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Influence of Coupling Delay on Noise Induced Coherent Oscillations in Excitable Systems

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Abstract Influence of small time-delays in coupling between noisy excitable systems on the coherence resonance and self-induced stochastic resonance is studied. Parameters of delayed coupled deterministic excitable units are chosen such that the system has only one attractor, namely the stationary state, for any value of the coupling and the time-lag. Addition of white noise induces qualitatively different types of coherent oscillations, and we analyzed the influence of coupling time-delay on the properties of these coherent oscillations. The main conclusion is that time-lag $\tau \geq 1$, but still smaller than the refractory period, and sufficiently strong coupling drastically change signal to noise ratio in the quantitative and qualitative way. An interval of noise values implies quite large signal to noise ratio and different types of noise induced coherence are greatly enhanced. We also observed coincident spiking for small noise intensity and time-lag proportional to the inter-spike interval of the coherent spike trains. On the other hand, time-lags $\tau < 1$ and/or weak coupling induce negligible changes in the properties of the stochastic coherence.

Keywords Neurons · Delay · Noise

1 Introduction

Excitability is a common property of many physical and biological systems. Although there is no unique definition [1] the intuitive meaning is clear: A small perturbation from the

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single stable stationary state can result in a large and long lasting excursion away from the stationary state before the system is returned back asymptotically to equilibrium. Further more, as an external parameter is changed, the global attractor in the form of the stationary point bifurcates into a stable periodic orbit, and the excitability is replaced by the oscillatory dynamics.

Typical example of excitable behavior is provided by the dynamics of neurons. However, realistic models of coupled neurons, must include the following two phenomena: (a) influence of different types of noise and (b) different time scales of the creation of impulses on one hand and their transmission between neurons on the other. It is well known that neurons *in vivo* function under influences of many sources of noise [2]. It is also well known that the noise of an appropriate small intensity can change the systems dynamics by turning the quiescent state of the neuron into the state of periodic firing [3]. There are different types of noise induced coherent oscillations [4, 5] that could occur in examples of excitable systems without [6] or with time-delay [7, 8], as will be discussed later. Description of interactions between neurons should include the details of the electrochemical processes in real synapses which occur on much slower time scale then the occurrence of an impulse and its transport along axons [9]. Alternatively, the transport of information between neurons can be phenomenologically described by time-delayed inter-neuronal interaction. It is well known that, depending on the parameters the time-delay can, but need not, induce drastic qualitative changes on the evolution of coupled deterministic excitable systems (please see for example [10–15]). However, a system of delay-differential equations is infinite dimensional with initial states represented by a vector functions on the interval $(-\tau, 0)$. Stability of stochastic delay-differential equations has been studied by mathematicians [16, 17]. Due to the time-delay the generated stochastic process is not Markovian so that the well known techniques, like the equivalent Focker-Plank equation, are not applicable. Nevertheless, there are some analytical methods, like generalization of the Lyapunov functional on the problem of stochastic stability. Approximations by stochastic differential equations without time-delay, by treating the time-delay as a small perturbation, lead to the replacement of the non-Markovian evolution with the Markovian and in some cases analytical treatment of the resulting Fokker-Plank equation can provide useful information [18]. However, even the stationary solution of the Fokker-Planck equation for a single stochastic FitzHugh-Nagumo neuron is known only for special values of the parameters. There is no applicable analytic treatment of the second order statistics of coupled stochastic FitzHugh-Nagumo systems (with or without delay) which is needed for the description of noise induced coherence [3].

Influence of noise on time-delay induced bifurcations and properties of synchronization have been analyzed elsewhere, for example in [19–22]. On the other hand the influence of coupling delay on different types of coherent oscillations that have been induced solely by the noise has been studied much less [23–25]. Noise induced resonant jumping between different attractors of systems with time-delayed feedback has been studied in [26, 27]. Such an analyzes would supply information complementary to the research on the effects of noise on the properties of oscillations and synchrony introduced by sufficient time-lag in the delayed coupling. It is our goal in this paper to study the effects of time-delay in the coupling between two excitable units on different types of noise induced coherent oscillations in each of the units.

The structure of the paper is as follows. In the next section we present the model of two FitzHugh-Nagumo excitable systems with noise perturbations and coupled by delayed electrical synapses. We restrict the parameter values to such domain that the deterministic system has the stable stationary state as the only attractor for any value of the time-delay. Both units are perturbed by noise which can induce different types of coherent oscillations. In Sect. 3

we present and discuss the results of our numerical computations. We have analyzed effects of time delay on coherence in the case that both units display the same type of noise induced coherent oscillations and the situation when the units display different types of oscillations. In each case we study the effects of time-delay on coherence properties of both single units and coincidence of spiking between the units. Finally, in Sect. 4, we summarize our results and propose some future projects.

