Synchronization of the minimal models of bursting neurons coupled by delayed chemical or electrical synapses*

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The minimal two-dimensional model of bursting neuronal dynamics is used to study the influence of time-delay on the properties of synchronization of bursting neurons. Generic properties of bursting and dependence of the stability of synchronization on the time-lag and the strength of coupling are described, and compared with the two common types of synaptical coupling, i.e., time-delayed chemical and electrical synapses.

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1. Introduction

Synchronization of coupled nonlinear dynamical systems is a widespread phenomenon occurring in physical and biological systems.[1,2] The observations of synchronous neural activity in the central nervous system have stimulated a great deal of theoretical work on synchronization in coupled neural networks.[3,4] These observations suggest that neural activity is a cooperative process of neurons and synchronization plays a vital role in information processing in the brain, such as in processing information from different sensory systems to form a coherent and unified perception of the external world. Many studies have been carried out on synchronization in limit cycle systems and, more recently, chaotic systems.[2] Phenomenological or qualitative models (or models of the generic bifurcation type as they are sometimes called) have been employed in many studies on synchronization in networks.[5−8] Small world and scale-free networks of various neuronal models with noise and synaptic delays have been studied numerically, for example in Refs. [9]–[14].

Generic bifurcation models, depending on the model, are able to display, to a greater or lesser extent, behaviour beyond simple spiking, thus capturing what is believed to be the essence of neocortical diversity. The important advantages of a good qualitative model are that it describes generic properties and is more transparent and easier to analyse. The simplicity of generic models has been achieved by using the minimal number of variables needed to capture the relevant dynamical behaviour. For example, the famous FitzHugh–Nagumo (FN) neuron model,[15,16] is a two-dimensional nonlinear neuron model, and it is used as a paradigm for type II spiking behaviour in neurons.[6] It has been often used to study synchronization of excitable neuronal dynamics (see for example Refs. [17], [18] and references therein). In addition, a three-dimensional Hindmarsh–Rose (HR) model[19] is a commonly used example of a model that can exhibit more complex behaviour than only periodic movement. It is capable of producing bursting solutions for a wide range of parameters (i.e., a series of spikes which are chaotically interspersed with the quiescence behaviour). Stability and bifurcations of the stationary solution and the exact synchronization of the bursting dynamics for delayed coupled HR neurons have been analysed for example in Refs. [20]–[24].

It is believed that a burst of spikes is more reliable than a single spike in producing responses in postsynaptic neurons, so it is important to study burst-

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ing neuronal dynamics[5,6] Among the various types of models that can exhibit bursting dynamics, the most elementary one, and in this sense the generic model, has been given by the two-dimensional system of ordinary differential equations introduced by Izhikevich.[5,25] Our goal in this paper is to present some synchronization properties of bursting neurons, described by the minimal Izhikevich model, that can be expected to be generic. In particular, our investigation will concentrate on the influence of the time-delay and coupling strength on bursting synchronization with the two types of coupling: electrical and chemical couplings.

In most synchronization studies, the coupling between the elements in the network is assumed to be electrical (also called linear or diffusive), and is represented as the difference between the membrane potentials of the interacting neurons. Although there are synapses which are well approximated by the electrical coupling, the majority are in fact the so-called chemical synapses.[3,7] The fast threshold modulation (FTM) model proposed by Somers and Kopell[26] is a simple mathematical model that represents this kind of coupling well. FTM differs from electric linear coupling in that the coupling term is a nonlinear function of the state variables of the coupling system.

In modelling qualitative neuronal networks, it is useful and also important to use explicitly the time-delays in the description of the transfer of information between the neurons. Obviously, the information flow in coupled systems is not instantaneous. On the contrary, finite speed of signal transmission over a distance gives rise to a finite time-delay. For example, the speed of signal conduction through unmyelinated axonal fibres is on the order of 1 m/s, resulting in time delays of up to 80 ms for propagation through the cortical network.[3] Furthermore, the complicated succession of processes that take place in real synapses can be modelled by a single interaction term with an explicit time-lag in the dynamical equations of the interacting neurons. In addition, it is known that values of the time-lag in a realistic domain can change the qualitative properties of dynamics: introduce or destroy stable oscillations and enhance or suppress synchronization between different units. In this paper, we will study the synchronization of two elementary two-dimensional bursters with an explicit time-delay in the coupling.

