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Dynamics of noisy FitzHugh–Nagumo neurons with delayed coupling

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Abstract

Results of an extensive numerical study of the influence of additive white noise on the dynamics of a pair of delayed coupled FitzHugh–Nagumo neurons are presented. An intuitively clear simple method is utilized to predict the critical intensities of the noise. In general, the qualitative properties of the noiseless dynamics are stable under the influence of the noise of a reasonable magnitude. However, there are regions of the coupling and time-lag parameters where the noise of a physically acceptable magnitude does cause qualitative changes of the dynamics. These regions are studied in detail.

1. Introduction

The primary qualitative property of a neuron is its excitable behavior. The interaction between the neurons is transmitted via synapses, and this mechanism can be conveniently modelled by a delayed diffusive coupling. In real neuronal systems, it is plausible to distinguish relatively strong coupling between selected neurons that determine the pathway of the impulse, and much weaker coupling of each of the selected neurons with many others. The influence of this weak coupling between a single neuron and many neurons in the background can be modelled by a small additive noise.

Thus, to model the dynamics of the set of neurons we shall use a set of delayed coupled convenient excitable systems with small additive noise acting on each unit. The excitable units will be modelled by a typical type II excitable system, the coupling will always be of the delayed diffusive type, and the initial impulse will be realized as a small displacement from the rest state of one of the neurons. We shall suppose that each of the neurons is perturbed by additive white noise with the same intensity.

In this paper, we shall report mainly the results of our analyses concerning the case of only two selected neurons, where each is modelled by the two dimensional FitzHugh–Nagumo system [1]. Thus the stochastic delay-differential equations of the model read

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$$\begin{aligned}
\mathrm{d}x_1 &= (-x_1^3 + (a+1)x_1^2 - ax_1 - y_1 + c(x_1 - x_2^\tau))\mathrm{d}t + \sqrt{2D}\mathrm{d}W,\\
\mathrm{d}y_1 &= (bx_1 - \gamma y_1)\mathrm{d}t,\\
\mathrm{d}x_2 &= (-x_2^3 + (a+1)x_2^2 - ax_2 - y_2 + c(x_2 - x_1^\tau))\mathrm{d}t + \sqrt{2D}\mathrm{d}W,\\
\mathrm{d}y_2 &= (bx_12 - \gamma y_2)\mathrm{d}t,
\end{aligned} \tag{1}$$

where $x^\tau_{1/2}(t) = x_{1/2}(t-\tau)$, τ is fixed but arbitrary time-lag, D is the intensity of the noise and $\mathrm{d}W$, formally written as $\mathrm{d}W = \xi(t)\mathrm{d}t$, is the stochastic increment $\mathrm{d}W$ of the Wiener process $\xi(t)$ for which

$$\begin{aligned}
&E(\xi) = 0\\
&E(\xi(t)\xi(t')) = \delta(t-t'),
\end{aligned} \tag{2}$$

where $E()$ denotes the mean with respect to the stochastic process. The increments satisfy

$$E(\mathrm{d}W) = 0, \qquad \mathrm{d}W\mathrm{d}W = \mathrm{d}t. \tag{3}$$

We shall consider that the noise is small if $D^2/2 < c$. Notice that the noise is assumed to affect the excitable variable x, that 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 (1) is the simplest. The particular form of the single FitzHugh–Nagumo unit with $D = 0$ does not admit periodic solutions for any values of the parameters. Furthermore we shall restrict our analysis to the range of the parameter values where each of the units for $D = 0$ exhibits excitability, with only one attractor in the form of a stable fixed point at the origin. For this to be the case, b and γ should be of the same order of magnitude and considerably smaller than a. Thus, oscillations might appear only due to the coupling between the excitable units or due to the noise.

We shall be interested in (a) the stability of the rest state of (1),and (b) in the properties of synchronization between the oscillatory dynamics, caused either by the coupling or by the noise.

Local bifurcations and synchronization in delayed coupled excitable systems of the two canonical types [2] in the excitable regime but without noise were analyzed in [3] following the work presented in [4] (where an extensive list of relevant references is given). This paper analyzes the influence of noise on the dynamical features of the noiseless systems presented in [3,4]. Many properties of single or instantaneously coupled excitable systems with noise, like the coherent or stochastic resonance, have been studied before. These studies have been collected in numerous reviews,-for example, in [5] (see also the articles in the special issue of Chaos, Solitons and Fractals [6]). Time-delayed feedback in a single noise neuron was also studied before, for example, in [7]. Instantaneously coupled noisy neurons have also been analyzed [8]. Stability of stationary solutions of ODE's perturbed by multiplicative stochastic perturbations has been studied for long time [9–11], using generalizations of the Lyapunov second method. Stability in systems with noise involving DDE was studied analytically, for example, in the context of coupled realistic and formal neural networks. Liao and Mao [12] have initiated the study of stability in stochastic neural networks, and this was extended to stochastic neural networks with discrete time-delays in Refs. [13,14]. Some analytical techniques relevant for delayed systems with noise have also been used in the study of coupled oscillator systems with delays and in noisy oscillators with delayed feedback [15,16]. However, influence of the additive noise on the important effects of the synaptic delays in the coupling, such as the death of oscillations or different types of synchronization, has not been analyzed before.

