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COUPLED STOCHASTIC OSCILLATORS WITH DELAYS IN COUPLING *

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Abstract. Stochastic coherence (SC) and self-induced stochastic resonance (SISR) are two distinct mechanisms of noise-induced coherent motion. Influence of small time-delays on the coherence resonance in weak and strong coupled, stochastic,type II excitable pairs of SC and SISR systems is studied. It is shown that the transition between different phenomena when the coupling strength is gradually changed from weak to strong coupling is quite homogenous with some differences between SC and SISR neurons, and that small time-delays can have interesting effect on the noise induced coherent oscillations.

1. Introduction

Excitability is a common property of many physical and biological systems. Although there is no unique definition [7] the intuitive meaning is clear: A small perturbation from the 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. Furthermore, in the framework of the bifurcation theory, 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 [14]. 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

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neuron into the state of periodic firing [12]. There are different types of noise induced coherent oscillations that could occur in examples of excitable systems [11], 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 [18, 2, 3, 5, 16]). 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 [13, 1]. Influence of noise on time-delay induced bifurcations and properties of synchronization have been analyzed elsewhere, for example in [4, 8, 17]. On the other hand our aim here is to investigate the influence of coupling delay, on different types of coherent oscillations that have been induced solely by the noise, when the neurons are both weak and strong coupled. Such a detailed and extensive 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. We would like to emphasis, that our goal in this paper, is to study the effects of interplay between the time-delay, coupling strength and noise, on different types of noise induced coherent oscillations in each pair of the coupled 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, coupled by delayed electrical synapses, with different strengths of coupling included in the model. 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 section 3 we present and discuss the results of our extensive numerical computations. We have analyzed effects of small time delay on coherence in the case that both units display the same type of noise induced coherent oscillations, for weak and toward strong coupling units. We study the effects of strength coupling and time-delay on coherence properties of both single units. Finally, in section 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 [7]. 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, modeled by the FitzHugh-Nagumo differential equations [7], 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:

$$\begin{aligned} \epsilon dx &= f(x,y) = (x - x^3/3 - y)dt + \sqrt{\epsilon}\sqrt{2D_1}dW_1 \\ dy &= g(x,y) = (x+a)dt + \sqrt{2D_2}dW_2, \end{aligned} \tag{2.1}$$

where $dW_{x,y}$ are independent increment of normalized Winer processes, i.e. $E(dW_i) = 0$, $E(dW_i dW_j) = \delta_{ij}$, $i,j = 1,2$ and $E(\dots)$ 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 $a = 1.05$. 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 [15]. The effect is traditionally called coherence resonance [12], but we shall use the term stochastic coherence (SC) [19] 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 oscillations 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 [11], 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 [11]. 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.

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:

$$\begin{aligned} \epsilon dx_i &= f(x_i,y_i) + c(x_j(t-\tau) - x_i)dt \\ dy_i &= g(x_i,y_i), \qquad i,j = 1,2 \end{aligned} \tag{2.2}$$

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, $c = 0.01$ for weak and $c = 0.1$ for strong coupling, 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, quite small time delay for 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 [11]. 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 [6] for the case of equal units, and in [19] 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 weak and strong coupling between the neurons on the properties of SC and SISR, for both units either in the SC or in the SISR state.

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:

$$SNR = \frac{\overline{T_k}}{[\mathrm{Var}(T_k)]^{1/2}} \tag{3.1}$$

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 SNR 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 [10], 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. Values of SNR that are presented in what follows represent values that have been obtained with single typical sample paths.

Results of our numerical calculations are illustrated in figures 1, 2, 3, 4 and 5 where on each figure a), b), c), d) corresponds to two SC and e), f), g), h) to two SISR neurons. We fix the noise intensity of one of the neurons, say D_2 to the maximal coherence of SC type (a, b, c, d on all the figures) or D_1 to the maximal coherence of SISR type (e, f, g, h on all the figures) and study the dependence of firing coherence of both neurons on the noise intensity D_1 or D_2 of the adjustable unit, on the time-lag τ and on coupling strength: $c = 0.01$(fig.1); 0.03(fig.2); 0.05(fig.3); 0.07(fig.4); 0.1(fig.5). We consider only relatively small time-lags up to the refractory period of a single spike of an isolated excitable FHN neuron, which is about $\tau \leq 1.3$. On each of the figures 1-5 values of time-lags are: $\tau = 0$ and $\tau = 0.4$ (on the a, e); $\tau = 0$ and $\tau = 0.7$ (on the b, f); $\tau = 0$ and $\tau = 1$ (on the c, g); $\tau = 0$ and $\tau = 1.3$(on the d, h).