The paper is organized as follows: in the next section, we present the models for connectivity used for the coupling between the neurons. Each of the neurons is modelled by the Izhikevich equations and, for the chemical synapse, we use the FTM model with explicit time-lag. In Section 3, we derive the delay-differential equations for small deviations from the manifold of the exact synchronization that we used to study the stability of the synchronization. The equations are analogous to those derived in Ref. [9] for HR neurons coupled by the delayed electrical synapses. Results of our analyses of the effects of the synaptic time delay on the bursting dynamics and synchronization are presented in Section 4. The conclusion is given in Section 5.

2. Basic models of bursting and synaptic connections

Izhikevich[25] introduced the minimal, qualitative, generic-type model of bursting behaviour, which requires only two variables and is of the form

$$\begin{aligned} \dot{x} &= x - \frac{x^3}{3} - y + \frac{4}{1+\exp(5(1-x))}\cos(40y), \\ \dot{y} &= \mu x, \end{aligned} \tag{1}$$

where $\mu = 0,01$, x is the rescaled membrane potential of the neuron and y corresponds to the slow current, for example Ca^+. Slow oscillations of y variable drive the fast variable x through periods of oscillatory and quiescent behaviour. An isolated Izhikevich neuron shows a two-dimensional hedgehog-like limit cycle attractor because the parameters are fixed to the values typical for bursting behaviour and the system has an unstable stationary solution. The burst in the dynamics of the fast(x) variable occurs for such (c, τ) that imply oscillatory behaviour of the slow variable y, and in particular during the periods when $\mathrm{d}y/\mathrm{d}t > 0$. Typical orbit of the Izhikevich model is illustrated in Fig. 1 by presenting its phase portrait (Fig.1(a)) and the time series $x(t)$ and $y(t)$ (Fig. 1(b)).

Synapses are of two types: chemical and electrical, both of which occur in the neocortex, although the chemical ones are much more frequent.[3] Chemical synapses have complex morphology and correspondly complex dynamics that operate on many different time scales, thus providing memory function. They have a steep activation function and therefore only transmit information about the timing of the spikes (or bursts) in the presynaptic cell. The fast threshold modulation model was, as a model for chemical coupling,

proposed by Somers and Kopell in 1993:[26] It is called fast, because no dynamics are incorporated, and called threshold modulation, because the model exhibits a threshold-like behaviour, either a hard threshold, or a more gradual, continuous threshold.

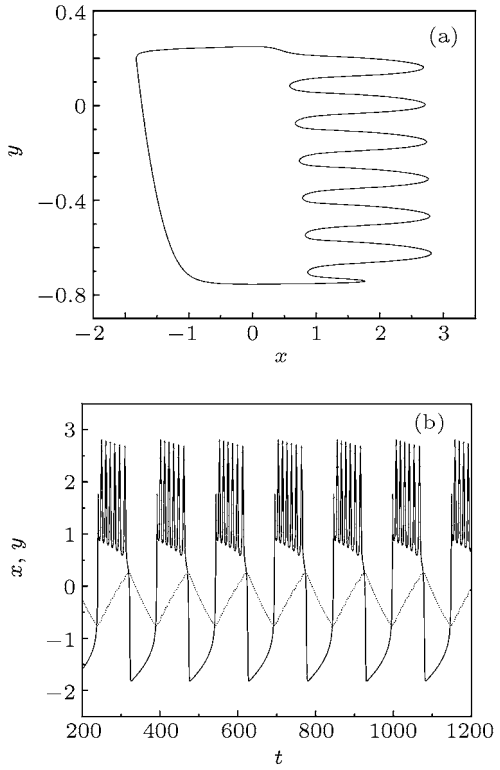


Fig. 1. The bursting dynamics on the attractor for the Izhikevich neuron ($\mu = 0.01$). (a) The phase portrait of the attractor, (b) the time series $x(t)$ (solid line) and $y(t)$ (dotted line).