2 The Model

Excitable behavior of a single neuron could be of two qualitatively different types [1]. They are distinguished phenomenologically by different properties of the frequencies and the amplitudes of the oscillatory dynamics in each of the two types, and the corresponding qualitative mathematical models are characterized by different bifurcation mechanisms. In this paper we shall consider typical type II excitable systems, as modeled by the FitzHugh-Nagumo differential equation [1], where the excitable behavior bifurcates into the oscillatory regime via the Hopf bifurcation. Each of the excitable neurons in the model is subjected to white noise that could appear in the model equations in two qualitatively different ways. Thus each neuron is described by the following stochastic differential equations:

$$\begin{aligned} \epsilon dx &= f(x, y) = (x - x^3/3 - y)dt + \sqrt{\epsilon}\sqrt{2D_1}dW_1 \\ dy &= g(x, y) = (x + a)dt + \sqrt{2D_2}dW_2, \end{aligned} \tag{1}$$

where $dW_{x,y}$ are independent increment of normalized Winer processes, that is $E(dW_i) = 0$, $E(dW_i dW_j) = \delta_{ij}$, $i, j = 1, 2$ and $E(\ldots)$ denotes expectation with respect to the stochastic process. The small parameter ϵ, which is in our paper fixed as $\epsilon = 10^{-2}$, takes care of the different time scales in the dynamics of the excitatory variable x (membrane potential) and the recovery variable y. The parameter a is the bifurcation parameter. For $|a| > 1$ the deterministic system (1) is excitable and for $|a| < 1$ the stationary state is unstable and there exists a stable limit cycle. In this paper a is fixed to $a = 1.05$. Membrane potential during an impulse in a real neuron varies between approximately -80 mV and 20 mV and the refractory period is roughly 1 to 2 ms. This values can be used to rescale the variable x and the time t in (1) if a comparison with trains of spikes from a real specific neuron are attempted. However, the model is usually used for qualitative studies of the type II excitability rather then for simulations of real neuronal activity.

There are many different sources of noise in real neurons. Some are due to random synaptic inputs from other neurons, random switching of ion channels and stochastic release of neurotransmitters in synapses. In (1) these random processes are modeled by the additive white noise terms in the first and the second equation. The two noise terms can produces series of spikes in the x variable which for certain values of the parameters D_1 or D_2 occur regularly so that the dynamics appears simply periodic i.e. coherent with quite well defined frequency. However the coherent oscillations induced by $D_1 = 0$, $D_2 \neq 0$ are qualitatively different from those that occur due to $D_1 \neq 0$, $D_2 = 0$. The first case, i.e. $D_1 = 0$, $D_2 \neq 0$ has been extensively studied, since it was reported in [28]. The effect is traditionally called coherence resonance [3], but we shall use the term stochastic coherence (SC) [29] in order to emphasize the noisy origin of the coherent oscillations. SC occurs only when the parameter a is close to its bifurcation value, the properties of the ensuing oscillation resemble the Hopf limit cycle of the deterministic system, and the properties of SC follow from this fact. The oscillations in the other case, $D_1 \neq 0$, $D_2 = 0$ are induced by quite different mechanism from that of the SC. It has been studied in details for example in [6], where it has been called self-induced stochastic resonance (SISR). The main properties of SISR (and the name) follow from the fact that the system (1) asymptotically resembles a particle in a double well potential [6], and thus the coherent oscillations resemble the well known effect of the stochastic resonance [4, 5]. In particular SISR happens even when a is far from the bifurcation value, and the resulting stochastic limit cycle does not resemble anything that could occur in the deterministic system. Of course, models with colored and parametric or multiplicative noise could also be justified [30]. However, our goal is to study the qualitative influence of time-delay on the SC and SISR which are induced by the two types of noise as in (1).

We shall study a pair of excitable FHN neurons (1) coupled by the electrical synapses. This type of synapse is modeled by delayed diffusive coupling between the membrane potentials of the coupled neurons. The model equations are as follows:

$$\begin{aligned} \epsilon dx_i &= f(x_i, y_i) + c(x_j(t-\tau) - x_i)dt \\ dy_i &= g(x_i, y_i), \quad i, j = 1, 2 \end{aligned} \tag{2}$$

where $f(x_i, y_i)$ and $g(x_i, y_i)$ are given by (1). The coupling constant c in this paper always assumes positive values, which ensures that the system (2) with $a = 1.05$ and for D_1, D_2 all equal to zero, has the stable stationary state as the only attractor *for any value of the time-lag* τ. Thus, possible oscillatory behavior of (2) can occur only because of the noise, and not because of strong coupling or time-delay. However, as we shall see, once the noise has produced spike trains that look coherent, relatively small time delay of the order of the refractory period and with sufficiently strong coupling can induce important qualitative changes in the SC and SISR as well as in the properties of synchronization between the two units.

