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Exact synchronization of noisy bursting neurons with coupling delays

Nikola Burić [a,*], Kristina Todorović [b], Nebojša Vasović [c]

[a] *Institute of Physics, University of Beograd, P.O. Box 68, 11080 Beograd-Zemun, Serbia*
[b] *Department of Physics and Mathematics, Faculty of Pharmacy, University of Belgrade, Vojvode Stepe 450, Belgrade, Serbia*
[c] *Department of Applied Mathematics, Faculty of Mining and Geology, P.O. Box 162, Belgrade, Serbia*

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Abstract

Exact synchronization of a pair of stochastically perturbed Hindmarsh–Rose bursting neurons with delayed electrical coupling is studied. Possibility of stochastically stable exact synchronization with sufficiently strong coupling is proved for arbitrary time-lags and sufficiently small noise. Various effects of the interplay and influence of noise and time-delay on the exact synchrony are studied by numerical computations.

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1. Introduction

Synchronized neuronal dynamics has been observed at all levels of the nervous system and was suggested as particularly important in information processing [1–3]. There are two different broad types of oscillatory dynamics of a single neuron [4]: (a) Bursting is a neuronal activity such that a neuron fires two or more spikes followed by a period of quiescence, which is again followed by similar periods of spikeing and quiescence; (b) spikeing is the dynamical regime when a sequence of spikes continues, more or less regularly, for a relatively large period of time uninterrupted by periods of quiescent state. It is believed that burst of spikes is more reliable than single spike in producing responses in postsynaptic neurons. On the other hand, the synchronization between the bursting neurons has been much less studied than the synchronization between simple or chaotic oscillators. In this paper we shall analyze the synchronization of bursting neurons under realistic conditions that include time-delays and noise.

It has recently become clear (please see later for a selection of relevant references) that mathematical modelling of synchronization of realistic neurons must take into the account two important effects: (a) finite transmission times, and (b) stochastic perturbation of each neuron. It is well known that the explicit time-lag of physically reasonable duration can have profound effects on the dynamics of coupled neurons [5,8,7], (and [6] and the references there in). For example, an important effect, that has been recently demonstrated [9,10], is that the time-lag facilitates exact synchronization

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[*] Corresponding author.
E-mail address: buric@phy.bg.ac.yu (N. Burić).

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among bursting electrically coupled neurons. Another important effect is the time-delay induced oscillation death [11,6], which can lead to synchronization onto a quiescent state instead of the synchronous bursting or spikeing. Response of real neurons to synaptic or external stimuli is always influenced by many processes that are commonly modelled by different types of noise [12]. It is well known that the noise can induce qualitatively new and important effects, like noise induced neuronal bursting [13] or coherence and stochastic resonances [14–16], (see also the collection of articles in [17]).

We shall investigate the interplay of effects induced by time-delay and noise on the exact synchronization among bursting neurons. For example, we shall see that an arbitrary small white noise can wash out completely the constructive effects of time-delay on the exact synchronization, but induces only proportionally small perturbation of the exact synchronization achieved by sufficiently strong coupling.

Mathematically, the problem of stable exact synchronization of noisy systems with delayed coupling is equivalent to the problem of stochastic stability of a stationary state of a system of stochastic delay-differential equations (SDDE). Most of the methods employed by physicists in the analyzes of the noisy systems relay on the Markov property of the stochastic process modelling the systems dynamics [18]. However, delay-differential equations with noise do not satisfy the Markov assumption [19–21]. Stability of such SDDE's has been studied using extensions of the Lapunov method by Russian mathematicians long time ago [19]. More recently, stability of synchronization in systems with noise involving DDE was studied analytically in the context of coupled realistic and formal neural networks. Liao and Mao [22] (see also [20]) have initiated the study of stability in stochastic neural networks, and this was extended to stochastic neural networks with discrete time-delays in references [23,24]. An interesting method to study stability of SDDE has been developed recently and applied on large collections of neurons in [21]. Some analytical techniques relevant for delayed systems with noise have also been used in the study of coupled bistable systems with delays [25], and in noisy oscillators with delayed feedback [26–30].

The paper is organized as follows. After the description of the model of two delayed coupled noisy bursting neurons in Section 2, we prove, in Section 3, a theorem that claims existence of stable exactly synchronous dynamics in the system of noisy bursters with sufficiently strong instantaneous and time-delayed coupling for arbitrary time-lags. The sufficiency conditions are illustrated by numerical computation in Section 4. There we also present results of our extended numerical study of the interplay between the noise and time-lag on the exact synchrony in the studied model. Our results are summarized and discussed in Section 5.