Our main goal in this paper is to study the influence of time-delay on the synchronization of two electrically or chemically coupled elementary bursters, given by the following delay-differential equations (DDE):

$$\begin{aligned}
\dot{x}_1 &= x_1 - \frac{x_1^3}{3} - y_1 + \frac{4}{1+\exp(5(1-x_1))} \\
&\quad \times \cos(40y_1) + C(x_1, x_2^\tau), \\
\dot{y}_1 &= \mu x_1, \\
\dot{x}_2 &= x_2 - \frac{x_2^3}{3} - y_2 + \frac{4}{1+\exp(5(1-x_2))} \\
&\quad \times \cos(40y_2) + C(x_2, x_1^\tau), \\
\dot{y}_2 &= \mu x_2, \qquad (2)
\end{aligned}$$

where $x_i^\tau \equiv x_i(t-\tau)$, and $\tau \geq 0$ is a measure of the time-delay. The function $C(x_i, x_{i+1}^\tau)$, $i = 1, 2$, $x_3 \equiv x_1$, describes the time delayed coupling between the units.

Two types of coupling will be analysed. The electrical coupling

$$C(x_i, x_{i+1}^\tau) = c(x_{i+1}^\tau - x_i), \qquad (3)$$

and the chemical coupling in the following FTM form:

$$C(x_i, x_{i+1}^\tau) = c(x_i - V_\mathrm{s}) \frac{1}{1+\exp[-k(x_{i+1}^\tau - \theta_\mathrm{s})]}. \quad (4)$$

The parameter V_s is the synaptic reversal potential. It determines the type of coupling. If V_s is larger than the membrane potential x, then the membrane potential x is de-polarized, thus exciting the cell. If, on the other hand, V_s is smaller than the membrane potential, then the membrane potential x is hyper-polarized, thus the cell is inhibited. The variable parameter c is the coupling strength between the first neuron at time t and its neighbour at some previous time $t-\tau$. The model exhibits either a hard or more gradual threshold-like behaviour, depending on the size of the parameter k, with $k \to \infty$ corresponding to the hard threshold. In this study, the values of the parameters θ_s, V_s and k will be fixed as $\theta_\mathrm{s} = -0.25$, $V_\mathrm{s} = 3$, and $k = 10$.

The time-delay plays a crucial role in the dynamics of the coupled system (2). For example, in the case of electrically time-delayed coupled bursters[23] or relaxation oscillators,[17,27] the time-lag in a certain domain leads to stabilization of the quiescent behaviour, i.e., to the phenomenon of oscillation death. Furthermore, it has been shown that the time-delay facilitates exact synchronization among bursting electrically coupled HR neurons,[22] but this phenomenon is unstable under an arbitrary small white noise perturbation.[24]

3. Linear stability analyses of synchronization

In a system of coupled bursting neurons (2), one can think of different degrees of synchronization. For example, a type of weak synchronization is achieved when the bursts in the two units occur roughly at the same time without synchronization of spikes within the bursts. The strongest type of synchronous dynamics is the exact synchronization. In Fig. 2, different types of asynchronous and synchronous bursting dynamics are illustrated. The two neurons in Eq. (2) are exactly synchronous if the following conditions are satisfied for all t:

$$\delta x = x_1 - x_2 = 0, \quad \delta y = y_1 - y_2 = 0. \qquad (5)$$

In order to study the stability of the exact synchronization of system (2), we have employed the method of numerical calculations of the Lyapunov exponent near the stationary solution of the equations that describe the dynamics of small deviations from the manifold of exact synchronization.[22]