The paper is organized as follows. In the next section, we propose a simple anzac to analyze the stability of the rest state of delayed coupled noisy FitzHugh–Nagumo neurons. In Section 3, an approximate formula for the critical noise intensities is compared with numerical computations. In Section 4, the influence of noise on the properties of synchronization for the same system is studied. Finally, we present a summary and discussion of our conclusions.

2. Stability of the excitable behavior

We shall first analyze stability of the rest state of system (1). Mathematically correct definitions of various types of stochastic stability of the rest state for a system of SDE's are formulated in terms of the probabilities given by the stochastic process that is a solution of the SDE's [9–11]. However, our approach will be heuristic, and is based on the fact that the sample paths of the solution process of (1) can be clearly distinguished into two classes. The sample paths that are attracted into a small domain around the state $(x_1, x_2, y_1, y_2) = (0, 0, 0, 0)$ (see Fig. 1b) belong to the first class. The evolution on such paths represents small fluctuations around the rest state for most of the time. The other class of paths quickly approaches the attractor of the deterministic system which corresponds to the relaxation oscillations, and the only effect of the noise on such paths is a small stochastic perturbation of the relaxation oscillations (see Fig. 1b). We shall consider an initial state to be in the stability domain of the rest state if a large majority of the sample paths with

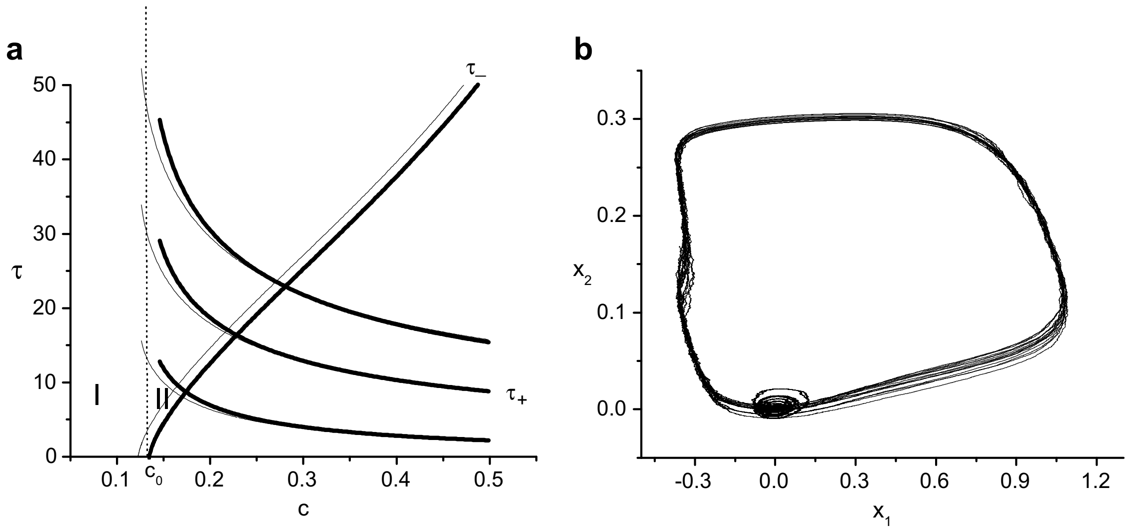

Fig. 1. (a) A representation of bifurcation curves of the rest state for system (1) with $a = 0.25$, $b = \gamma = 0.02$; $D = 0.01$. (b) Projections onto (x_1,y_1) plane of typical representatives of stable and unstable sample paths.

this initial state belong to the first class. The initial state for which most of the paths belong to the second class is considered unstable. Finally, we define the rest state to be unstable if all initial states are unstable in the above sense. Numerical evidence indicates that there is indeed a quite clear distinction between the parameter values which render an initial state stable or unstable, *i.e.*, the domain of the parameter values with a similar percentage of stable and unstable paths from an initial state is rather small, and we shall neglect it in the presentation of our results. We shall argue later that this way of describing the dynamics generated by (1) is more appropriate than, for example, presentation of the averages over many sample paths.

Relevant results for the system without the noise are given in [3,4]. We chose the values of the internal parameters which correspond to excitable behavior of noninteracting deterministic FitzHugh–Nagumo neuron. The rest state of the pair of delayed interacting deterministic neurons corresponds to coordinates $x_1 = x_2 = y_1 = y_2 = 0$, and can be stable or unstable depending on the values of the coupling parameter c and the time-lag τ. When the rest state is stable the whole system displays excitability in the sense that two following types of initial conditions could be distinguished. The rest state is surrounded by a quite small neighborhood which contains the initial conditions that immediately approach the rest state. On the other hand, a deviation from the rest state which is outside of this small domain can cause a large excursion through the state space before the system asymptotically returns to the rest state.