From fig.1 and fig.2 we can see that the coherence of noise induced spiking for both SC and SISR type neurons is not qualitatively affected by weak coupling ($c = 0.01$ and $c = 0.03$) for time-delay $\tau \leq 1$, but for $\tau = 1.3$ even for still weak coupling value $c = 0.03$ we can see first "reaction on the coupling strength" in both SC and SISR cases, which is shown in fig.2d and 2h respectively. Stronger coupling introduces significant modifications which very much depend on the time-lag and is illustrated in fig.3,4 and 5.

Figures 3a,b,c,d ($c = 0.05$) and fig.2a,b,c,d (c=0.03) (SC type) are qualitatively the same, but the qualitative and quantitative changes in curves $SNR_1(\log_{10} D_1)$ and $SNR_2(\log_{10} D_1)$ for SISR type in fig.3h (for $\tau = 1.3$) are obvious which means significant improvement in coherence comparing with the previous fig.2h (for same value of the time-delay).

Figure 4 presents improvement in coherence for lower intensity of the noise $-4 < \log_{10} D_2 < -2.5$ of the curves $SNR_1(\log_{10} D_2)$ and $SNR_2(\log_{10} D_2)$ for coupled neurons of SC type in the fig.4d for $\tau = 1.3$, while the other diagrams are qualitatively the same as in previous figure 3.

Typical effects of the influence of small time lag are shown in fig.5b and illustrated with $\tau = 0.7$, when both neurons are of the SC type and the noise intensity of one of them is held fixed at the SC maximum for single neuron. Other values of the time-lag less then $\tau < 1$ cause similar small modifications of the dependencies $SNR_1(\log_{10} D_2)$ and $SNR_2(\log_{10} D_2)$. However, large influence of the time-delay on $SNR_1(\log_{10} D_2)$ and $SNR_2(\log_{10} D_2)$ is demonstrated for all $\tau \geq 1$, as is illustrated in fig. 5c,d for $\tau = 1$ and $\tau = 1.3$ respectively. The curves $SNR_1(\log_{10} D_2)$

and $SNR_2(\log_{10} D_2)$ 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 bifurcations or other qualitative changes 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 5e, f, g, h 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 $SNR_1(\log_{10} D_1)$ and $SNR_2(\log_{10} D_1)$ drastically. Observe that the influence of time-delay for $\tau = 1$ in the SC-SC case is quite different from the SISR-SISR case.

In summary we can conclude that for any coupling strength 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 induced coherence SNR_1 and SNR_2, for SISR type neurons even for weaker coupling (c=0.05) then for the SC type where similar changes are not observed until strong coupling $c = 0.1$. In general the curves acquire several local maxima and minima that depend on τ. 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 respectively. In the case b) the firing coherence of both neurons is measured by $SNR_1(\log_{10} D_{1,2})$ and $SNR_2(\log_{10} D_{1,2})$ and is significantly smaller for any $D_{1,2}$ for $\tau = 1$ then for $\tau < 1$. In the case a) $SNR_1(\log_{10} D_{1,2})$ and $SNR_2(\log_{10} D_{1,2})$ for $\tau = 1$ and small D are larger then for $\tau < 1$. In either of the considered cases the large local maxima in $SNR_1(\log_{10} D_{1,2})$ and $SNR_2(\log_{10} D_{1,2})$ 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. Let us stress once again that the two deterministic FHN neurons in the considered range of the parameters with delayed coupling do not display any 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 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 coupling strength and 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. 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 varying the coupling strength from weak ($c = 0.01$) to strong ($c = 0.1$). 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. Transition toward strong coupling is quite uniform, with remark that pair of SISR neurons are more sensitive to the intensity of the coupling strength, than SC pair of neurons. Even 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 manner. New local minima and maxima of the signal to noise ratio as a function of the noise intensity are created by the time-lag $\tau > 1$, and the coherence of spiking measured by (3.1) can be greatly enhanced.

In this paper we have used the "homogeneous pair" of FitzHugh-Nagumo neurons (SC-SC and SISR-SISR) 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 "heterogenous pair" SC-SISR, and it will be interesting to see the influence of coupling strength and coupling delay in those cases (it might be different), which deserves to be studied. Obviously it would be interesting to perform the analysis of the influence of internal time-delay introduced in both neurons on noise induced coherence in all the cases we have previously mentioned.