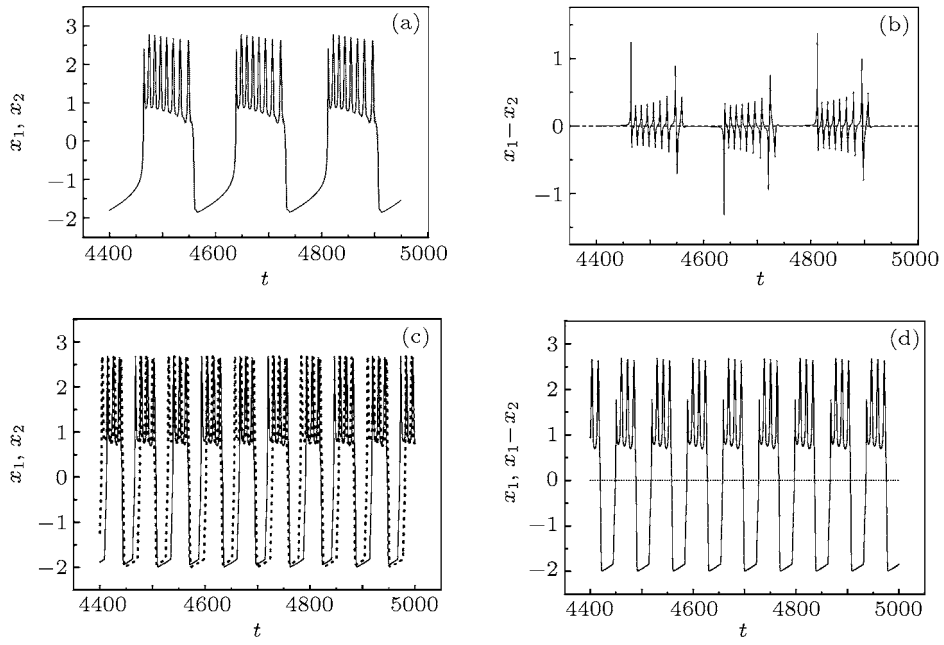


Fig. 2. Different types of dynamics, such as weak synchronization ((a),(b)) when neurons are electrically coupled, asynchronous bursting (c) and exact synchronization (d) achieved by increasing the values of the time-lag τ when neurons are FTM coupled. Values of (c, τ) and the plotted curves are (a) (0.1, 5), x_1 (solid line), x_2 (dotted line); (b) (0.1, 5), $(x_1 - x_2)$; (c) (0.3, 60), x_1 (solid line), x_2 (dotted line); (d) (0.3, 66), x_1 (solid line), $x_1 - x_2$ (dotted line).

On synchronization manifold (5), the dynamical equation is

$$\begin{aligned}\dot{x} &= x - \frac{x^3}{3} - y + \frac{4}{1+\exp(5(1-x))} \\ &\quad \times \cos(40y) + C(x, x^\tau), \\ \dot{y} &= \mu x, \\ x &= x_1 = x_2,\ y = y_1 = y_2, \end{aligned} \tag{6}$$

where $C(x, x^\tau)$ is in the form of Eq. (3) for electrical or Eq. (4) for chemical coupling.

The motion transverse to the synchronization manifold can be described in terms of infinitesimally small variations $\delta x \sim o(x), \delta y \sim o(y)$ by the equations

$$\begin{aligned}\dot{\delta}x &= \left[1 - x^2 + \frac{20}{[1+\exp(5(1-x))]^2}\right. \\ &\quad \left. \times \cos(40y)\exp(5(1-x)) + A\right]\delta x \\ &\quad - \left[1 + \frac{160}{1+\exp(5(1-x))}\sin(40y)\right]\delta y \\ &\quad + B\delta x^\tau, \\ \dot{\delta}y &= \mu\delta x, \end{aligned} \tag{7}$$