We might expect that relatively small noise should be enough to turn this excitable dynamics into oscillatory dynamics with superimposed small fluctuations. The mechanism of such bifurcation is intuitively clear. Small additive noise replaces the rest state by slightly fluctuating state. This fluctuations could be large enough to shift the state into the excitable domain whenever, or for a majority of times, it enters a small neighborhood of zero. Then the relaxation oscillations will continue with the help of the noisy perturbations. On the other hand, the noise could be so small that the state close to the rest state is never shifted into the excitability domain. This destabilization mechanism is similar to the one that occurs in a single noisy FitzHugh–Nagumo or other types of excitable systems [5]. Obviously, the timing of spikes will be a random variable, i.e., the noise-induced oscillations will have stochastically time dependent frequency, and will also depend on the particular realization of the stochastic process. A meaningful prediction of the critical D for fixed values of (c, τ) could be given only in the sense of the expectation over the stochastic process (1). Nevertheless, the previous intuitive argument suggests that a simple method can be used to obtain a rough estimate of the minimal D that could replace the fluctuating rest state by the fluctuating relaxation oscillations. The method consists in replacing the rest state $(x_{10}, y_{10}, x_{20}, y_{20}) = (0, 0, 0, 0)$ in the standard linear stability analysis by the state $(x_{10}, y_{10}, x_{20}, y_{20}) = (D, D, D, D)$, shifted from zero by the distance given by the intensity of the noise D. As we shall see, such a crude anzac gives estimates of the critical values D which agree remarkably well with numerical calculation.

Linear stability analyses of the rest state for the DDE's (1) without the noise was given in all the details in [3], and shall not be repeated here. The final results are the bifurcation curves in the (c, τ) plane for conveniently fixed but arbitrary values of the parameters a, b and γ, given by the following formulas:

$$\tan(\omega\tau^c) = \frac{\pm\omega(\gamma^2 + \omega^2 - b)}{\pm A\gamma^2 \pm A\omega^2 \mp b\gamma}, \tag{4}$$

where

$$\omega_\pm^2 = \left(-M \pm \sqrt{M^2 - 4N}\right)\Big/2. \tag{5}$$

The symbols M, N and A are expressed in terms of the parameters in (1) and in terms of the coordinates of the rest state $(x_{10}, y_{10}, x_{20}, y_{20})$. In the present case, we substitute $(x_{10}, y_{10}, x_{20}, y_{20}) = (D, D, D, D)$ resulting in

$$\begin{aligned} M &= A^2 + \gamma^2 - 2b - c^2, \\ N &= A^2\gamma^2 + b^2 - 2Ab\gamma - c^2\gamma^2, \\ A &= a - c - 2(1 + a)D + 3D^2. \end{aligned} \tag{6}$$

The thick curves shown in Fig. 1a represent pairs of values of (c, τ) which correspond to the Hopf bifurcation of the rest state given by (2)–(4) for $D = 0$. The type of the Hopf bifurcation is indicated by the subindex $\pm$, where $+$ indicates the supercritical and $-$ the subcritical bifurcation. Thus, upon passing the curves $\tau_{+,i}$ ($\tau_{-,i}$) in the direction of increasing τ, the dimension of the unstable manifold is increased (decreased) by 2. The thin curves shown in Fig. 1a represent the same bifurcation curves but for $D = 0.01$ in (4). By inspection of Fig. 1a, we see that the rest state is stable for $c < c_0$ and any τ (domain I), and in a small region bounded by the segments of the three curves $\tau_{1,+}$, $\tau_{1,-}$ (domain II) indicated in