3 Numerical Results

Each of the isolated noisy FHN neurons can display a train of spikes due to the noise even when the only attractor of the deterministic system is the stable stationary solution. Time distribution of the spikes can be regular with almost constant inter-spike interval. Occurrence of coherent series of spikes for particular values of the noise intensity is the common manifestation of both SC and SISR. However, the two cases occur via quite different mechanisms and have different properties, like dependence of the inter-spike period and on the noise intensity. Mechanisms of SC and SISR, and their properties, have been compared in [6]. Coupling between the neurons which are in the state of SC or SISR could preserve the coherence of each of the units and furthermore lead to synchronization of noise induced oscillations. This effects have been studied in the case of instantaneous coupling (no time-delay) for example in [31] for the case of equal units, and in [29] for the case of one unit in the state of SC and the other in the state of SISR. In this section we illustrate the main effects of the time-delay in the coupling on the properties of SC and SISR, for both units either in the SC or in the SISR state or when one unit displays SC and the other SISR.

The coherence of noise induced series of spikes in each of the neurons is commonly characterized by a kind of signal to noise ratio defined by:

$$S = \frac{\overline{T_k}}{[\mathrm{Var}(T_k)]^{1/2}} \tag{3}$$

where $T_k = t_k - t_{k-1}$ is the k-th inter-spike time interval and the overline, like in $\overline{T}_k$, denotes time averaging. Large S corresponds to high coherence of the noise induced spike trains.

There are different types of synchronization between the two coherently spiking neurons that could be of interest. For example, the strongest kind is the exact synchronization, i.e. $x_1(t) = x_2(t)$ for all $t > t_0$, and another commonly studied is the synchronization between the phases of the two oscillators. We shall analyze the kind of synchronization such that each spike of one of the neurons occurs within the duration of some spike of the other neuron. This notion of synchrony is motivated by neurological considerations [32], and is quantified by the so called coincidence function (CF). This is defined as the time average of the ratio between the number of spikes of one of the neurons, which are coincident with some of the spikes of the other neuron, and the average number of spikes per neuron. Two spikes are considered coincident whenever the sum of $x_1(t) + x_2(t)$ is larger then some threshold, say the hight of spikes $\max\{x_i\}$. This type of synchrony does not assume coherent spiking and is weaker than either exact or phase synchronization.

In our numerical integration we have used the Runge-Kutta 4-th order routine for the deterministic part of (2) and the Euler method for the stochastic part. Many sample paths for each value of the variable parameters $D_{1,2}$ and τ have been calculated. Results are compared with examples of other published work [29] and with computations performed using ready made programs for solving SDDE's available within the XPP package [33]. Values of S and C that are presented in what follows represent values that have been obtained with single typical sample paths. The sample paths were always sufficiently long so that the time average in (3) and the value of S did not change (on the scale of the figures) by increasing the length of the paths.

Results of our numerical calculations are illustrated in Figs. 1, 2, 3 and 4, where Fig. 1 corresponds to two SC and Fig. 2 to two SISR neurons, and Figs. 3 and 4 to the cases of nonequal units. We fix the noise intensity of one of the neurons, say D_2 to the maximal coherence of SC type (Fig. 1) or D_1 to the maximal coherence of SISR type (Fig. 2) and study the dependence of firing coherence of both neurons and coincidences on the noise intensity D_1 or D_2 of the adjustable unit and on the time-lag τ. We consider only relatively small time-lags up to the refractory period which is about $\tau \leq 1.3$. Coherence of noise induced spiking is not qualitatively affected by weak coupling with arbitrary time-delay. However, stronger coupling introduces significant modifications which also very much depend on the time-lag as is illustrated in Figs. 1, 2, 3 and 4.

In Fig. 1a we show typical effects of small time-lag, illustrated with $\tau = 0.7$, on functions $S_1(\log_{10} D_2)$ and $S_2(\log_{10} D_2)$, when both neurons are of the SC type and the noise intensity of one of them is held fixed at the SC maximum. Other values of the time-lag less then $\tau < 1$ cause similar small modifications of the dependencies $S_1(\log_{10} D_2)$ and $S_2(\log_{10} D_2)$. However, large influence of the time-delay on $S_1(\log_{10} D_2)$ and $S_2(\log_{10} D_2)$ is demonstrated for all $\tau \geq 1$, as is illustrated in Fig. 1b, c for $\tau = 1$ and $\tau = 1.3$ respectively. The curves $S_1(\log_{10} D_2)$ and $S_2(\log_{10} D_2)$ with $\tau \geq 1$ are qualitatively and quantitatively different from those with $\tau < 1$. Let us stress that deterministic systems with delayed coupling of the same coupling strength $c = 0.1$ show no bifurcation or other qualitative change for any $\tau \geq 0$. Thus, qualitative change in the properties of noise induced spiking coherence achieved with $\tau \geq 1$ should be attributed to the simultaneous action of noise and time-delay.

Figures 2a, b, c illustrate the same effects in the case when the two neurons are of the SISR type with fixed noise intensity in one of them. The situation is qualitatively similar to the previous case: small $\tau < 1$ introduces only small quantitative changes, but $\tau \geq 1$ changes the curves $S_1(\log_{10} D_1)$ and $S_2(\log_{10} D_1)$ drastically. Observe that the influence of time-delay for $\tau = 1$ in the SC-SC case is quite different from the SISR-SISR case.