where we have used $x_1^3 - x_2^3 \sim 3x^2\delta x$,

$$\begin{aligned}&\frac{4}{1+\exp(5(1-x_1))}\cos(40y_1) \\ &- \frac{4}{1+\exp(5(1-x_2))}\cos(40y_2) \\ &\sim \left[\frac{20}{[1+\exp(5(1-x))]^2}\cos(40y)\exp(5(1-x))\right]\delta x \\ &\quad - \left[\frac{160}{1+\exp(5(1-x))}\sin(40y)\right]\delta y, \end{aligned}$$

and

$$\begin{aligned}&c\left[(x_1 - V_\mathrm{s})\frac{1}{1+\exp[-kx_2^\tau + k\theta_\mathrm{s}]}\right. \\ &\left. -(x_2 - V_\mathrm{s})\frac{1}{1+\exp[-kx_1^\tau + k\theta_\mathrm{s}]}\right] \\ &\sim \left[\frac{c}{1+\exp[-k(x^\tau - \theta_\mathrm{s})]}\right]\delta x \\ &\quad - \left[c(x - V_\mathrm{s})\frac{k\exp[-k(x^\tau - \theta_\mathrm{s})]}{(1+\exp[-k(x^\tau - \theta_\mathrm{s})])^2}\right]\delta x^\tau. \end{aligned}$$

In the case of the electrical coupling, we have

$$A = -c, \qquad B = -c,$$

and in the case of the chemical FTM coupling, we have

$$\begin{aligned}A &= \left[\frac{c}{1+\exp[-k(x^\tau - \theta_\mathrm{s})]}\right], \\ B &= -\left[c(x - V_\mathrm{s})\frac{k\exp[-k(x^\tau - \theta_\mathrm{s})]}{(1+\exp[-k(x^\tau - \theta_\mathrm{s})])^2}\right]. \end{aligned}$$

Equation (7) can be treated as a nonautonomous system of DDEs for the dynamics of small variations δx, δy, where the time dependence of x, y are determined by Eq. (6). The synchronization manifold is

stable or unstable, depending on whether the solutions of (7) ($\delta x(t)$, $\delta y(t)$) shrink to zero or grow asymptotically as $t \to \infty$. Sufficient condition for the stability is that the largest Lyapunov exponent associated with (7) is negative. The largest Lyapunov exponent of (7), which can be obtained by numerical solutions of joint equations (6) and (7), thus provides information of the local stability of the synchronization manifold.

4. Bursting and synchronization

We have studied the conditions for synchronization on parameters c and τ by numerical solutions of Eqs. (2), (6) and (7). The main questions that we want to answer are: a) for which values of c and τ, exactly synchronous bursting dynamics is stable and b) in which way the properties of the bursts, like the frequency of their occurrence and the average number of spikes in each burst, depend on the values of the coupling strength c and the time-delay τ.

The computations of the largest Lyapunov exponent for the motion transverse to the synchronization manifold (6) are used to determine the domain of (c, τ) parameters that imply stability or instability of the synchronization manifold. Application of this method to DDEs has been described in details elsewhere,[9,17,18] and will not be repeated here.

For $\tau = 0$ and for both types of coupling, the units are synchronized or non synchronized, depending on the sign of the value c: for $c > 0$, the units are synchronized and in the opposite case, i.e., when $c < 0$, the units are non-synchronized. For $\tau > 0$, a much more complex behaviour emerges. The results of our numerical study of the properties of the bursts and their synchronization in terms of the coupling c and the time-delay τ are presented by discussing Figs. 3–5.