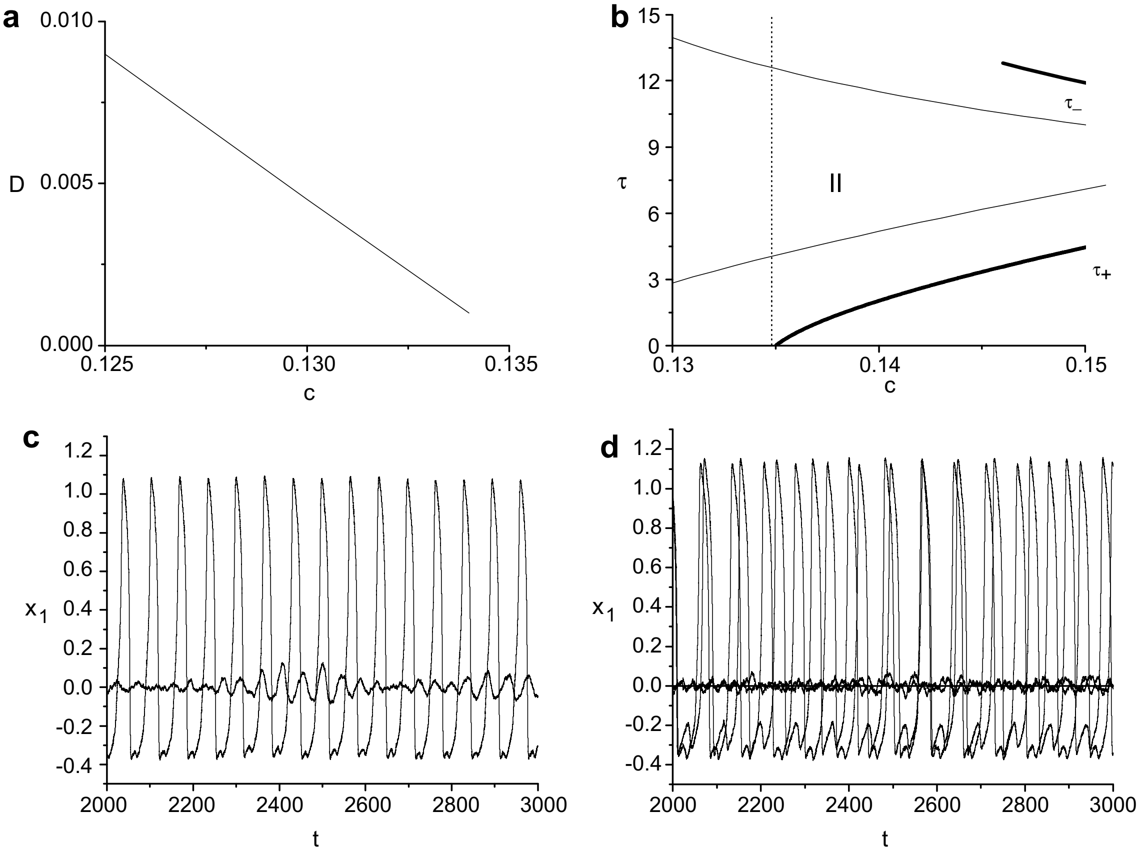

Fig. 2. An illustration of numerical tests of the simple approximate formulas for bifurcation values of parameters (c,D) (a and c) and (c, τ) (b and d). Times series in figures (c) and (d) illustrate $x_1(t)$ and should be compared with approximate predictions on figures (a) and (b), respectively. The parameters are $a = 0.25$, $b = \gamma = 0.02$ and in (a) and (c) are $\tau = 0$; $c = 0.125$ and the two paths in (c) are for $D = 0.0065$ (stable) and $D = 0.01$ (unstable). The parameters in (b) and (d) are $\tau = 0$; $c = 0.14$ and the two stable paths in (d) are for $\tau = 6.5$; $\tau = 10.5$ and two unstable for $\tau = 5$; $\tau = 12.5$.

the figure. In this domain there are two attractors, corresponding to the stable rest state and the stable large limit cycle [3,4]. The two attractors of the noise system for a small value of $D = 0.01$, i.e., the fluctuating rest state and the relaxation limit cycle, are illustrated in Fig. 1b.

Fig. 2a is relevant for the domain I, and gives the values of D such that at least one of the four eigenvalues of the deterministic form of (1) with $\tau = 0$ linearized at $(x_{10}, y_{10}, x_{20}, y_{20}) = (D, D, D, D)$ has positive real part. This represents the estimate of the critical values of the noise intensity D_c such that the initial conditions from any small neighborhood of the rest state end up on an attractor away from the rest state. The estimated values D_c are to be compared with numerical calculations.

3. Discussion and numerical tests of the approximate bifurcation curves

We have performed numerical calculations to check if a relatively small noise could introduce qualitative changes in the dynamics in a small neighborhood of the stable rest state of the deterministic system, and to test the predictions for D_c and τ_c for fixed D that are given by the simple anzac. Notice that the deterministic system in the domain I for sufficiently large τ could have an additional attractor besides the stable rest state. However, we shall first concentrate on the stability properties of the rest state only.

