Influence of noise on dynamics of coupled bursters

Nikola Burić,[1,*] Kristina Todorović,[2] and Nebojša Vasović[3]
[1]*Institute of Physics, University of Beograd, P.O. Box 68, 11080 Beograd-Zemun, Serbia*
[2]*Department of Physics and Mathematics, Faculty of Pharmacy, University of Belgrade, Vojvode Stepe 450, Belgrade, Serbia*
[3]*Department of Applied Mathematics, Faculty of Mining and Geology, P.O. Box 162, Belgrade, Serbia*
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The influence of white noise on the dynamics of a delayed electrically coupled pair of Hidmarsh-Rose bursting neurons is studied. In particular a simple method to predict the intensity of noise that can destabilize the quiescent state is proposed and compared with numerical computations. Furthermore, it is demonstrated that quite small noise completely destroys the exact synchronization of bursting dynamics, and a qualitative explanation of this effect is discussed.

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I. INTRODUCTION

Bursting is one of the three main regimes of neuronal membrane dynamics [1]. Its time pattern is distinguished from that of quiescent or spiking dynamics by the appearance of groups of spikes interspersed by periods of quiescent or subthreshold oscillatory behavior. It is expected that a burst of spikes is much more reliable for inducing responses in postsynaptic cells than a single spike, hence the importance of understanding its dynamical properties.

The bursting can occur as a reaction of a single neuron to proper external excitation, but it can also occur due to the synaptic coupling between pairs of neurons. Synaptic transmission is a process much more complicated and much slower than the propagation of spikes along an axon. Thus, in modeling the dynamics of synaptically coupled neurons one should either include the details of the synapses or resort to simple phenomenological models, which then need to include the time lag explicitly. It is well known that an explicit time lag of physically reasonable duration can have profound effects on the dynamics of coupled neurons. For example, an important effect, which has been recently demonstrated [2], is that the time lag facilitates exact synchronization among bursting electrically coupled neurons.

The response of real neurons to synaptic or external stimuli is always influenced by many processes that are commonly modeled by different types of noise. Thus, only the effects observed in models of neuronal dynamics which are stable under the influence of noise should be seriously considered as realistic.

In this paper we shall analyze the generation and synchronization of bursting in a delayed coupled pair of Hidmarsh-Rose (HR) neurons [3] influenced by white noise. The model is given by the following system of stochastic delay-differential equations (SDDEs):

$$dx_1 = [F_x(x_1,y_1,z_1) + c(x_1 - x_2\ (t-\tau)]dt + \sqrt{2D}\,dW,$$

$$dx_2 = [F_x(x_2,y_2,z_2) + c(x_2 - x_1\ (t-\tau)]dt + \sqrt{2D}\,dW,$$

$$dy_i = F_y(x_i,y_i,z_i)dt, \quad i = 1,2,$$

$$dz_i = F_z(x_i,y_i,z_i)dt, \quad i = 1,2, \tag{1}$$

where F_x, F_y, and F_z are the components of the HR fast-slow neuronal model [3],

$$F_x = y + 3x^2 - x^3 - z + I, \quad F_y = 1 - 5x^2 - y,$$

$$F_z = -rz + rS(x+1.6), \tag{2}$$

and the term $c(x_i(t) - x_j(t-\tau)$ represents delayed electrical coupling. We shall illustrate the results of our analysis for two sets of fixed typical values of the parameters $I=3.2$, $r=0.006$, $S=4$ and $I=0$, $r=0.0021$, $S=4$, with variable parameters c, τ, and D. The parameter D measures the intensity of the noise, and dW is the stochastic increment of the Wiener process, satisfying $E(dW)=0$, $dWdW=dt$, where $E(\cdots)$ denotes the expectation with respect to the process. Notice that the noise is assumed to affect the excitable variable x, which is interpreted as the membrane potential. Other choices of types of noise and its coupling to the neurons are also plausible, but the one in Eqs. (1) is the simplest.