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FIGURE CAPTIONS

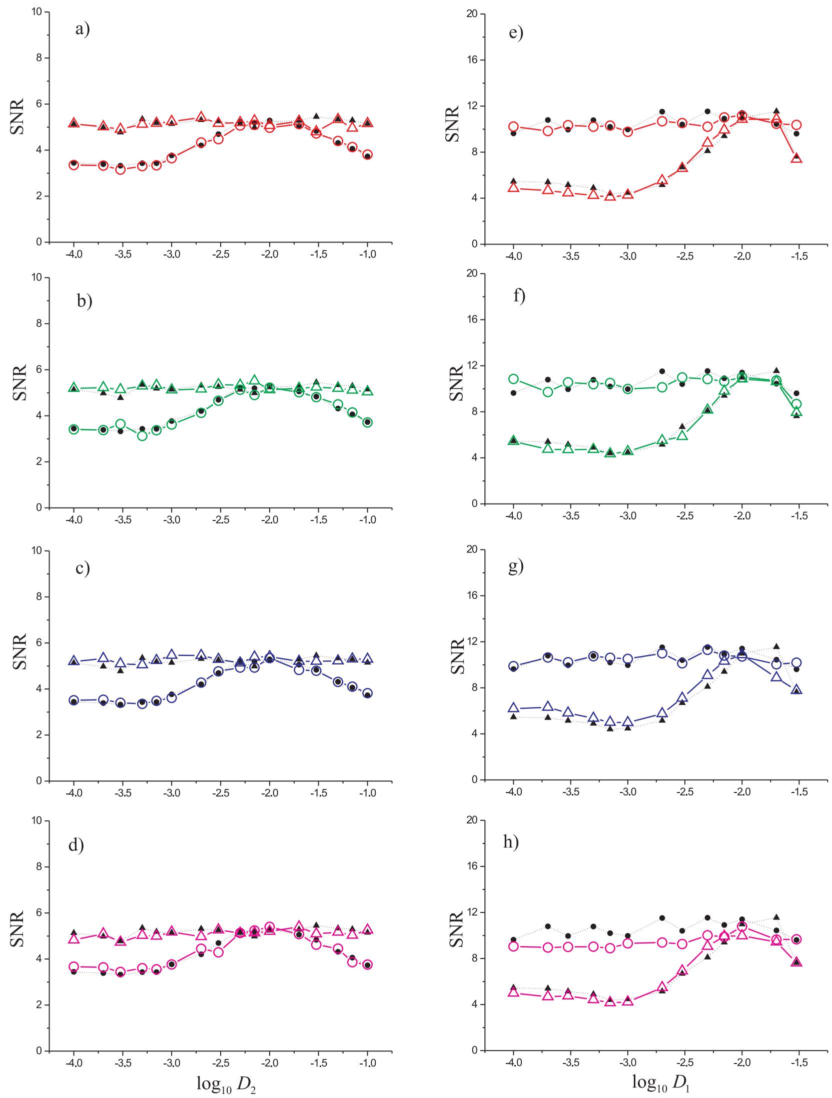

Figure 4.1.

Figure 4.1: Illustrates coherence in the (a,b,c,d) SC-SC case, and (e,f,g,h) in the SISR-SISR case, for $c = 0.01$ (weak) coupled pair of neurons. SNR_1(circles) and SNR_2 (triangles) full for $\tau = 0$ and hollow for $\tau = 0.4$ (a,e), $\tau = 0.7$ (b,f), $\tau = 1$ (c,g) and $\tau = 1.3$ (d,h). Calculated values of $SNR_{1,2}$ are indicated by symbols and the lines (dotted fot $\tau = 0$, and full for $\tau = 0.4 - 1.3$) serve only to connect the values corresponding to the same τ and different $\log_{10} D_{1,2}$.