The results are illustrated in Fig. 2. Fig. 2c and d represents the time series $x_1(t)$ generated by representative sample paths of the stochastic process (1), for various values of the parameters (c, τ, D) close to the bifurcation curves predicted

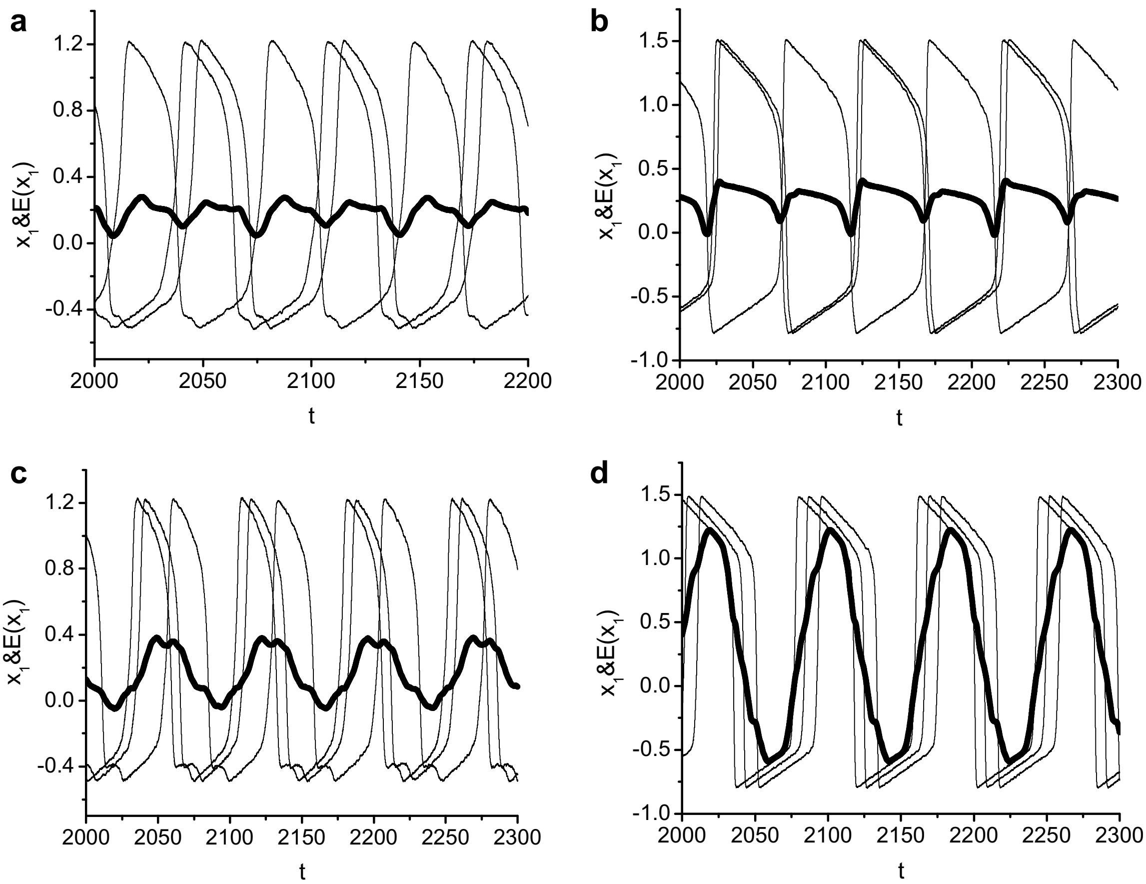

Fig. 3. An illustration of the effects of averaging as discussed in the main text, for $a = 0.25$, $b = \gamma = 0.02$; (a and b) $c = 0.2(a)$; $c = 0.4(b)$, $\tau = 0$, $D = 0.01$ and (c and d) $c = 0.2(c)$; $c = 0.4(d)$, $\tau = 40$, $D = 0.01$. Segment of $x_1(t)$ for three typical sample paths is illustrated by thin and the mean values over only 50 sample paths by the thick curves.

by the simple anzac. The average behaviour of the system for fixed (c, τ, D) and fixed initial conditions could be obtained by averaging over many realizations, but the qualitative features of the dynamics are more clearly illustrated with a typical realization. In fact, distribution of the random spiking times is usually such that the random spikes can occur at any time in between two successive spiking of the deterministic system. In this case an average over many sample paths has dynamical properties which are different in important features from those of each of the sample paths. This is illustrated in Fig. 3, where we have plotted segments of three typical sample paths and the average over only 50 sample paths, for two values of the coupling and time-lags. The same conclusions, concerning the relation between the qualitative properties of the sample paths and of the average, have been obtained for all other values of the parameters c, τ and for relevant values of the noise intensity D.

In Fig. 2a and c, we concentrate on the area in the (c, τ) plane, where $0 < c < c_0$ and $0 \leqslant \tau < \infty$. For small or zero τ the deterministic system is excitable with the stable rest state. Relatively small additive noise is only manifested by corresponding small fluctuations in a small neighborhood of the rest state. Such a fluctuating rest state is still considered as stable. However, relatively large noise destabilizes the rest state. An orbit from an arbitrary initial condition then ends up on a noisy attractor, which resembles the attractor of a relaxation oscillator with added fluctuations (Fig. 1b). The size of noise, characterized by the parameter D, that is needed to produce this qualitative change depends on the coupling and is quite correctly estimated by the values given in Fig. 2a which have been obtained using the simple anzac. The critical D_c decreases as c approaches c_0. Let us point out that for c much smaller than c_0, combined effect of noise and sufficiently large time-lag enhances the oscillatory behavior. On the other hand, for c close to c_0 but still $c < c_0$