2. The model

In this paper we shall analyze the exact synchronization of bursting in delayed coupled pair of Hidmarsh–Rose (HR) neurons [31] influenced by white noise. The model is given by the following system of stochastic delay-differential equations (SDDE)

$$\begin{aligned}
\mathrm{d}x_1 &= [F_x(x_1,y_1,z_1)+c_1(x_2-x_1)+c_2(x_2(t-\tau)-x_1)]\,\mathrm{d}t+x_1\sqrt{2D}\,\mathrm{d}W\\
\mathrm{d}x_2 &= [F_x(x_2,y_2,z_2)+c_1(x_1-x_2)+c_2(x_1(t-\tau)-x_2)]\,\mathrm{d}t+x_2\sqrt{2D}\,\mathrm{d}W\\
\mathrm{d}y_i &= F_y(x_i,y_i,z_i)\,\mathrm{d}t,\quad i=1,2\\
\mathrm{d}z_i &= F_z(x_i,y_i,z_i)\,\mathrm{d}t,\quad i=1,2
\end{aligned}\tag{1}$$

where F_x, F_y, F_z are the components of the HR fast–slow neuronal model [31]

$$\begin{aligned}
&F_x = y+3x^2-x^3-z+I,\qquad F_y = 1-bx^2-y\\
&F_z = -rz+rS(x-C_x)
\end{aligned}\tag{2}$$

and the terms $c_1(x_j(t)-x_i(t))+c_2(x_j(t-\tau)-x_i(t))$, $i=1,2$; $j=2,1$ represent mixtures of instantaneous and delayed electrical coupling. We shall suppose that the dynamical regime displayed by the two isolated neurons is the same, which is the case for example if the internal parameters and the external stimulus have the same values for both neurons. Stochastic perturbations are modelled by the multiplicative white noise $x_i\sqrt{2D}\mathrm{d}W, i=1,2$ in the equations for the membrane potentials of the ith neuron, where $\mathrm{d}W$ is the stochastic increment of the Wiener process. The intensity of the noise D and the stochastic properties of the noise are assumed to be the same for both neurons, but, of course, single realizations of the Wiener processes in the equations for x_1 and x_2 need not be the same functions of t.

The HR equation (2) describe the dynamics of the single neuron subject to external stimulus I. Depending on the values of the parameters r, S, C_x and the external current I the model can have qualitatively different attractors corresponding to quiescent state, periodic firing and bursting with regular or chaotic sequences of bursts [32–35]. The bursting dynamics is driven by the oscillations of the slow z variable, and occurs when the oscillations of z have sufficiently large amplitude. The beginning of a bursts of spikes corresponds to a minimum of the oscillating $z(t)$, endures during the period when z is increasing and the termination of the burst coincides with the change of the sign of $\mathrm{d}z/\mathrm{d}t$. Quiescent state endures while $\mathrm{d}z/\mathrm{d}t < 0$, and terminates at the next minimum.

In our numerical study we shall concentrate on two set of values of the parameters in (2) corresponding to different regimes of isolated neurons and different origin of bursting dynamics in the coupled pair

$$(\text{case } \alpha) : I = 3.2;\; b = 5;\; C_x = 1.6;\; r = 0.006;\; S = 4 \tag{3}$$

that correspond to situations when each of the isolated neurons displays bursting due to non-zero external current, and

$$(\text{case } \beta) : I = 0;\; b = 5;\; C_x = 1.6;\; r = 0.0021;\; S = 4 \tag{4}$$

when the isolated neurons are in the quiescent state but the bursting occurs for sufficiently strong coupling, i.e. sufficiently large $c_1 + c_2$ in Eq. (1). Nonsynchronized bursting in $x_1(t)$ and $x_2(t)$ is illustrated in Fig. 1a (case α) and Fig. 3a (case β).