We shall analyze the influence of noise in the following four cases of exactly synchronous dynamics that occur in the noiseless pair of delayed coupled HR neurons: (α) $I=I_0 \neq 0$ $\tau=0$, $c<0$, $|c|$ large; (β) $I=I_0\neq 0$, $\tau\neq 0$, $c<0$, $|c|$ small; (γ) $I=I_0\neq 0$, $\tau\neq 0$, $c>0$, $|c|$ small; and (δ) $I=0$, $\tau\neq 0$, $c>0$, $|c|$ sufficiently large. In cases α and β, analyzed in [2], the dynamics of each of the neurons is that of bursting even when they are exactly synchronous. In case γ the neurons behave as relaxation oscillators for the coupling and the time lag that imply exact synchronization. In case δ (analyzed in [4]) and for $0<c<c_0$ the neurons have only one attractor corresponding to the quiescent state. For $c>c_0$ and $\tau=0$ the bursting starts and the bursting periods of one of the neurons coincide with the quiescent phase of the other. The time lag in an interval around sufficiently large τ leads to exact synchronization. In what follows we shall study: (i) the influence of noise on the stability of the stationary state in case δ that represents the quiescent behavior and (ii) the stability to noise of the exact synchronization in the four cases. Here, the main conclusion will be that a small noise completely destroys the exact synchrony achieved by an appropriate time

*buric@phy.bg.ac.yu

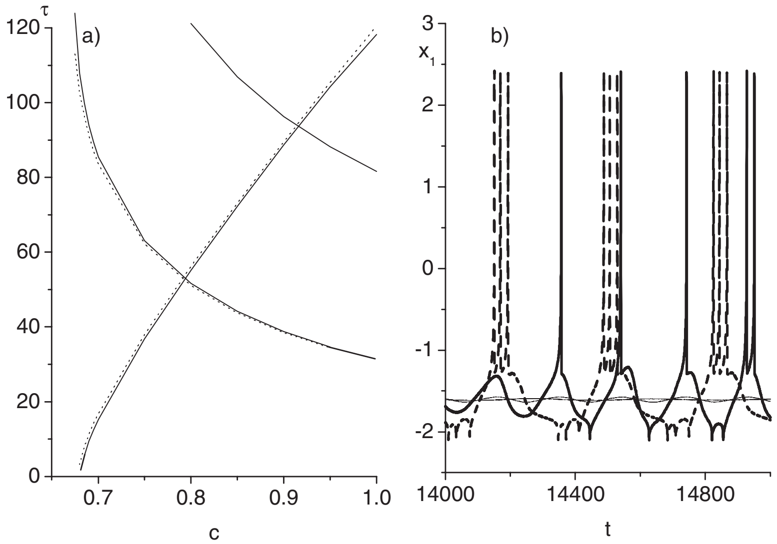

FIG. 1. (a) Hopf bifurcations curves $\tau(c)$ for the noiseless system (solid lines) and those predicted by $x_0 \to x_0 + D$ for $D=0.001$. (b) Sample time series of bursting $x_1(t)$ for $(c,\tau) = (0.7, 17.5)$ (thick solid line), (0.7,84) (thick dashed line) and quiescent $(c,\tau)=(0.7,18.7)$, (thin solid line) (0.7,82) (thin-dashed line) states. Other parameters are $D=0.001$ and $I=0$, $r=0.0021$, $S=4$.

delay with weak coupling (cases β and γ), and only slightly disturbs the exact synchrony that occurs with sufficiently strong coupling [with (case δ) or without (case α) the nonzero time lag].

Many properties of single or instantaneously coupled excitable systems with noise, like coherent or stochastic resonance, have been studied before. These studies have been collected in numerous reviews, for example, in [5]. Time-delayed feedback in a single noise neuron was also studied before, for example, in [6]. Instantaneously coupled noisy neurons have also been analyzed [7]. Bifurcations and synchronization in delayed coupled excitable neurons without noise have been studied for example in [8] (see the references therein) [9]. The stability of delay-differential systems with noise was studied analytically, for example, in the context of coupled realistic and formal neural networks. Liao and Mao [10] have initiated the study of stability in stochastic neural networks, and this was extended to stochastic neural networks with discrete time delays in Refs. [11,12]. However, the influence of noise on delayed coupled bursting neurons, in particular the influence on the important effects, such as the delay induced death of bursting or facilitation of bursting synchronization by delay, have not been analyzed before.

II. NOISE AND STABILITY OF THE QUIESCENT STATE

The parameter values $I=0$, $r=0.0021$, and $S=4$ imply that an isolated Hidmarsh-Rose neuron (2) has only one attractor: the stable stationary state at $(x_0,y_0,z_0)=(-1.60453, -11.8726, -0.01812)$. The noiseless system (1) for $D=0$ is characterized by the fact that the coupling destabilizes the stationary state for $c=c_0=0.674\,522$, $\tau=0$, and then slow oscillations of the z variable lead the system through the bursting behavior. The bifurcation at $c=c_0$ is the generalized Hopf bifurcation (Bautin bifurcation). Increasing the time lag from zero leads to a sequence of Hopf bifurcations, illustrated in Fig. 1(a) by thick curves. The thick curve with positive slope corresponds to the subcritical Hopf, and the thick curves with negative slope represent the supercritical Hopf bifurcations. Similarly to the case of coupled FitzHugh neurons [8,9], there is a region between the two lowest Hopf curves where the stationary state is stabilized by the appropriate nonzero time lag. We shall be interested in the effects of noise on the stability of the stationary state.