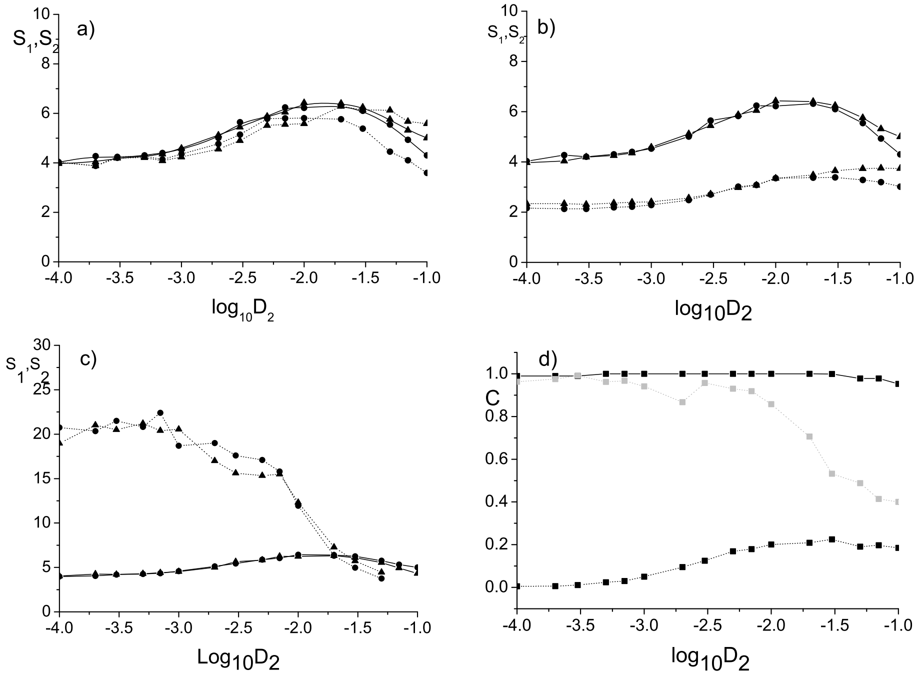

Fig. 1 Illustrates coherence (**a**, **b**, **c**) and spiking coincidence (**d**) in the SC-SC case. D_2 of the second (SC) neuron is fixed to $D_2 = 0.01$. D_2 of the first (SC) neuron, shown on the x axes as $\text{Log}_{10}(D_2)$, is adjustable. S_1 (*circles*) and S_2 (*triangles*) for $\tau = 0$ (**a**, **b**, **c** *full line*) and $\tau = 0.7$ (**a**, *dotted*) $\tau = 1$ (**b**, *dotted*) and $\tau = 1.3$ (**c**, *dotted*) are shown. In (**d**) coincidence functions C for $\tau = 0$ (*black full*), $\tau = 1$ (*black dotted*) and $\tau = 2.7$ (*gray dotted*) are shown. Calculated values of $S_{1,2}$ and C are indicated by symbols and the lines serve only to connect the values corresponding to the same τ and different $\log_{10} D_2$

In Figs. 3 and 4 we illustrate influence of the time-delay on $S_1(\log_{10} D_{1,2})$ and $S_2(\log_{10} D_{1,2})$ when fixed SC is coupled with adjustable SISR (Fig. 3) and adjustable SC is coupled with fixed SISR neurons (Fig. 4). Conclusions are qualitatively the same as in the corresponding cases of coupled equal neurons. For $\tau < 1$ there are no important changes in $S_1(\log_{10} D_{1,2})$ and $S_2(\log_{10} D_{1,2})$. For $\tau = 1$ and if SC neuron is fixed and SISR is adjustable $S_1(\log_{10} D_1)$ and $S_2(\log_{10} D_1)$ are significantly smaller then for $\tau < 1$ or $\tau > 1$. On the other hand if the fixed neuron is of the SISR type then $\tau = 1$ implies larger and qualitatively different $S_1(\log_{10} D_2)$ and $S_2(\log_{10} D_2)$. Time-lag $\tau > 1$ introduces important qualitative and quantitative changes paralleling the cases of equal units.

Figures 1d, 2d, 3d, and 4d illustrate the influence of time-delay on coincidence of spiking of the two neurons as measured by the coincidence function. Obviously, when there is no interaction time-delay spike in one neuron immediately causes the other neuron to fire so the spikes largely overlap and are considered coincident. Spikes also coincide when the time-lag is close to the inter-spike interval, if such is relatively well defined. Otherwise nonzero interaction time-lag destroys the coincidence of spiking. As the noise becomes larger the coincidence that occurs at special values of the time-lag decreases.