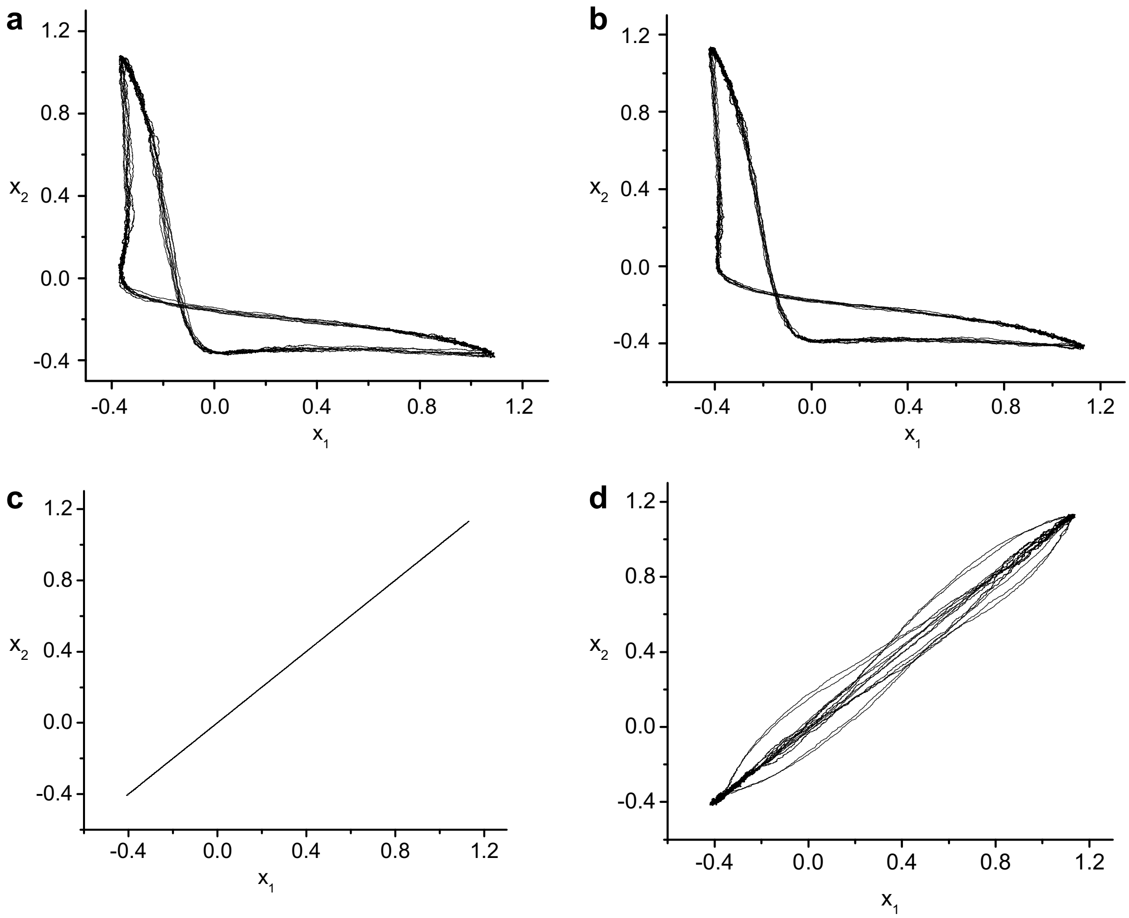

Fig. 4. An illustration of the effects of noise on out-of-phase synchronization (a and b) and the exact synchronization (c and d). Representative sample paths are illustrated by projections on (x_1,x_2) for parameters (a) $c = 0.125$; $D = 0.01$; $\tau = 0$; (b) $c = 0.15$; $D = 0.01$; $\tau = 0$; (c) $c = 0.15$; $D = 0.0$; $\tau = 35$ and (d) $c = 0.15$; $D = 0.01$; $\tau = 35$.