Mathematically correct definitions of various types of stochastic stability of the rest state for a system of SDEs are formulated in terms of the probabilities given by the stochastic process that is a solution of the SDEs [13]. However, our approach will be heuristic. We might expect that when the system is close to the Hopf bifurcation relatively small noise should be enough to push the stationary state from its small stability neighborhood. The minimal D that could destabilize the small fluctuations near the rest state and lead to large oscillations of z variable, with consequent bursting dynamics, can be roughly estimated as follows. The method consists in shifting the coordinates of the rest state in the standard linear stability analysis by an amount that is likely to occur in the time interval dt due to small noisy fluctuations—that is, by the distance equal to the intensity of the noise D. It is remarkable that such a crude ansatz gives estimates of the critical values of D that agree well with numerical calculations.

The stability of the stationary state of the noiseless system (1) does not depend on the values y_0 and z_0 but depends on x_0. The substitution $x_0 \to x_0 + D$ provides estimates of the critical D. Figure 1(a) represent the Hopf bifurcation curves $\tau(c)$ for x_0 corresponding to the noiseless system (solid lines) and with $x_0 \to x_0 + D$ (dotted curves) for fixed $D=0.001$. Figure 1(b) illustrates the numerical tests of the predictions given by the dotted curves in Fig. 1(a). Let us first observe that the domain of (c,τ) that corresponds to the stationary state stabilized by the time delay, the domain between dotted curves, is shrunk by noise, but still exists for quite large values of D. All sample time series in Fig. 1(b) correspond to (c,τ) values in between the solid lines—i.e., to the stability domain of the noiseless system. Since the value $D=0.001$ is quite small, the difference between the dotted and solid curves is almost undetectable on the scale of the figure. Nevertheless, the simple ansatz predicts that for (c,τ) values that are below the lower dotted and above the upper dotted curve

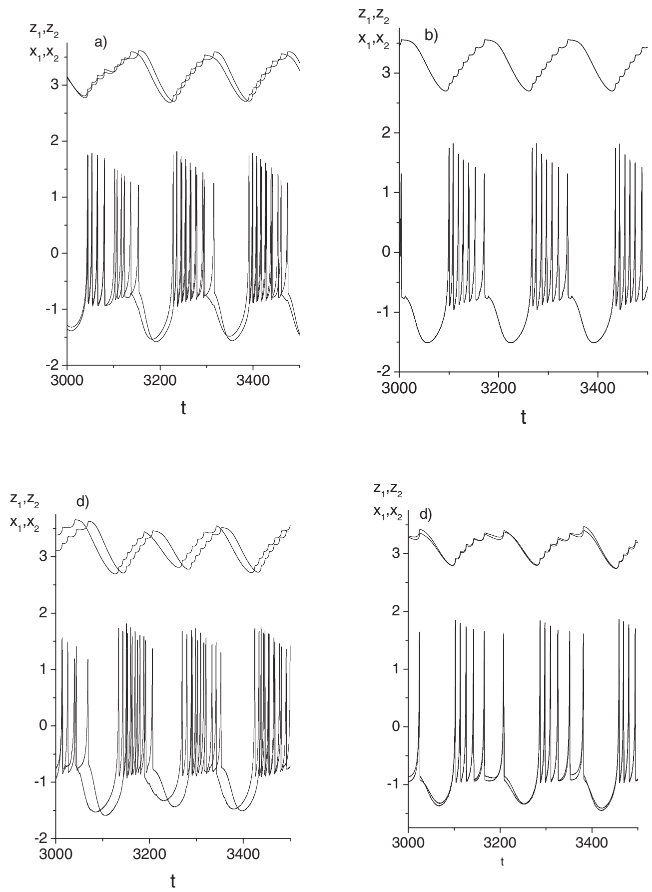

FIG. 2. The effect of a small noise in cases α and β. The parameters are I=3.2, r=0.006, S=4 and (a) c=−0.1, τ=0, D=0, (b) c=−0.1, τ=8, D=0 (like in [2]), (c) c=−0.1, τ=8, D=0.001, and (d) c=−0.45, τ=0, D=0.001. Shown are $z_1(t)$ and $x_1(t)$ (solid line) and $z_2(t)$ and $x_2(t)$ (dotted line).