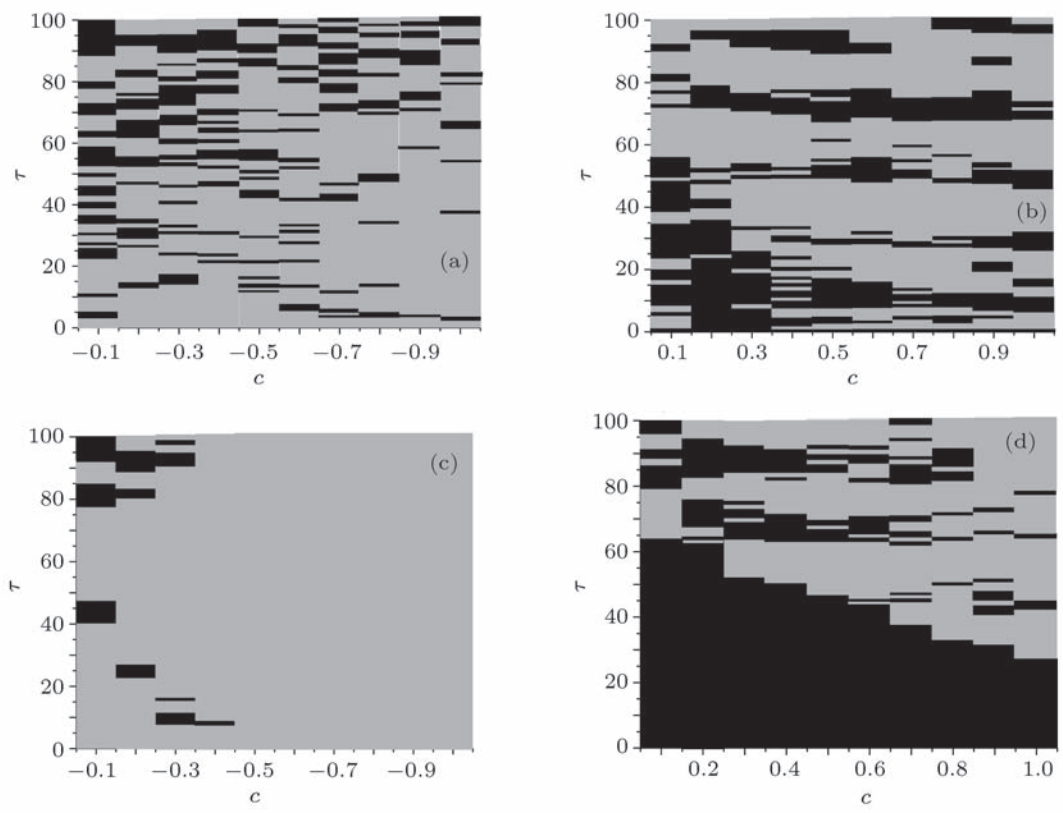


Fig. 3. Domains in (c, τ) parameter plane that imply synchronous (black) or asynchronous (white) bursting behaviour for electrical ((a), (b)) and chemical ((c), (d)) coupling.

Generally, Figs. 3–5 show an important and fundamental influence of time-delay on synchronization and bursting and spiking properties of coupled Izhikevich neurons.

figure 3 indicates that the regions of the parameter space (c, τ), where the largest Lyapunov exponents are larger or smaller than zero, i.e., the regions of the parameter space where units are non-synchronized (gray) or synchronized (black), respectively. The sign of the largest Lyapunov exponent is illustrated on a net of 10×20 (c, τ) values for $c > 0$ and $c < 0$. We choose the values of the coupling strength and the time-delay in the realistic domain, i.e., in our calculations, we set $|c| \leq 1$ and $0 \leq \tau \leq 100$. In the case of an

electrical coupling, the regions in the parameter space (c, τ) are much more interspersed than that in the case of the chemical coupling, i.e., the transitions from synchronized to non-synchronized behaviour (and vice versa) occur much more often than that in the case of the FTM coupling. Figures 3(c) and 3(d) (when the neurons are FTM coupled) show the existence of large areas of both synchronized and non-synchronized behaviour.