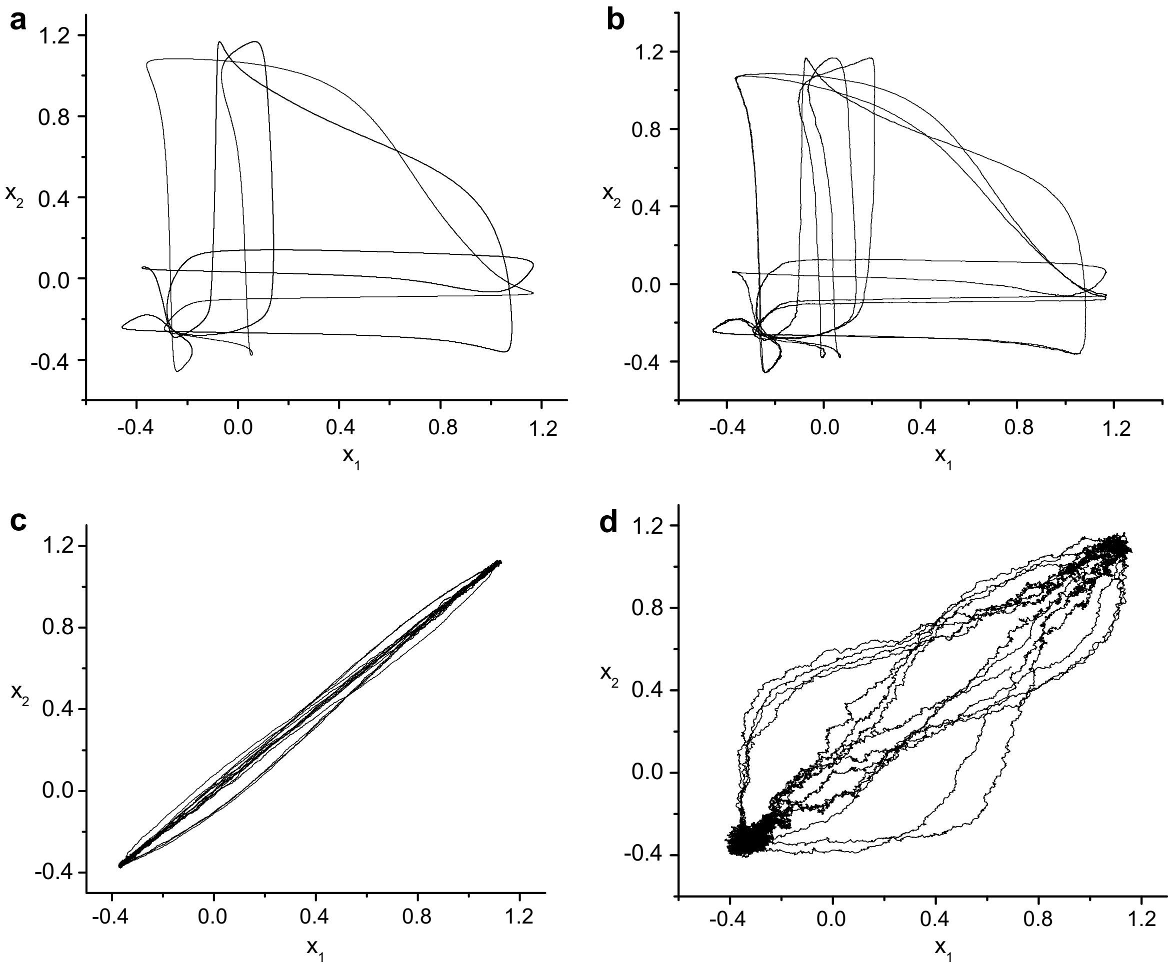

Fig. 5. The effects of noise on the complicated type of synchronization illustrated in (a) for $D = 0$, $c = 0.14$; $t = 40$. Small noise $D = 0.001$ (b) implies small perturbations, but the larger noise $D = 0.005$ (c) implies sample paths which are approximately synchronous. The effect of still larger noise $D = 0.14$ is shown in (d). Other parameters are as always $a = 0.25$, $b = \gamma = 0.02$.

nonzero time delay can stabilize the rest state, which is unstable for given values of c and D. This is an important effect, which occurs also for (c, τ) in the domain II, as is discussed in the next paragraph.

Let us now discuss the stability of the rest state for parameters in the domain II, illustrated in Fig. 2b and d. Below the curve $\tau_{-,1}$ and for $c > c_0$ the rest state of the deterministic system is unstable. Time-delay $\tau \in (\tau_{-,1}(c), \tau_{+,1}(c))$ stabilizes the rest state for $c > c_0$ and c smaller than the value corresponding to the intersection of the bifurcation curves $\tau_{-,1}(c)$ and $\tau_{+,1}(c)$. In this domain, besides the stable rest state the deterministic system has yet another attractor corresponding to relaxation oscillations. The major qualitative effect on the stability of the rest state of the additive noise in this domain II of the parameters (c, τ) is to shrink the domain along the τ axis and to extend it to the values of c slightly smaller than c_0. In other words, the rest state, which is unstable either due to the coupling $c > c_0$ or due to noise for c slightly smaller than c_0, is stabilized by the nonzero time-delay with τ in the domain that depends on c and on D. Thus, convenient time-lag suppresses the instability of the rest state due to the noise or the coupling. The predictions given by formulas (2)–(4) excellently agree with the numerical calculations. This is illustrated in Fig. 2d, which represent single typical realizations for fixed $c = 0.14$, the noise parameter $D = 0.01$, and the few values of the time-lag τ close to the bifurcation points that bound the domain II. As the intensity of the noise D is increased the domain of the time-delay induced stability shrinks to nothing.