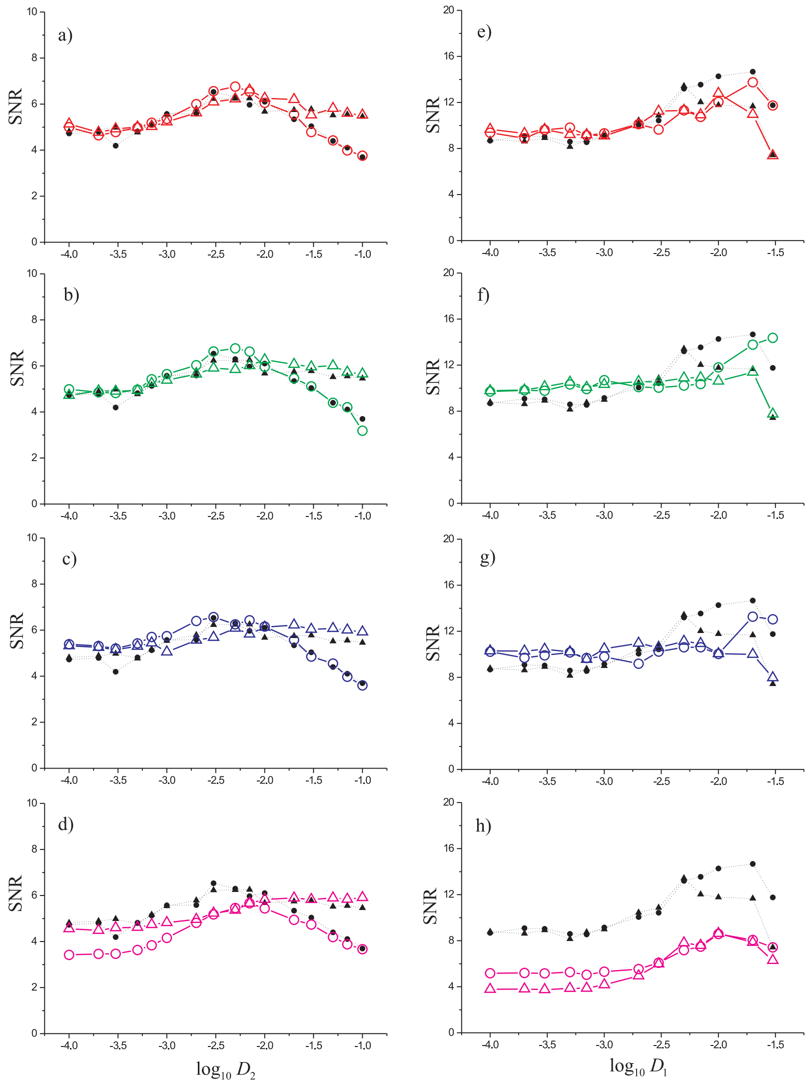

Figure 4.2.

Figure 4.2: Illustrates coherence in the (a,b,c,d) SC-SC case, and (e,f,g,h) in the SISR-SISR case, for $c = 0.03$ coupled pair of neurons. SNR_1(circles) and SNR_2 (triangles) full for $\tau = 0$ and hollow for $\tau = 0.4$ (a,e), $\tau = 0.7$ (b,f), $\tau = 1$ (c,g) and $\tau = 1.3$ (d,h). Calculated values of $SNR_{1,2}$ are indicated by symbols and the lines (dotted fot $\tau = 0$, and full for $\tau = 0.4 - 1.3$) serve only to connect the values corresponding to the same τ and different $\log_{10} D_{1,2}$.