3. Stochastic stability of exact synchronization

In this section we prove that the exact synchronization between stochastically perturbed HR systems in the general form (1) and (2) is globally stable in the mean, for sufficiently large instantaneous coupling constant. To study the

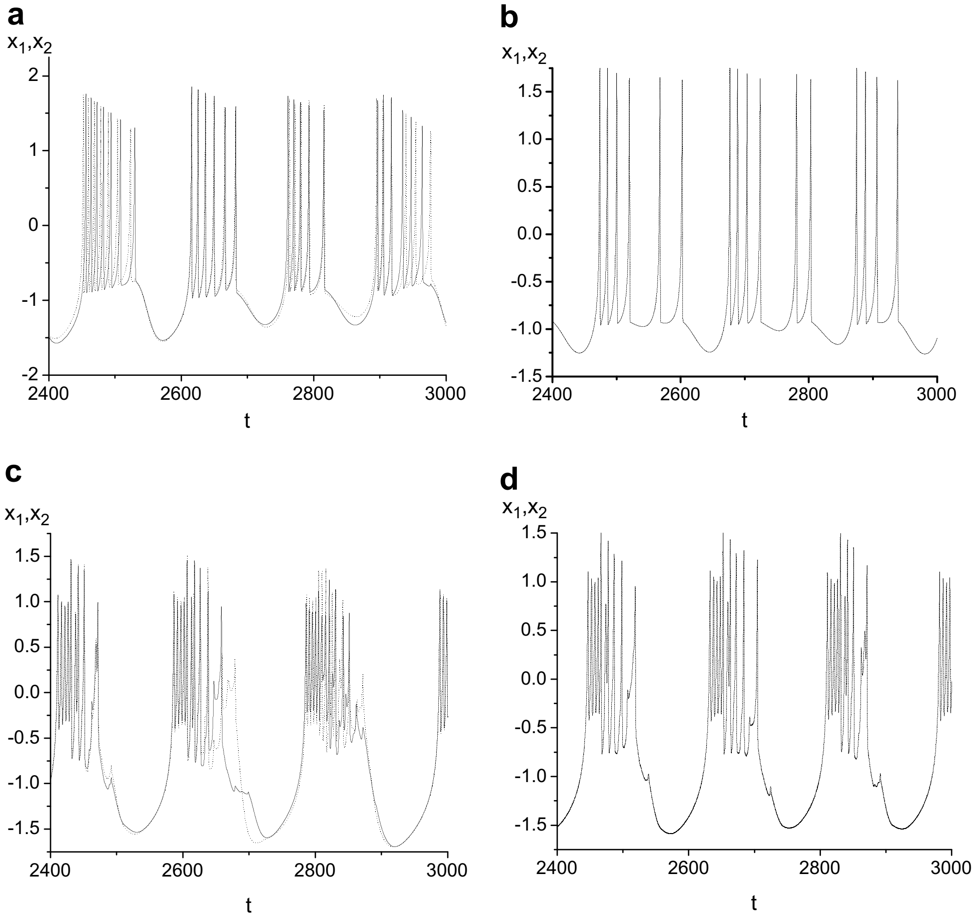

Fig. 1. Case α: (a) $c_1 = 0.1,\ c_2 = 0,\ D = 0$; (b) $c_1 = 0.5,\ c_2 = 0,\ D = 0$; (c) $c_1 = 0.2,\ c_2 = 0.5,\ \tau = 20,\ D = 0$; (d) $c_1 = 0.5,\ c_2 = 0.45,\ \tau = 20,\ D = 0.001$.

stability of the exact synchronization between the *1*st and the *2*nd unit it is convenient to analyze the dynamics of the difference

$$\varDelta_1(t) = x_1(t) - x_2(t), \quad \varDelta_2(t) = y_1(t) - y_2(t), \quad \varDelta_3(t) = z_1(t) - z_2(t) \tag{5}$$

Globally stable stationary state of the evolution equations for the differences corresponds to globally stable exact synchronization. The Ito stochastic equations governing the evolution of the differences are

$$\begin{aligned} d\varDelta_1(t) &= [\varDelta_2(t) + 3\varDelta_1(t)(x_1(t)+x_2(t)) - \varDelta_1(t)(x_1^2(t) + x_1(t)x_2(t) + x_2^2(t)) - \varDelta_3(t) - (2c_1+c_2)\varDelta_1(t) \\ &\quad - c_2\varDelta_1(t-\tau)]\,\mathrm{d}t + \varDelta_1(t)\sqrt{2D}\,\mathrm{d}W \\ d\varDelta_2(t) &= [-b\varDelta_1(t)(x_1(t)+x_2(t)) - \varDelta_2(t)]\,\mathrm{d}t \\ d\varDelta_3(t) &= [-r\varDelta_3(t) + rS\varDelta_1(t)]\,\mathrm{d}t \end{aligned} \tag{6}$$

Notice that the equations for the differences process explicitly contain unknown solutions $x_1(t)$ and $x_2(t)$. Our strategy will be to show that these solutions are bounded and then to use this fact for the analyzes of the stability of the trivial stationary state $\varDelta_i(t) = 0$, $i = 1,2,3$. To this end we shall utilize a stochastic extension of the Lyapunov method for DDE's [5,36,37].