For the values of the coupling c larger than the one that corresponds to the intersection of the bifurcation curves $\tau_{-,1}(c)$ and $\tau_{+,1}(c)$ the rest state is unstable for any value of the time-lag and zero or nonzero noise. There is no interesting effects due to the noise as far as the dynamics in a small neighborhood of the rest state is considered.

4. Stability of synchronization

Synchronization of the oscillations in a chain of deterministic delayed coupled FitzHugh–Nagumo systems was studied in detail for arbitrary number of units in Ref. [3]. In the case of two deterministic neurons the properties of synchronization can be summarized as follows. For $c < c_0$ and sufficiently large τ, there is a stable limit cycle which exists besides the stable rest state. The oscillations of the two neurons on the limit cycle are coherent but asynchronous, and this type of synchronization persists for all larger τ. For $c > c_0$ oscillations of the two neurons are also always coherent but could be asynchronous, like they are for small τ, or exactly synchronous for some intermediate intervals of τ. There are also regions in the parameter (c, τ) plane where there are two types of attractors with oscillatory dynamics and different types of synchronization. On one of them, the oscillations are exactly synchronous and on the other the oscillations are coherent but asynchronous. The first one attracts the initial conditions that are close to the unstable rest state, and the other attracts the rest of the state space. Besides these domains, there is also domain II which was already mentioned in connection with the stability of the rest state. In this parameter domain the stable rest state is one attractor and the other corresponds to coherent asynchronous oscillations of the two neurons.

The influence of the additive noise on the typical cases of synchronization is illustrated in Figs. 4 and 5. The general conclusion is as follows. If the deterministic system possesses only one attractor, be it the one with exactly synchronous or the one with the asynchronous oscillations, the additive noise does not introduce any qualitative changes. Fluctuations around the synchronization manifold are proportional to the intensity of the noise D. This is illustrated in Fig. 4a and b for the case of coherent asynchronous oscillations and in Fig. 4c and d for the exactly synchronous case.

Let us now describe some situations that occur in relatively small domains of the parameters (c, τ) plane. For (c, τ) parameters such that with no noise there are two attractors, then sufficient, but still relatively small, noise destroys the attractor which corresponds to the exactly synchronous dynamics. Then, all initial conditions are attracted towards the attractor that corresponds to the asynchronous dynamics. Thus, if the asynchronous and synchronous oscillations coexist in the deterministic system for some (c, τ) domain, the asynchronous oscillations are in general more stable with respect to the noise perturbations. However, somewhat opposite situation also occurs, as is illustrated in Fig. 5. For the illustrated values of the parameters (c, τ) the deterministic system shows a quite complicated type of synchronization (Fig. 5a). Small noise just slightly perturbs the complicated attractor (Fig. 5b), but larger noise (Fig. 5c and d) forces the two neurons to oscillate in synchrony with fluctuations proportional to the noise intensity, for any initial conditions.

5. Summary and discussion

We have studied the influence of noise on the stability of the rest state and the synchronization properties of delayed coupled excitable systems. The excitable units are modelled by the FitzHugh–Nagumo equations, which provide a typical representative of the type II excitable systems. The studied model includes two important features of real coupled neurons, that is the synaptic delay and the influence of many neurons that are only very weakly coupled to considered neurons, and could be treated as a noisy background.

Stability of the rest state is analyzed first. Sufficient, but still small noise can turn fluctuating rest state into relaxation oscillations with superimposed fluctuations. Very simple, although intuitively justified, idea is utilized to modify the standard linear stability analyses of stationary solutions for the deterministic delay–differential system, to provide us with predictions of the critical values of the noise intensity. The predictions remarkably agree with the numerical calculations. It should be remarked that the domain of delay induced stability exists for quite significant noise intensities. Again the relevant noise intensities and time-lags are correctly predicted by the simple method.

The influence of noise on the properties of synchronization, in the general case when there is only one attractor, is rather trivial. If the attractor of the deterministic system supports exactly synchronous oscillations or some form of coherent but asynchronous dynamics the noise does not change the qualitative properties of the synchronization. The only effect is addition of fluctuations proportional to the noise intensity. However, it is interesting to observe that for some values of the parameters, increasing the noise intensity results in the transition from stochastic asynchronous oscillations to something that looks more like strongly perturbed synchronous dynamics. For exceptional domains of the (c, τ) parameters both the stable exactly synchronous and the stable asynchronous oscillations are possible in the deterministic system. Then, quite a small noise destroys the attractor with the synchronous dynamics, and all initial states are attracted to the fluctuating asynchronous oscillations.

We have analyzed the effects of noise added to a typical type II excitable systems coupled by time-delayed interaction. The influence of the same type of noise on the type I delayed coupled excitable systems could be different and should be studied. Also coloured noise is justified and could induce quite different effects from the case of the additive white noise that was studied here.

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