Results presented in Fig. 1 to Fig. 4 illustrate dependence of coherence on noise as measured by $S_1(D_i)$, $S_2(D_i)$ when the noise in one of the neurons D_j is fixed and the other D_i is variable. The fixed value D_j always corresponds to the maximal SC or SISR for the decoupled units, which is approximately $D_j = 0.01$ (for $a = 1.05$). The influence of the

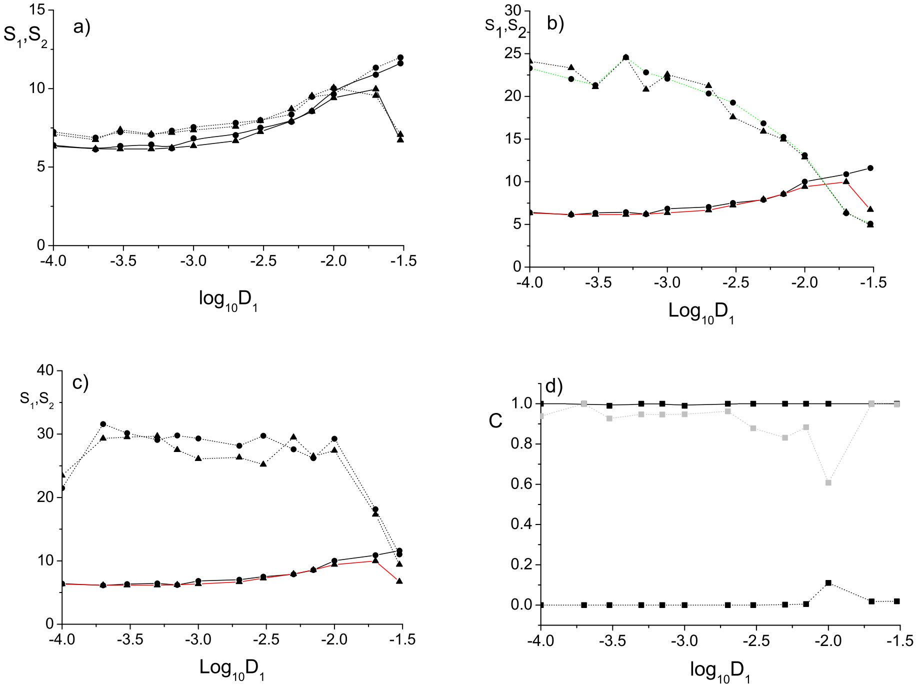

Fig. 2 Illustrates coherence (**a**, **b**, **c**) and spiking coincidence (**d**) in the SISR-SISR case. D_1 of the first SISR neuron is fixed to $D_1 = 0.01$. D_1 of the second SISR neuron, shown on the x axes as $\mathrm{Log}_{10}(D_1)$, is adjustable. S_1 (*circles*) and S_2 (*triangles*) for $\tau = 0$ (**a**, **b**, **c** *full line*) and $\tau = 0.7$ (**a**, *dotted*) $\tau = 1$ (**b**, *dotted*) and $\tau = 1.3$ (**c**, *dotted*) are shown. In (**d**) coincidence functions C for $\tau = 0$ (*black full*), $\tau = 1$ (*black dotted*) and $\tau = 2.7$ (*gray dotted*) are shown. Calculated values of $S_{1,2}$ and C are indicated by symbols and the lines serve only to connect the values corresponding to the same τ and different $\log_{10} D_1$

time-delay of the size up to the refractory period on the curves $S_{1,2}(\log_{10} D_i)$ for such fixed $D_j = 0.01$ is illustrated in Fig. 1 to Fig. 4. For $\tau > 1$ the curves $S_{1,2}(\log_{10} D_i)$ can be considered as monotonically decreasing with increasing D_i. Such monotonic dependence is due to relatively large value of the fixed noise D_j. Significantly smaller values of the fixed noise lead to the characteristic bell shaped dependence of $S_{1,2}(\log_{10} D_i)$, illustrated in Fig. 5a, b.

We can conclude that small time-lag $\tau < 1$ only slightly changes the properties of noise induced coherence in each of the considered cases. On the other hand, $\tau \geq 1$ introduces significant qualitative and quantitative changes in the functions which characterize the noise induces coherence S_1 and S_2. In general the curves acquire a plateau of large values for an intermediate interval of noise intensities. Time-delay $\tau > 1$ significantly increases the coherence and shifts the corresponding noise parameters towards smaller values. Dependence of the values of $S_{1,2}(\log_{10} D_i)$ on τ at D_i that corresponds to the maximum coherence for $\tau = 0$ is illustrated in Fig. 6a, b. When $\tau = 1$ two cases can be distinguished: (a) the noise intensity in the SISR neuron is fixed to the coherence maximum of the isolated neuron or (b) the noise intensity in the SC neuron is fixed to the coherence maximum of the isolated neuron and in both cases the adjustable neuron is either SISR or SC. In the case (b) the firing coherence of both neurons as measured by $S_1(\log_{10} D_{1,2})$ and $S_2(\log_{10} D_{1,2})$ is significantly smaller for any $D_{1,2}$ for $\tau = 1$ then for $\tau < 1$. In the case (a) $S_1(\log_{10} D_{1,2})$ and $S_2(\log_{10} D_{1,2})$ for $\tau = 1$ and small D are larger then for $\tau < 1$. In either of the considered cases the large local