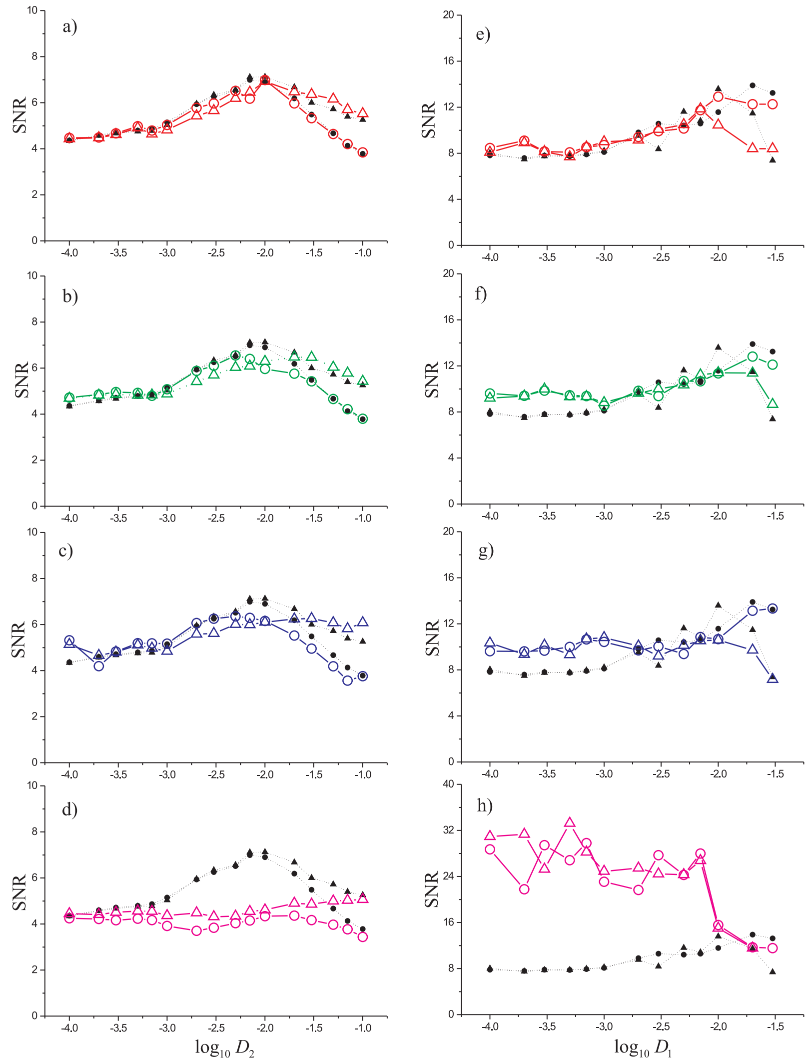

Figure 4.3.

Figure 4.3: Illustrates coherence in the (a,b,c,d) SC-SC case, and (e,f,g,h) in the SISR-SISR case, for $c = 0.05$ coupled pair of neurons. SNR_1(circles) and SNR_2 (triangles) full for $\tau = 0$ and hollow for $\tau = 0.4$ (a,e), $\tau = 0.7$ (b,f), $\tau = 1$ (c,g) and $\tau = 1.3$ (d,h). Calculated values of $SNR_{1,2}$ are indicated by symbols and the lines (dotted fot $\tau = 0$, and full for $\tau = 0.4 - 1.3$) serve only to connect the values corresponding to the same τ and different $\log_{10} D_{1,2}$.

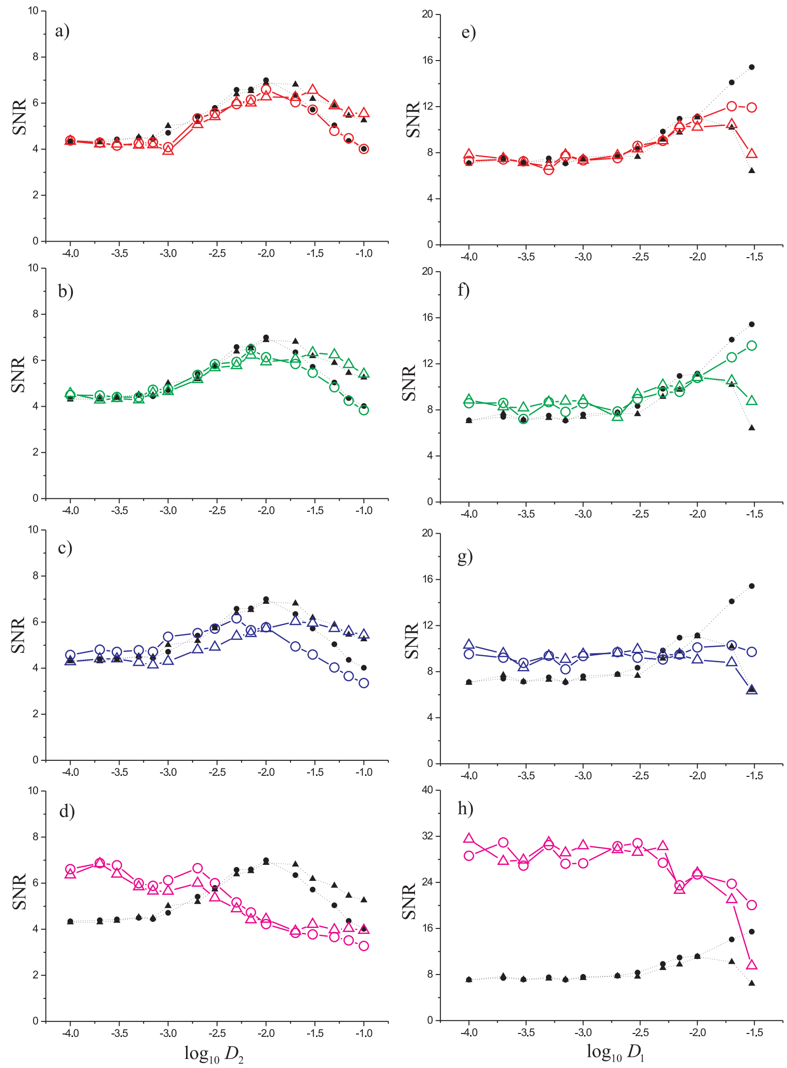

Figure 4.4.