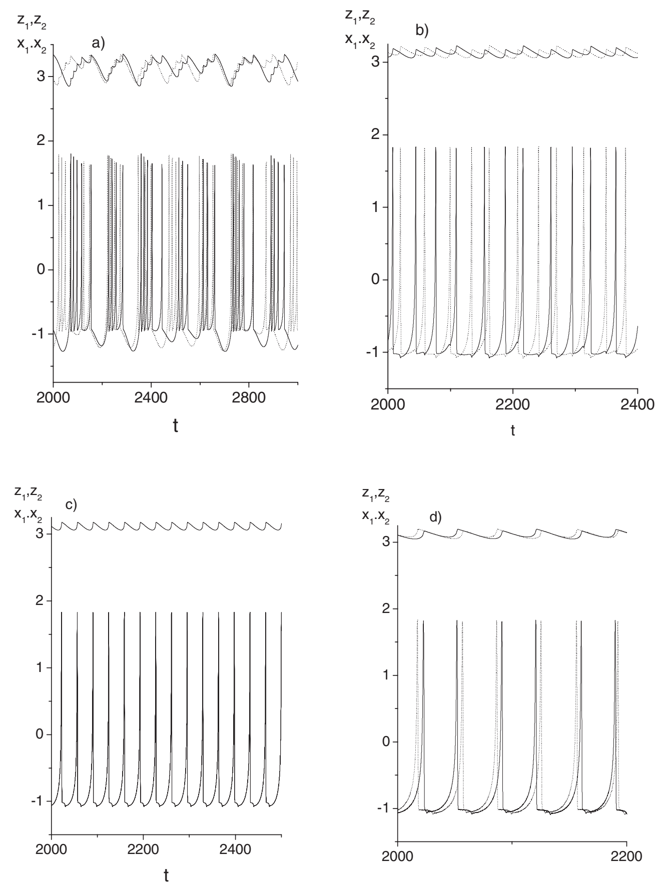

FIG. 3. The effect of a small noise in case γ. The parameters are I=3.2, r=0.006, S=4 and (a) c=0.0, τ=0, D=0, (b) c=0.1, τ=0, D=0, (c) c=0.1, τ=8, D=0.0, and (d) c=0.1, τ=8, D=0.001. Shown are $z_1(t)$ and $x_1(t)$ (solid line) and $z_2(t)$ and $x_2(t)$ (dotted line) in (a), (b), (c), and $(x_1(t), x_2(t))$ in (d).

in Fig. 1(a) the quiescent state should be unstable, illustrated in Fig. 1(b) where two of the sample time series represent stable bursting [thick lines in Fig. 1(b)] and stable [represented by thin lines in Fig. 1(b)] for (c, τ) values that are in between the dotted curves in Fig. 1(a).

III. NOISE AND EXACT SYNCHRONIZATION

The exact synchronization of a delayed coupled pair of noiseless HR neurons was studied in [2] for the case β and in [4] for the case δ. The main result of [2] and [4] is the observation of the potentially important fact that the time delay in a proper interval facilitates exact synchronization. However, we shall now demonstrate that quite small values of the noise destroy the exact synchrony achieved with the help of an appropriate time lag, contrary to the exact synchronization at sufficiently strong coupling. Consequently the facilitation of synchronization by time delay should be considered as an unstable effect, which is certainly much less preferable in realistic systems than exact synchronization with strong coupling (and or without the time delay).

We shall discuss the results of our numerical computations by commenting on the data presented in Figs. 2–4.

Cases α and β are illustrated in Fig. 2. Figures 2(a) and 2(b) illustrate exact synchronization for small negative c, achieved by a nonzero time lag, and Fig. 2(c) illustrates the unproportionally large effects of a quite small noise. 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. 2(c) is as asynchronous as that in Fig. 2(a). On the other hand, Fig. 2(d) illustrates the effect of noise on the exact synchrony due to strong coupling (no time delay). The effect is proportional to the intensity of the noise.

In Figs. 3(a)–3(d) we illustrate case γ—i.e., exact synchronization with weak positive coupling and an appropriate time delay between the HR bursters [Figs. 3(a)–3(c)] and the effects of small noise [Fig. 3(d)]. The exactly synchronized neurons display periodic spiking. The exact synchrony achieved by the time delay is completely destroyed by very small noise, but the time difference between the spiking times of the two neurons is smaller than in the nonsynchronized noiseless situation [Fig. 3(b)].