In order to prove that $x_i(t)$ are bounded we consider the following functional:

$$U = \sum_{l=1,2} x_l^2/2 + y_l^2/2b^2 + z_l^2/2rS. \tag{7}$$

After some calculations, using $E(x_l^2(t)\sqrt{2D}\,\mathrm{d}W) = 0$, $x_1(t)x_2(t-\tau) \leqslant x_1(t)/2 + x_2(t-\tau)/2$ and similarly for 1 ↔ 2 interchanged, we obtain

$$\begin{aligned} E(\mathrm{d}U(t)) &\leqslant \frac{SC_x^2}{4}\,\mathrm{d}t - c_1(x_1(t)-x_2(t))^2 \\ &\quad + \sum_{l=1,2}\left[\frac{-(2z_l(t)+C_xS)^2}{4S} - \frac{(2y_l(t) - 1 - b^2x_l(t) + bx_l^2(t))^2}{4b^2} + F_1(x_l(t), x_l(t-\tau))\right]\mathrm{d}t \end{aligned} \tag{8}$$

where

$$F_1(x_l(t), x_l(t-\tau)) = -3x_l^4(t)/4 + \frac{2b^2(6-b)x_l^3(t) + b(b^3 + 4bD - 2bc_2 - 2)x_l^2(t) + 2b^2x_l(t) + 1}{4b^2} + c_2x_l^2(t-\tau)/2 \tag{9}$$

Now, we see that due to term $-3x_l^4(t)/4$, there is a positive M such that the previous expression for $F_1(x(t), x(t-\tau))$ is bounded when $|x(t)|$ is bounded by positive $M : |x(t)| < M$ and has negative values for $|x(t)| \geqslant M$. It follows from (8) that in region remote enough from the origin the expectation $E(\mathrm{d}U(t))$ is negative and, therefore, almost all trajectories beginning is this region are attracted into a bounded domain around the origin.

We shall now use the boundedness of $x_1(t)$, $x_2(t)$ to study the sufficient conditions for the exact synchronization, i.e. for the stability of the trivial stationary state of the difference equations (6). To that end we consider the following candidate for the Lyapunov functional for (6):

$$L = \varDelta_1^2(t)/2 + 2\varDelta_2^2(t)/b^2 + \varDelta_3^2(t)/2rS + e\int_{-\tau}^{0}\varDelta_1(t+\theta)\,\mathrm{d}\theta \tag{10}$$

where e is a free parameter. If we can show that there are such values of the parameters c_1 and c_2 such that for some value of e the expectation of the Ito derivative is never positive along the solutions of (6), i.e. $E(\mathrm{d}L(t)) \leqslant 0$ than the stationary state $\varDelta_i = 0$, $i = 1,2,3$ is stochastically stable [19,20].

Using Ito formula, the equations of the process (6),and the equations for the differences we obtain

$$\begin{aligned} \mathrm{d}L(t) &= -[8\varDelta_2(t) - b^2\varDelta_1(t) + 4b\varDelta_1(t)(x_1(t)+x_2(t))]^2\,\mathrm{d}t/16b^2 - \varDelta_1^2(t)[-x_1(t)x_2(t) + (b/2-3)(x_1(t)+x_2(t)) \\ &\quad - b^2/16 - D + c_1]\,\mathrm{d}t - (c_1+c_2)\varDelta_1^2(t)\,\mathrm{d}t - c_2\varDelta_1(t)\varDelta_1(t-\tau)\,\mathrm{d}t + e(\varDelta_1^2(t) - \varDelta_1^2(t-\tau))\,\mathrm{d}t - \varDelta_3^2(t)\,\mathrm{d}t/S \\ &\quad + \varDelta_1^2(t)\sqrt{2D}\,\mathrm{d}W \end{aligned} \tag{11}$$

