons

Let $V_{k1} = -0.87$ and $V_{k2} = -0.88$ where the isolated neuron fires chaotic bursts. Figures 6(a) and 7(a) present IBI and ISI bifurcation diagrams of two coupled neurons dependent on the coupling strength $C$.

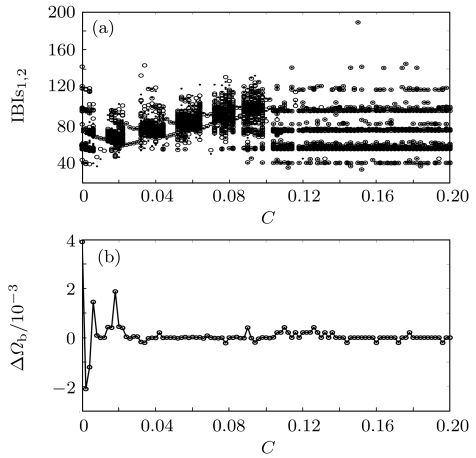



**Fig. 6.** Bifurcation diagrams of IBIs of two coupled neurons versus coupling strength $C$ (a), and mean burst frequency difference $\Delta\Omega_\mathrm{b}$ versus coupling strength $C$ (b).

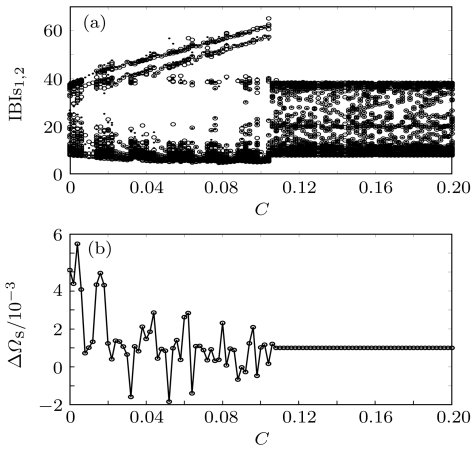



**Fig. 7.** Bifurcation diagrams of ISIs of two coupled neurons versus coupling strength $C$ (a), and mean spike frequency difference $\Delta\Omega_\mathrm{s}$ versus coupling strength $C$ (b).

It is shown in Figs. 6(a) and 7(a) that some similar bifurcation structures with chaotic bursting exist in an interval of $[0, 0.106]$. When $C > 0.106$, the two neurons generate spikes simultaneously, and even spikes involved

in each burst are the same, so burst synchronization coexists with spike synchronization when $C > 0.106$. The plot of mean spike frequency difference $\Delta\Omega_{\rm s}$ versus coupling strength $C$ shown in Fig. 7(b) also demonstrates that the critical coupling for spike synchronization is $C = 0.106$ when $\Delta\Omega_{\rm s} \to 0$. The curve for the difference of mean burst frequency $\Delta\Omega_{\rm b}$ versus $C$ is presented in Fig. 7(b); in the whole interval, the curve oscillates up and down near zero with a value on the order of $10^{-3}$.