The effects of noise in case δ of bursting induced by coupling and the exact synchronization by the time delay are illustrated in Fig. 4. In the exactly synchronized situation the two neurons are most of the time in the quiescent state which

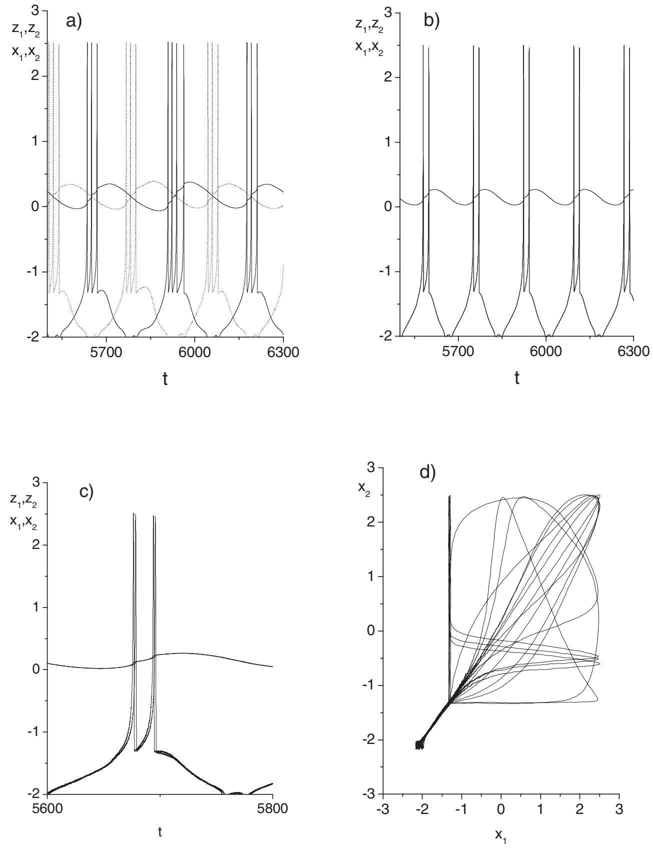

FIG. 4. The effect of a small noise in case δ. The parameters are $I=0$, $r=0.0021$, $S=4$ and (a) $c=0.8$, $\tau=0$, $D=0$, (b) $c=0.8$, $\tau=75$, $D=0$, and (c) and (d) $c=0.8$, $\tau=75$, $D=0.001$. Shown are $z_1(t)$ and $x_1(t)$ (solid line) and $z_2(t)$ and $x_2(t)$ (dotted line) in (a), (b), (c) and $(x_1(t),x_2(t))$ in (d).

is interrupted by short periods of bursts. The crucial effect of a small noise is to desynchronize the initiation of bursting periods and the spikes within the burst, but both neurons are still most of the time in the slightly fluctuating quiescent state. Nevertheless, a large part of the manifold of the exact synchronization is destabilized by the small noise [Fig. 4(d)].

A qualitative explanation of the destructive effect of noise on the exact synchrony is as follows. 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 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 a large difference in x_1 and x_2 variables.

The previous argument is based on the stochastic distribution of minima and maxima of the slowly oscillating function $z_i(t)$. Two-dimensional models of spiking neurons can be obtained by fixing z to different values. Consequently, and contrary to the bursting synchronization, in the case of spiking synchronization, small stochastic perturbations, in general, only slightly influence the type of synchronization that is present in the deterministic system. Even if the spiking in different neurons might start at slightly different times, like each of the bursting periods in the noisy bursters, the coupling soon leads to the type of synchronization that occurs in the noiseless case with only small fluctuations around the synchronization manifold.

In summary, we have studied the influence of white noise on the stability of the quiescent state and synchronization of bursting in a delayed coupled pair of Hidmarsh-Rose neurons. There is very little influence of noise on the stability of the quiescent state, which can be detected only when the system is near the bifurcations. In this domain, a simple ansatz provides relatively correct estimates of the critical noise intensity that can destabilize the stationary state. On the other hand, the noise has a devastating effect on the exact synchronization that occurs in the noiseless system due to proper time lags in the coupling. Already quite small noise completely destroys the effect of time delay on the exact synchronization. This suggests that facilitation by the time delay of the exact synchrony should not be expected in experiments with real bursting neurons.

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