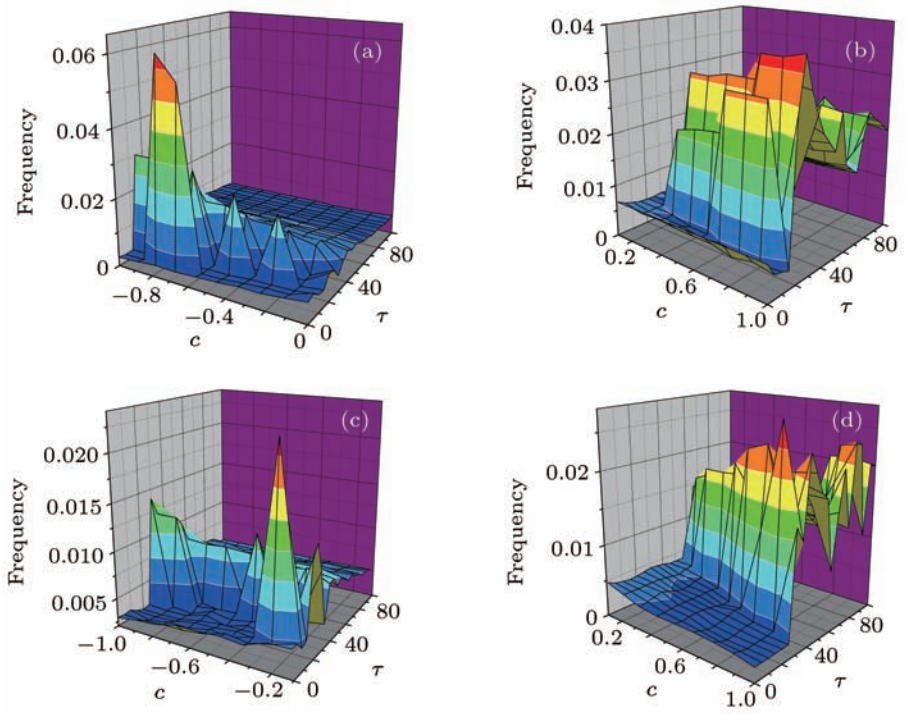


Fig. 4. (colour online) The dependence of the frequency of bursts on c and τ for electrical ((a), (b)) and FTM ((c), (d)) coupling.

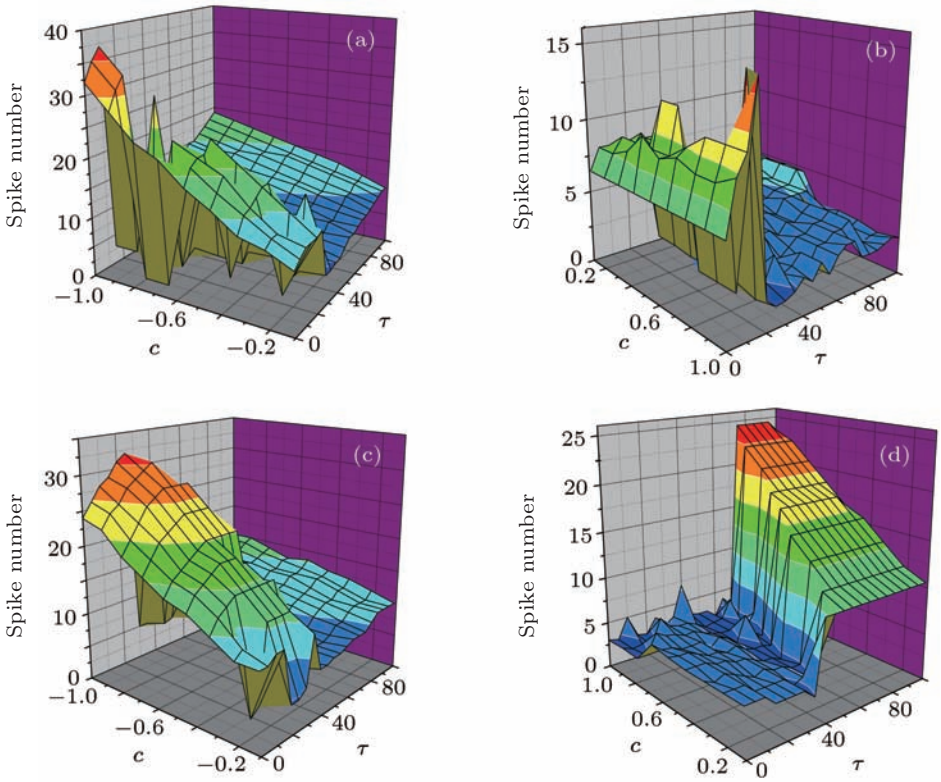


Fig. 5. (colour online) The dependence of the average number of spikes per burst on c and τ for electrical ((a), (b)) and chemical ((c), (d)) coupling.