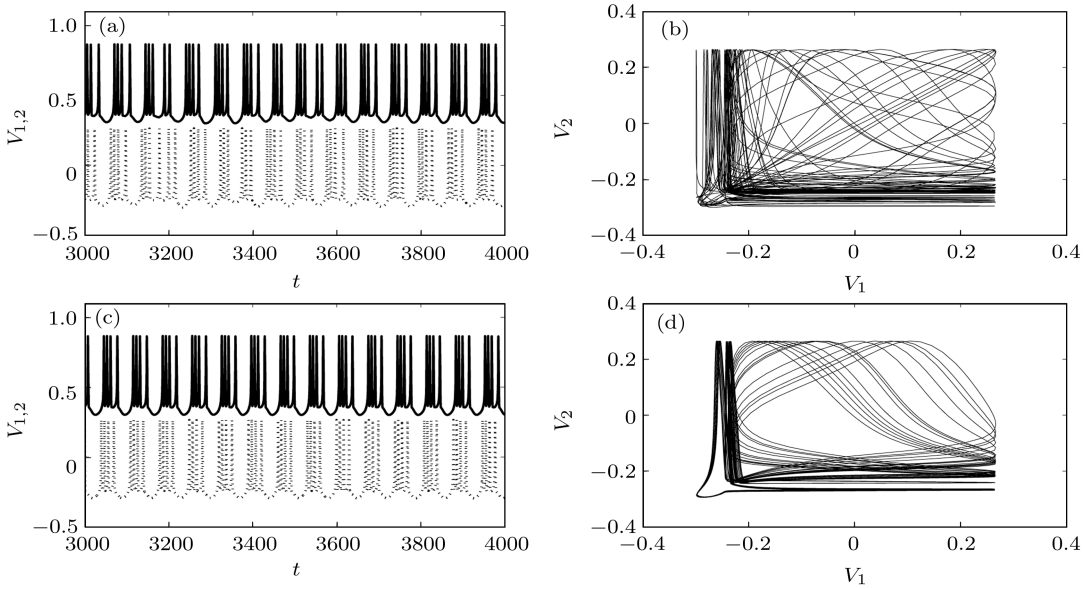



**Fig. 8.** Illustration of burst synchronization for (a), (b) $C = 0.005$, (c), (d) $C = 0.006$. Here panels (a) and (c) are the time series of two neurons before and after burst synchronization, while panels (b) and (d) display trajectories of two neurons in the $V_1$–$V_2$ plane before and after burst synchronization.

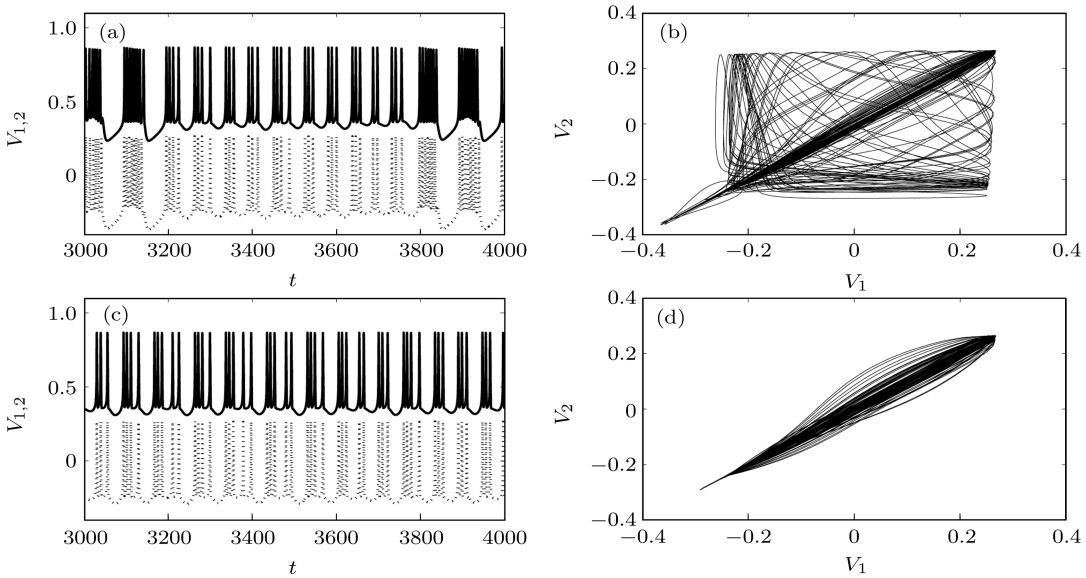



**Fig. 9.** Illustration of spike synchronization for (a), (b) $C = 0.09$, (c), (d) $C = 0.11$. Here panels (a) and (c) are the time series of two neurons before and after spike synchronization, while panels (b) and (d) display trajectories of two neurons in the $V_1$–$V_2$ plane before and after spike synchronization.

In order to find the critical value for burst synchronization clearly, we exhibit the time series and the phase planes of two neurons before and after burst, spike synchronizations in Figs. 8 and 9, where panels (a) and (c) in Figs. 8 and 9 are the time series of two neurons before and after burst, spike synchronization, respectively; the solid line denotes neuron 1 and the dot line represents neuron 2. Panels (b) and (d) in Figs. 8 and 9 are trajectories of two neurons in the $V_1$–$V_2$ plane before and after burst, spike synchronizations, respectively. Combining the above bifurcation diagrams and time series, we can find that the critical value for burst synchronization is $C = 0.0055$ which is much smaller than that for spike synchronization.

In summary, it can be seen that the transition route of two coupled bursting neurons is nonsynchronization $\longrightarrow$ burst synchronization $\longrightarrow$ spike synchronization $\longrightarrow$ nearly complete synchronization. Burst or spike synchronization is actually one form of phase synchronization; usually one does not imply the other, but there are regimes where both coexist.

## 5. Numerical confirmation based on the phase equation

In Section 3, we have converted the coupled neuronal model into a phase equation, and obtained a sufficient condition for the occurrence of phase synchronization. In the following, we will solve the phase equation (3) numerically by adjusting coupling strength $C$. Phase synchronization occurs when the phase difference $|\phi_1 - \phi_2| < 2\pi$.