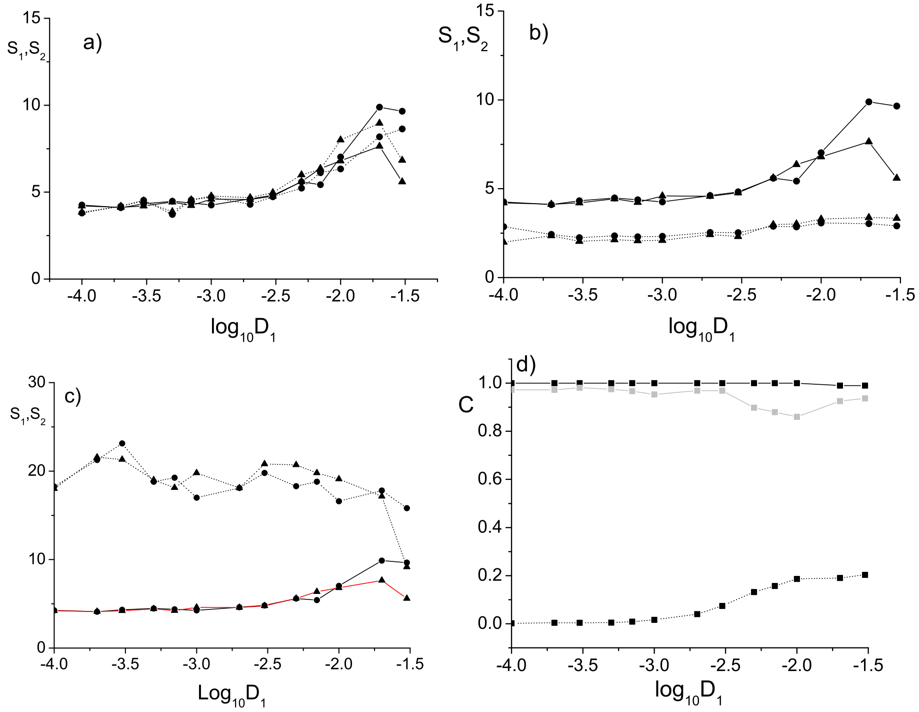

Fig. 3 Illustrates coherence (**a**, **b**, **c**) and spiking coincidence (**d**) in the SC-SISR case. D_2 of the first (SC) neuron is fixed to $D_2 = 0.01$. D_1 of the second (SISR), shown on the x axes as $\mathrm{Log}_{10}(D_1)$, is adjustable. S_1 (*circles*) and S_2 (*triangles*) for $\tau = 0$ (**a**, **b**, **c** *full line*) and $\tau = 0.8$ (**a**, *dotted*) $\tau = 1$ (**b**, *dotted*) and $\tau = 1.3$ (**c**, *dotted*) are shown. In (**d**) coincidence functions C for $\tau = 0$ (*black full*), $\tau = 1$ (*black dotted*) and $\tau = 2.7$ (*gray dotted*) are shown. Calculated values of $S_{1,2}$ and C are indicated by symbols and the lines serve only to connect the values corresponding to the same τ and different $\log_{10} D_1$

maxima in $S_1(\log_{10} D_{1,2})$ and $S_2(\log_{10} D_{1,2})$ that appear for $\tau > 1$ must be considered as a consequence of very small variance over long time of the values of the inter-spike intervals and not of large values of these intervals. In Fig. 7 we illustrate the coherent oscillations in the example of SC-SC case achieved with $\tau = 1.3$ and compare the time-series with that for $\tau = 1$ and $\tau < 1$. It is obvious that the coherence is significantly improved in the case $\tau = 1.3$ compared to $\tau \leq 1$ even though the frequency of the spiking is also increased. The reason for the significant increase of the maximal coherence for sufficiently large time-lag could be due to the fact that the time-lag becomes similar to the refractory period. However, we have no qualitative explanation for the sudden, bifurcation like, change of the curves $S_{1,2}(\log_{10} D_i)$ at $\tau = 1$. Let us stress once again that the two deterministic FHN neurons in the considered range of the parameters with delayed coupling do not have any bifurcations to oscillatory dynamics for any value of the time-lag.

4 Summary

We have studied a pair of FitzHugh-Nagumo neurons with noise coupled by time-delayed diffusive coupling. The bifurcation parameters of each of the neurons and the coupling