The stochastic analog of the Lyapunov condition for deterministic equations $\mathrm{d}L(t)/\mathrm{d}t$ is that the expectation of the Ito derivative $E(\mathrm{d}L(t)) \leqslant 0$. The expectation of (11), using $E(\varDelta_1^2(t)\sqrt{2D}\,\mathrm{d}W) = 0$, is given by

$$\begin{aligned}E(\mathrm{d}L(t)) = &-[8\Delta_2(t) - b^2\Delta_1(t) + 4b\Delta_1(t)(x_1(t) + x_2(t))]^2\,\mathrm{d}t/16b^2 - \Delta_1^2(t)[-x_1(t)x_2(t) + (b/2-3)(x_1(t)\\ &+ x_2(t)) - b^2/16 - D + c_1]\,\mathrm{d}t - (c_1+c_2)\Delta_1^2(t)\,\mathrm{d}t - c_2\Delta_1(t)\Delta_1(t-\tau)\,\mathrm{d}t + e(\Delta_1^2(t) - \Delta_1^2(t-\tau))\,\mathrm{d}t\\ &- \Delta_3^2(t)\,\mathrm{d}t/S \end{aligned} \tag{12}$$

The first line is obviously negative and the second line can be made negative with sufficiently large c_1. Consider the quadratic form given by the last two lines of (12). The Silvester conditions for its negative definiteness are satisfied if $c_1 > 0$; $c_2 > 0$; $c_1 > c_2$ and e is chosen to be $e = (c_1 + c_2)/2$. The second line in (15) is negative definite if c_1 is large enough, i.e.

$$c_1 > \max\{x_1(t)x_2(t) - (b/2-3)(x_1(t) + x_2(t)) + b^2/16 + D\} \tag{13}$$

Thus, we conclude that with c_1 sufficiently large and $c_2 < c_1$ the trivial stationary state $\Delta_i(t) = 0$, $i = 1,2,3$ will be stable with unit probability [19,20], i.e. the state of exact synchronization can be made globally stable with unit probability with large enough c_1 and for any D, τ and $c_2 < c_1$.

We would like to make few remarks concerning the obtained sufficient condition for the stability of exact synchrony. Obviously there is very little practical use of the obtained sufficiency condition for predicting values of the coupling constant that imply exact synchronization of bursting. The sufficiency condition should be understood as a qualitative result that the exact synchrony can be achieved with certainty despite the noise and arbitrary time-lag, provided that the coupling is sufficiently strong. The condition does not say anything about possibility of stable exact synchrony for weak coupling and particular values of the time-lag, neither it says anything about the exact synchronization for each particular realization of the process described by (1). However, one might expect that with sufficiently strong instantaneous coupling and for arbitrary time-delays and for small noise each sample path will only slightly fluctuate around the exactly synchronous motion. On the other hand, the obtained condition does not prevent the situation when the exact synchrony is achieved by particular time-lag and weak coupling with $c_2 > c_1$, but fluctuations due to very small noise completely destroy the exact synchronization. This indeed occurs, as will be illustrated in the next section.

4. Numerical illustrations

As was pointed out, the bursting regime of the HR pair of neurons could be achieved by an external stimulus (case α) or by the coupling between the neurons which are in the quiescent state when isolated (case β). The sufficiency conditions apply to both situations but the exact synchronization in the two situations displays different properties and will be discussed separately.

Let us first discuss the exact synchronization when the bursting is induced by the external stimulus. In Figs. 1 and 2 we show segments of the time series $x_1(t)$ and $x_2(t)$ for some illustrative values of the coupling parameters c_1, c_2, the time-lag τ and the intensity of the noise D in this case. In Fig. 1b we illustrate that, as claimed in Section 3, sufficiently strong instantaneous coupling c_1 implies exact synchronization for arbitrary time-lags and the delayed coupling $c_2 < c_1$. If the instantaneous coupling is weaker than the delayed one, for example $c_1 = 0.2 < c_2 = 0.5$ there is no exact synchronization for most values of the time-lag τ (in Fig. 1c $\tau = 20$). As will be discussed, there could be some exceptional values of the time-lag τ such that the dynamics of the two neurons is exactly synchronous even with $c_1 = 0$, but such a state is highly unstable with respect to the noise and/or variations of the time-lag. The point here is that if the instantaneous coupling is not strong enough than the exact synchronization cannot be guaranteed. On the other hand, as is illustrated in Fig. 1d sufficiently large c_1 guaranties the exact synchrony for arbitrary values of the time-lag (for example, in Fig. 1d $\tau = 20$ and $D = 0.001$). The stochastic fluctuations around the exactly synchronous state are proportional to the small noise intensity, contrary to the case when the exact synchrony is achieved by a particular choice of c_2 and τ but with small c_1, illustrated in Fig. 2c.