For Case 1: $V_{\rm k1} = -0.8$ and $V_{\rm k2} = -0.7$, the evolutions of phase difference $\phi_1 - \phi_2$ versus coupling strength $C$ are shown in Fig. 10 with $C = 0.05$, $C = 0.12$, $C = 0.13$ and $C = 0.14$ from top to bottom. It is obviously observed that when $C = 0.05$ and $C = 0.12$, the phase difference has $2\pi$-phase jumps or ascends monotonically, so the two neurons are nonsynchronized. When $C = 0.13$, the phase difference fluctuates near zero within the interval of $[0, 2\pi]$, which means that phase synchronization is achieved. So the transition point from nonsynchronization to phase synchronization is approximately $C = 0.13$. This value is close to 0.134 which is the critical value for spike synchronization in Case 1. When $C = 0.14$, the phase difference is bounded with the bound being $2\pi$. When the coupling strength is large enough, nearly complete synchronization appears.

For Case 2: $V_{\rm k1} = -0.87$ and $V_{\rm k2} = -0.88$, the evolutions of phase difference $\phi_1$–$\phi_2$ versus coupling strength $C$ are shown in Fig. 11 with $C = 0.03$, $C = 0.09$, $C = 0.1$ and $C = 0.13$ from top to bottom. It is shown that when $C = 0.03$ and $C = 0.09$, the phase difference is unbounded. When $C = 0.1$, the phase difference becomes bounded within an interval of $[0, 2\pi]$. When $C = 0.13$, the phase difference is bounded with a value of $2\pi$ in a very small interval. So phase synchronization occurs at about $C = 0.1$ which is close to the critical value $C = 0.106$ for the spike synchronization in Case 2. So the phase synchronization deduced through the theoretical analysis in Section 3 is actually spike synchronization.

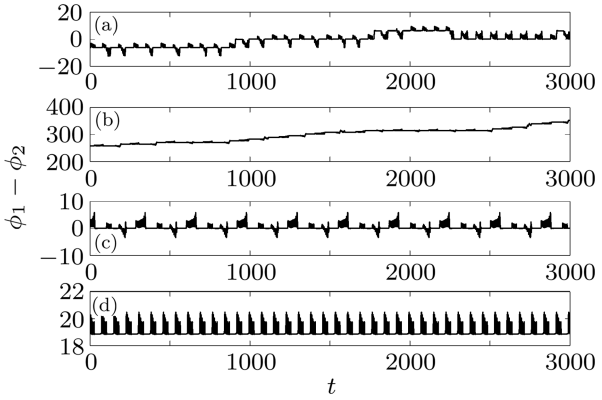



**Fig. 10.** Difference between the values of phase difference $\phi_1$–$\phi_2$ for two neurons for various values of coupling strength $C$: 0.05 (a), 0.12 (b), 0.13 (c) and 0.14 (d).

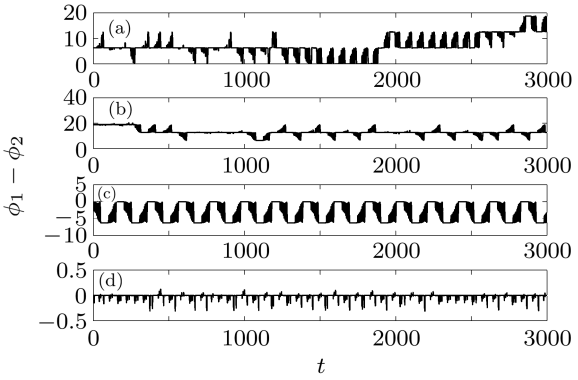



**Fig. 11.** Difference between the values of phase difference $\phi_1$–$\phi_2$ for two neurons for various values of coupling strength $C$: 0.03 (a), 0.09 (b), 0.1 (c) and 0.13 (d).

## 6. Summary and discussion

In this paper, we have theoretically and numerically studied phase synchronization and its transitions between burst synchronization and spike synchronization in two electrically coupled modified Morris–Lecar neurons. It is found that the occurrence of spike synchronization can be judged from the dynamics of the phase equation, and the corresponding sufficient condition is obtained. By coupling two bursting neurons, whether periodical or chaotic, when they are uncoupled, a transition from nonsynchronization to burst synchronization, then to spike synchronization, and finally toward nearly complete synchronization is discovered as the coupling strength increases. The presented results suggest that the synchronization of bursting activity is a multi-time-scale phenomenon and the burst synchronization is usually a precursor

to spike synchronization; a larger coupling can lead to a full coincidence of coupled neurons.

Although our results are obtained for two coupled neurons, the theoretical method can be easily generalized to neural networks, and the methods of interspike interval (ISI) and IBI bifurcations may help us better understand the multi-time-scale phenomenon of synchronization and neural coding mechanisms. It is well known that different synchronous regimes may correspond to different cognitive and pathological states. Hence, the results obtained in this paper have physiological significance.

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