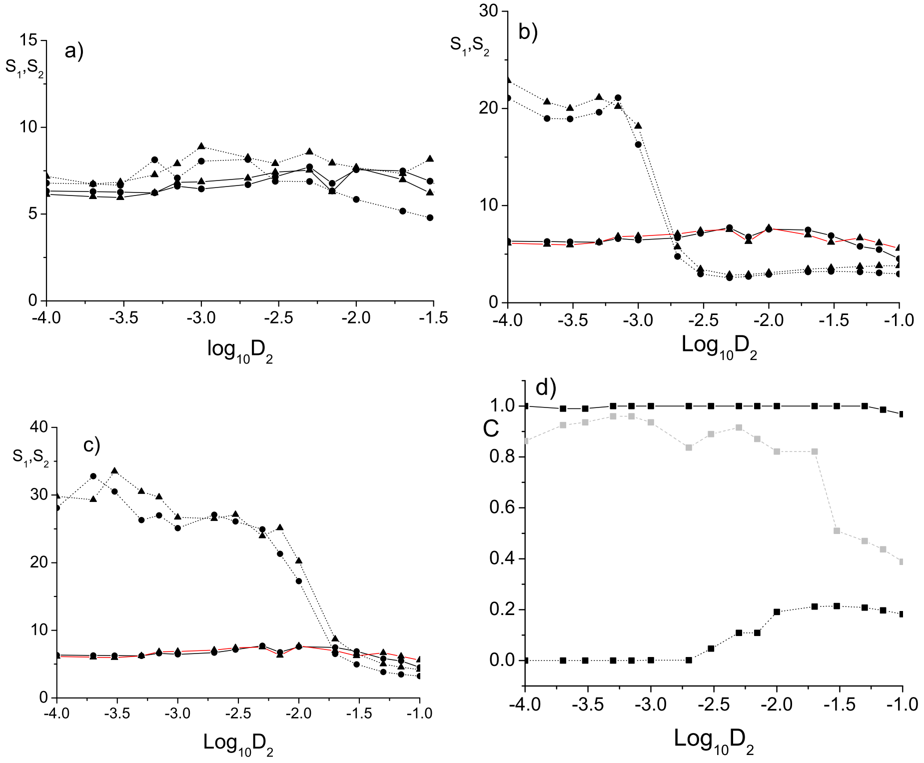

Fig. 4 Illustrates coherence (**a**, **b**, **c**) and spiking coincidence (**d**) in the SC-SISR case. D_1 of the second (SISR) neuron is fixed to $D_1 = 0.01$. D_2 of the first (SC), shown on the x axes as $\mathrm{Log}_{10}(D_2)$, is adjustable. S_1 (*circles*) and S_2 (*triangles*) for $\tau = 0$ (**a**, **b**, **c** *full line*) and $\tau = 0.8$ (**a**, *dotted*) $\tau = 1$ (**b**, *dotted*) and $\tau = 1.3$ (**c**, *dotted*) are shown. In (**d**) coincidence functions C for $\tau = 0$ (*black full*), $\tau = 1$ (*black dotted*) and $\tau = 2.7$ (*gray dotted*) are shown. Calculated values of $S_{1,2}$ and C are indicated by symbols and the lines serve only to connect the values corresponding to the same τ and different $\log_{10} D_2$

strength were such that the only attractor of the system without the noise terms is the stable stationary state for any value of the time-lag. Thus, the deterministic system is excitable with no oscillatory dynamics for any value of the time-lag. Addition of white noise in two different ways produces spiking that appears periodic for particular values of the noise strength. We have studied the influence of time-delay in the coupling on the coherent spiking induced by noise in the slow variable, called stochastic coherence (SC), and on that induced by the noise in the fast variable which is called self-induced stochastic resonance (SISR). This research is complementary to the analyzes of the effects of noise on the properties of oscillations and synchrony introduced by sufficient time-lag in the delayed coupling. Noise induced coherent spiking is studied using the signal to noise ratio and coincidence of spikes between the two neurons was measured using the coincidence function. As pointed before, the isolated neurons without noise were always in the excitable regime and the coupling strength was always positive, which guaranties that the train of spikes can only be introduced by noise, and not by time-delay. Then we numerically studied changes in the signal to noise ratio introduced by small time-delay for each of the neurons in the pairs like SC-SC, SISR-SISR and SC-SISR. Our main results can be summarized as follows: Weak coupling with any time-lag does not introduce any qualitative change of the signal to noise ratio.

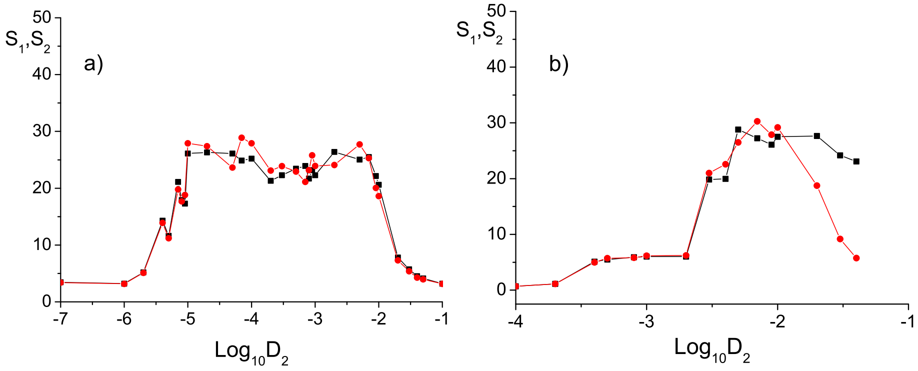

Fig. 5 Illustrates $S_1(\text{Log}_{10} D_2)$ (*triangle*), $S_2(\text{Log}_{10} D_2)$ (*circle*) for $D_1 = 0.001$ in SC-SC (**a**) and SISR-SISR (**b**) cases, for $\tau = 1.3$. Other parameters are $a = 1.05$, $c = 0.1$