Figure 4.4: Illustrates coherence in the (a,b,c,d) SC-SC case, and (e,f,g,h) in the SISR-SISR case, for $c = 0.07$ coupled pair of neurons. SNR_1(circles) and SNR_2 (triangles) full for $\tau = 0$ and hollow for $\tau = 0.4$ (a,e), $\tau = 0.7$ (b,f), $\tau = 1$ (c,g) and $\tau = 1.3$ (d,h). Calculated values of $SNR_{1,2}$ are indicated by symbols and the lines (dotted fot $\tau = 0$, and full for $\tau = 0.4 - 1.3$) serve only to connect the values corresponding to the same τ and different $\log_{10} D_{1,2}$.

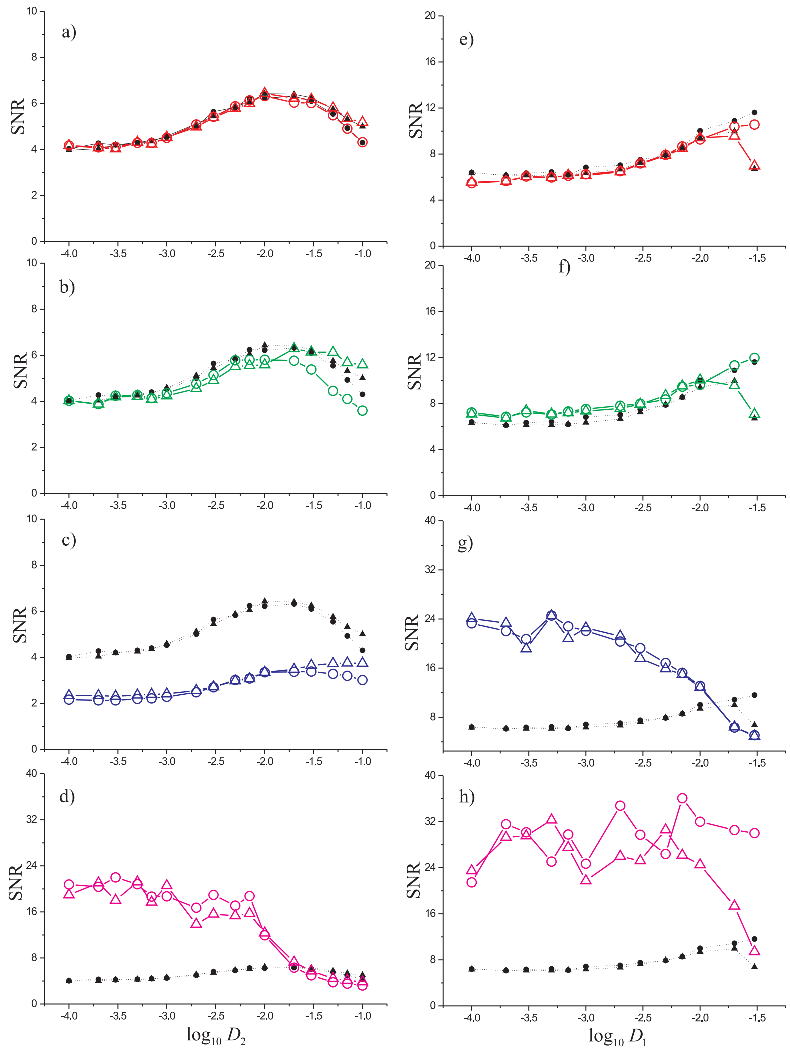

Figure 4.5.

Figure 4.5: Illustrates coherence in the (a,b,c,d) SC-SC case, and (e,f,g,h) in the SISR-SISR case, for $c = 0.1$ (strong) coupled pair of neurons. SNR_1(circles) and SNR_2 (triangles) full for $\tau = 0$ and hollow for $\tau = 0.4$ (a,e), $\tau = 0.7$ (b,f), $\tau = 1$ (c,g) and $\tau = 1.3$ (d,h). Calculated values of $SNR_{1,2}$ are indicated by symbols and the lines (dotted fot $\tau = 0$, and full for $\tau = 0.4 - 1.3$) serve only to connect the values corresponding to the same τ and different $\log_{10} D_{1,2}$.

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