In Fig. 2a–d we would like to illustrate the fact that if the instantaneous coupling is not strong enough than small variation of the time-lag or quite small noise radically destroys the exact synchronization that might occur for some particular c_2 and τ. Fig. 2a illustrates the exact synchrony for such particular values $c_1 = 0$, $c_2 = 0.1$ and $\tau = 8$ and no noise. However, the synchrony is achieved for τ in a small interval, and for example is lost with the time-lag $\tau = 9$ as shown in Fig. 2b. Similarly the exact synchrony is completely destroyed by rather small noise $D = 0.001$ as shown in Fig. 2c. Smaller or larger values of D induce qualitatively the same destruction of the exact synchrony. Obviously, small noise has completely destroyed what has been achieved by the time-delay, so that the dynamics in Fig. 3c is as asynchronous as that in Fig. 1a. On the other hand, if the instantaneous coupling is strong enough neither the time-lag nor a small noise cannot qualitatively change the state of exact synchronization, as is illustrated in Fig. 2d.

We suggest the following qualitative explanation of the destabilization by small noise of exactly synchronous bursting. The beginning of a burst in $x_i(t)$ corresponds to the minimum of $z_i(t)$ and the end of the burst occurs at the

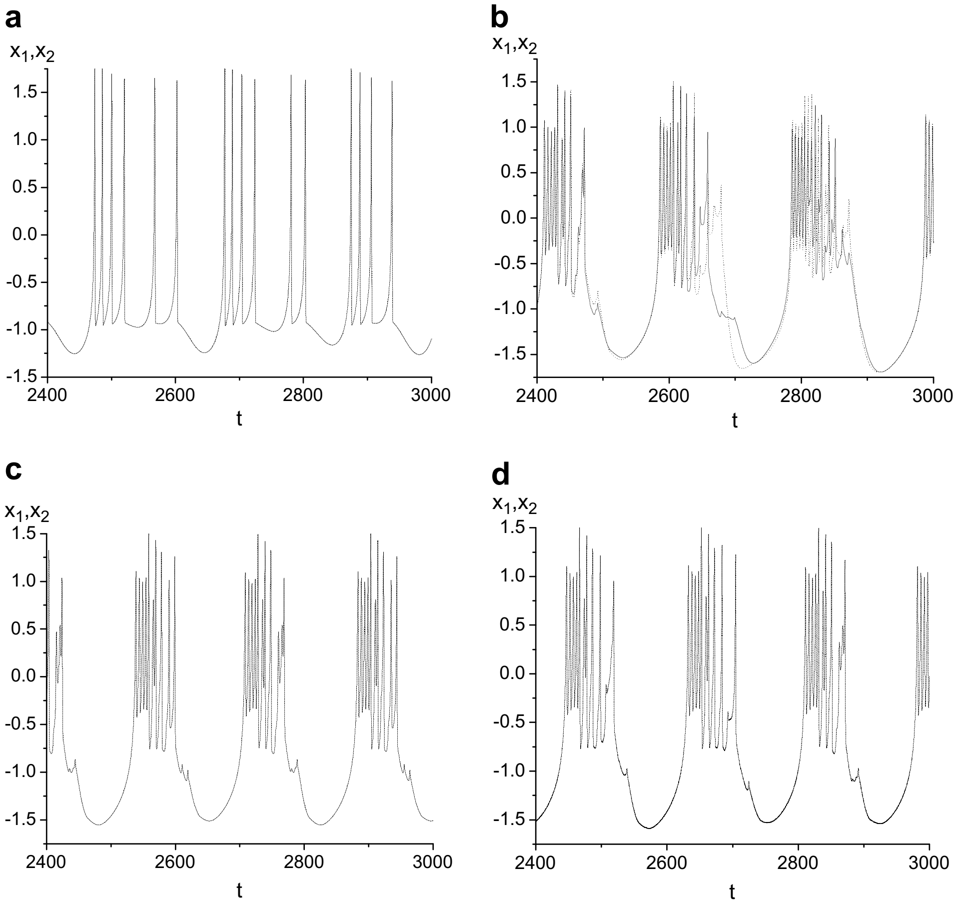

Fig. 2. Case α: (a) $c_1 = 0$, $c_2 = 0.1$, $\tau = 8$, $D = 0$; (b) $c_1 = 0$, $c_2 = 0.1$, $\tau = 9$, $D = 0$; (c) $c_1 = 0$, $c_2 = 0.1$, $\tau = 8$, $D = 0.001$; (d) $c_1 = 0.45$, $c_2 = 0.1$, $\tau = 9$, $D = 0.001$.