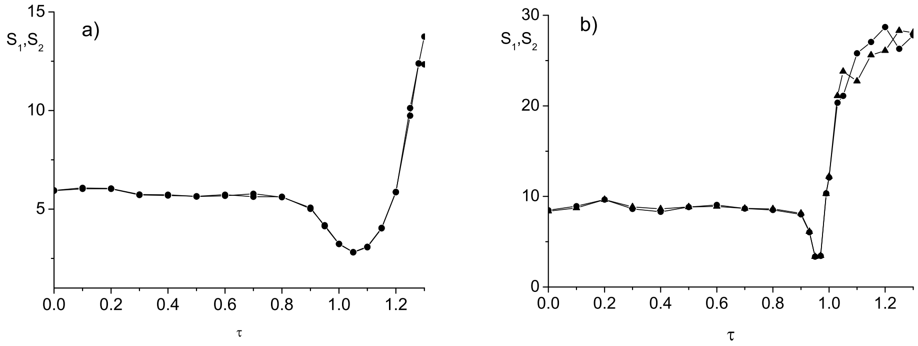

Fig. 6 Illustrates dependence of S_1 (*triangles*) and S_2 (*circles*) on the time-lag τ for the values of D_1, D_2 that imply in the maximal SC-SC $D_1 = 0.0$, $D_2 = 0.01$ (**a**) and maximal SISR-SISR $D_1 = 0.0$, $D_2 = 0.01$ (**b**) when there is no time-delay $\tau = 0$

Strong coupling with the time-lag $\tau < 1$ induces only small changes of the signal to noise ratio. However, time-lag $\tau \geq 1$ and sufficiently strong coupling drastically change signal to noise ratio in the quantitative and qualitative way. An interval of noise values implies quite large signal to noise ratio and SC or SISR is greatly enhanced. We also observed coincident spiking for small noise intensity and time-lag proportional to the inter-spike interval of the coherent spike trains.

In this paper we have used the FitzHugh-Nagumo neuron as the typical example of an excitable type II system, and the diffusive coupling as the model of an electrical synapse. We expect that noise can induce coherent spiking of excitable neurons of type I, as modeled for example by Terman-Wang system, and the influence of coupling delay in this case might be different, which deserves to be studied. Obviously it would be interesting to perform the analyzes of the influence of time-delay on noise induced coherence in the case of chemically coupled neurons.

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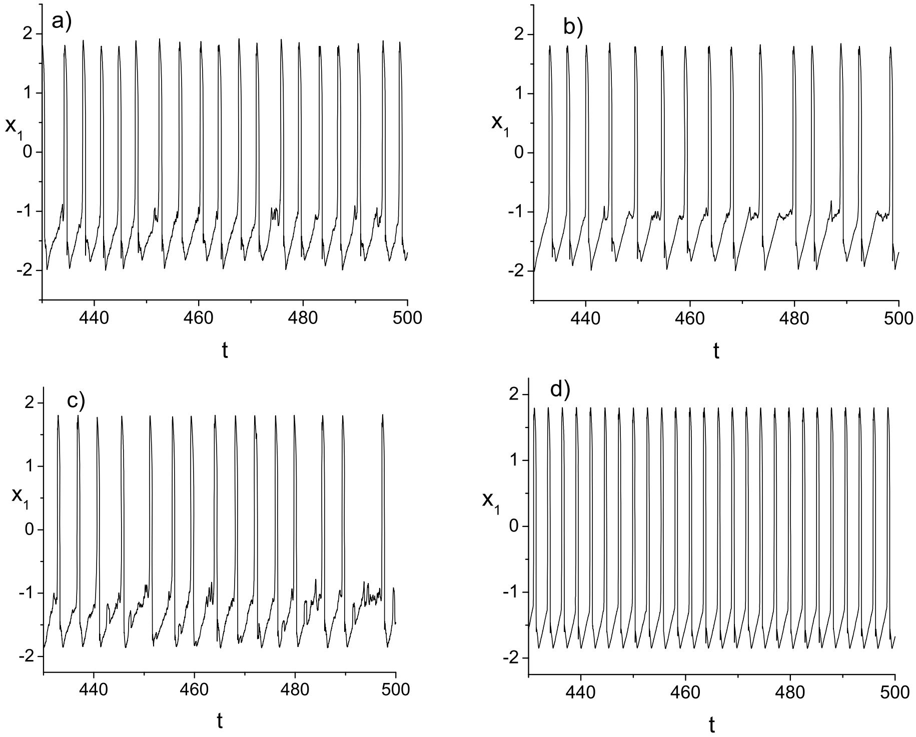

Fig. 7 Time series $x_1(t)$ in the case SC-SC with $D_2 = 0.01$ for the first neuron and for (**a**) $\tau = 0$, $D_1 = 0.01$ for the second; (**b**) $\tau = 0$, $D_2 = 0.001$ for the second; (**c**) $\tau = 1$, $D_2 = 0.01$ for the second and (**d**) $\tau = 1.3$, $D_2 = 0.001$, corresponding to a local coherence maxima in Fig. 1c, for the second

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