Figure 4 demonstrates the dependence of frequency of bursts on the parameters c and τ. The frequency of the bursts introduced by electrical coupling is much larger than the frequency introduced by FTM coupling (almost two times bigger for certain regions of (c, τ)). The electrical and chemical coupling leads to qualitatively similar diagrams. In addition, there is a qualitative difference for both types of coupling between the dynamics for $c < 0$ and $c > 0$. In other words, the qualitative difference is not so much between the electrical and chemical coupling as it is between the cases that $c < 0$ and $c > 0$.

Figure 5 shows the average number of spikes as a function of the relevant parameters. Sharp peaks can be seen, for certain values of c and τ, only in the case where the units are electrically coupled and for $c > 0$. All the three other diagrams look qualitatively similar.

5. Summary and discussion

We have studied the exact synchronization of bursting dynamics in a pair of neurons with both an electrical and an FTM model of the chemical synapse. An Izhikevich neuron was used as the minimal generic model of each of the bursting units and we have included explicitly the time-delay in the synapses. Although the model with explicit time-delay is an infinite dimensional dynamical system, and because there is an infinite number of Lyapunov exponents, we examined the stability of the synchronized behaviour by computing the maximum Lyapunov exponent for the transverse directions to the synchronization manifold. We have demonstrated that the time-delay in both the electrical and the chemical FTM synapse can lead to the exact synchronization of bursting. Numerical calculations are used to solve the DDE's of the model and calculate the largest Lyapunov exponent for the equations of perturbations transversal to the synchronization manifold. These calculations can serve to determine the domains of the values of the coupling strength and time-delay that imply asynchronous or exactly synchronous bursting dynamics for initial states in some domains near the (unstable) stationary state. We have concentrated on the effects of the synaptic time-delay on the stability of synchronous bursting dynamics. Time-delay-induced oscillation death was not observed in the domain of parameters (c, τ) we have investigated, but instead of that a simple spiking exists in the small domain of values (c, τ).

The focus of our investigation here was on 1) the synchronizing effect of time-delay as a function of the time-lag and coupling strengths, 2) the stability of synchronized states, and 3) the properties of the bursts, like the frequency of their occurrence and the average number of spikes in each burst, depending on the values of the coupling strength c and the time-delay τ.

The following conclusions are obtained from our calculations. For $\tau = 0$ and for both types of coupling, the units are synchronized or non synchronized, depending on the sign of the value c: for $c > 0$ the units are synchronized and, in the opposite case, i.e., when $c < 0$, the units are non-synchronized. For $\tau > 0$, a much more complex behaviour emerges. In the case of electrical coupling, the synchronization of the bursting neurons occurs most often through the weak synchronization, i.e., through the bursting of the coupled neurons which is not exactly synchronous but the periods of bursts of the two neurons coincide. On the other hand, the bursting of the two chemically FTM coupled units is mostly either asynchronous or exactly synchronous, and only a negligibly small (c, τ) parameter domain implies the weak synchronization.

Relations between the domains of synchronous and asynchronous bursting described in this paper have been obtained using the most elementary model of bursting dynamics. It remains to be studied whether the conclusions can be also applied qualitatively in the cases of more complicated neuronal models in the bursting regime, and deterministic neuronal models with perturbations by white noise. It is also important to study the relative importance of time-delay for cases of instantaneous electrical or chemical coupling on the synchronization in more complicated networks of elementary bursters.

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