following maxima. The time that corresponds to minima in z_i is a random variable, with not necessarily equal realizations for $i = 1$ and $i = 2$, i.e. for the two neurons. This leads to a small time difference between the timing of the initiation of bursts in the two neurons, but the large difference in x_1 and x_2 variables.

Let us now discuss the stability of the exact synchronization of bursting when the isolated neurons are in the quiescent state and the bursting dynamics is induced by instantaneous coupling. Bifurcations behind such bursting were analyzed in [7]. In this case the globally stable stationary solution, corresponding to quiescent state, is destabilized only if c_1 and c_2 are both less or equal to zero and at least one of them has large modulus. For positive c_1 and c_2 or if both have small absolute values the stationary state is stable for any τ and stochastically stable for small noise intensities. This situation includes the sufficiency conditions from Section 2. Thus the exact synchrony that is guarantied by the analytic argument for sufficiently large c_1 and $c_2 < c_1$ is somewhat trivial, i.e. the exactly synchronous state is the globally stable stationary state. However, synchronization for those negative values of the coupling when the bursting occurs can be studied numerically. We have illustrated in Fig. 1b the coupling induced non-synchronous bursting for particular negative values of the coupling c_1 and c_2. Numerical evidence shows that if $c_2 = 0$, i.e. with the instantaneous coupling the exact synchronization of bursting does not occur for any c_1. As mentioned, the only synchronous dynamics is that of the stable stationary state for large positive c_1. However, time-delay can lead to synchronization of bursting induced by coupling (with negative c_1 and c_2) if the time-lag τ is in a specific interval. This is illustrated in Fig. 3b. Similarly to the case of externally induced bursting, small noise is sufficient to destroy the exact synchrony induced by the time-delay. This is illustrated in Fig. 3c. Fig. 3d illustrates better the asynchronous spikeing of x_1 and x_2 within the bursts. However, it should be noticed that although the spikes within the burst are desynchronized by the small noise since the initiation times of the burst in one or the other neuron are perturbed by different realizations

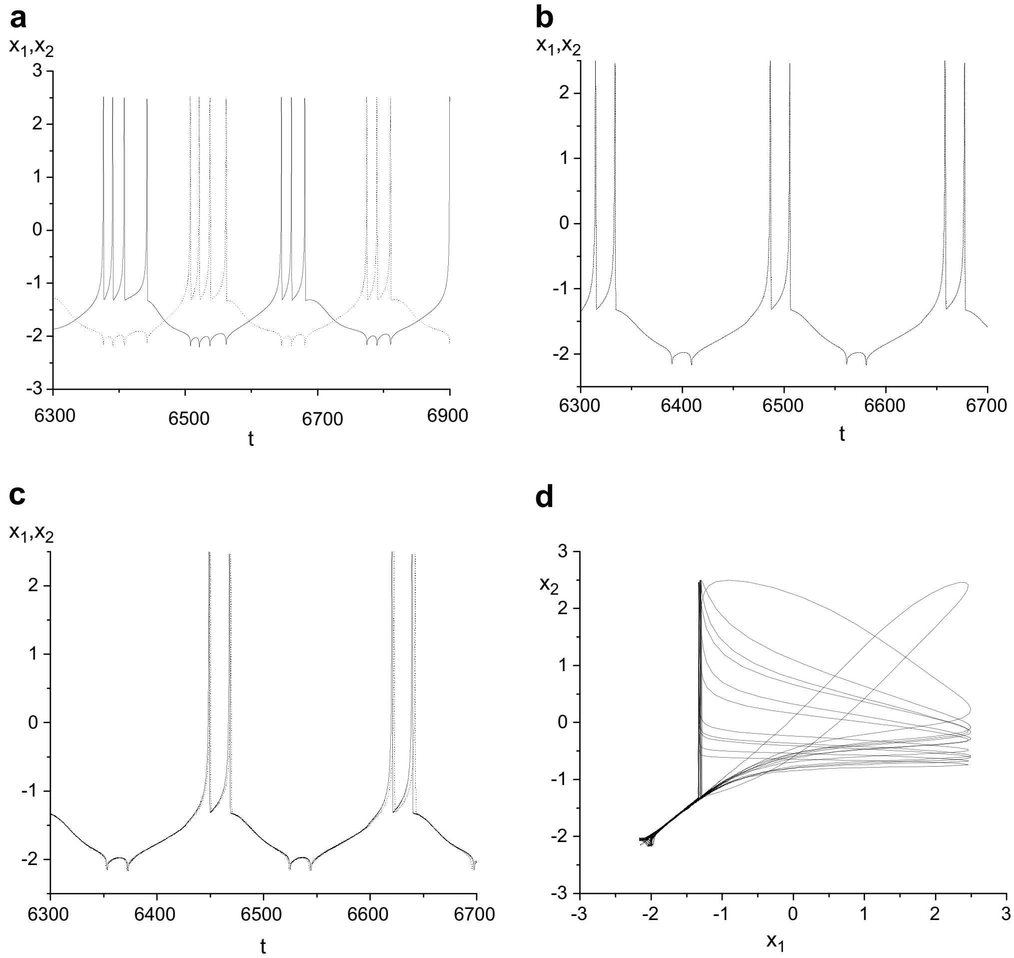

Fig. 3. Case β: (a) $c_1 = -0.8$, $c_2 = 0$; (b) $c_1 = 0$, $c_2 = -0.8$, $\tau = 75$, $D = 0$; (c) and (d) $c_1 = 0$, $c_2 = -0.8$, $\tau = 75$, $D = 0.001$.

of the stochastic process, the occurrence of bursts is still much more synchronous than when $\tau = 0$. Thus, there is a kind of synchronization induced by time-delay which is persistent under small noise. This is different from the previously discussed case of delay-facilitated exact synchronization of bursting, illustrated in Fig. 3, where very small noise is enough to completely undo the effects of time-delay.

5. Summary and discussion

We have studied the exact synchronization of bursting dynamics in a pair of realistic neurons. Hindmarsh–Rose neuron was used as the model of each of the bursting units, and we analyzed the coupling model corresponding to the electrical synapses. Two important aspects of the real systems have been included explicitly in the model: (a) Fluctuations of factors that could influence the state of each of the neurons was modelled by adding a stochastic term in the equation of the membrane potential; (b) transmission and synaptic delays are included in the form of the coupling terms. We have considered the coupling that represent a mixture with different strengths of instantaneous and delayed coupling. Thus, the mathematical model consisted of the set of stochastic delay-differential equations.

The possibility of stable exact synchronization was first analyzed analytically. We have shown that provided the instantaneous coupling constant is large enough and larger than the delayed one the exact synchronization will be stable with unit probability for any time-lag and small noise. This result represent a sufficient condition for the stable exact synchrony and cannot be used to actually predict realistic values of the coupling for which the synchronization occurs.

In our numerical calculations we have separately analyzed the synchronization that occurs among bursting induced by an external stimulus or by coupling between the neurons. We have concentrated on showing that the exact synchronization that might occur with weak instantaneous coupling and for properly chosen time-lags and the strength of the delayed coupling is unstable under small noise and variation of time-lags. On the other hand if the exact synchronization is achieved by strong instantaneous coupling then it is stable under variation of time-delay and only slightly perturbed by small noise. We should conclude that if the exact synchronization is to be observed in real neuronal systems than it is likely to involve strong coupling, rather then to relay on some finely tuned weak coupling with time-delays.

Explicitly included time-delay should be more important in models of neurons coupled by chemical synapses. Methods of Section 3 could be used to prove possibility of stochastically stable exact synchronization for some models of delayed chemical synapse, such as fast threshold modulation. We are currently pursuing numerical investigations of synchronization with similar models of chemical synapses. We have concentrated on the exact synchronization of bursting neurons. Other types of synchronization, i.e. synchronization of bursts without synchronization of spikes within a burst, are also important and behave differently with respect to time-delays and stochastic perturbations. It would also be interesting to study the relative importance of time-delayed and instantaneous coupling on the synchronization in more complicated networks of noisy bursting neurons.

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