

Influence of interaction delays on noise-induced coherence in excitable systemsNikola Burić,^{1,*} Kristina Todorović,² and Nebojša Vasović³¹*Institute of Physics, University of Beograd, P.O. Box 68, 11080 Beograd-Zemun, Serbia*²*Department of Physics, Faculty of Pharmacy, University of Belgrade, Vojvode Stepe 450, Belgrade, Serbia*³*Department of Applied Mathematics, Faculty of Mining and Geology, University of Belgrade, P.O. Box 162, Belgrade, Serbia*

(Received 15 April 2010; published 15 September 2010)

Influence of the interaction time delay on the noise-induced system size resonance in a system of all-to-all electrically coupled FitzHugh-Nagumo excitable neurons is studied. It is observed that small time lags decrease and that large time lags increase the coherence of spiking. Bifurcations of the system's stationary state are used to explain the observed nonmonotonic dependence of coherence on the time lag.

DOI: [10.1103/PhysRevE.82.037201](https://doi.org/10.1103/PhysRevE.82.037201)

PACS number(s): 05.45.-a, 05.40.Ca

I. INTRODUCTION

Collective variables of a system of stochastically evolving units can display regular coherent dynamics. Remarkably, the collective dynamics can be the most coherent for a certain small range of intermediate values of the parameters that characterize stochasticity of the single units. Stochastic resonance [1] is the most famous example of such constructive role of the dynamical noise. Other phenomena of the same type, such as coherence resonance [1,2], have been discovered and studied in various model systems and experiments [3]. One of more recently described properties of noise-induced coherence phenomena is the dependence of the level of coherence on the size of the system. It has been observed, for the first time in [4], that the level of coherence in the noise-induced oscillations of the collective variables depends on the size of the system, i.e., on the number of coupled units N , and that for systems with moderate N the maximum of coherence, for fixed noise amplitude, is obtained for an intermediate value of N . In this note we study the influence of interaction time delay on the noise-induced coherence and in particular on the effects of time delay on the system size coherence resonance (SSCR).

The phenomenon of SSCR has been studied in examples of neuronal networks [5] and suggested to be an important mechanism in dynamics of real networks of neurons [5]. However, in the model studies of SSCR in neuronal networks [5] the interneuronal connections have been modeled by instantaneous interaction, which is an oversimplification with potentially important consequences. It is well known from numerous studies (please see for example [7–9] and the references therein) that the interaction time delay of moderate and biologically relevant size can influence, for example, the stability and synchronization of the neuronal dynamics. Effects of the standard coherence resonance, observed in collections of neurons, are also strongly influenced by the varying time delay. In this note we shall describe the influence of the interaction time delay on the phenomenon of SSCR in a system of excitable neurons, and discuss the bifurcations that are relevant for the observed dependence of the coherence on the interaction time delay.

II. MODEL

We shall study a system of excitable neurons modeled by the following set of stochastic delay-differential equations (SDDE),

$$\epsilon dx_i = (x - x^3/3 - y + I)dt + \frac{c}{N} \sum_{j=1}^N [x_j(t - \tau) - x_i]dt, \\ dy_i = (x + b)dt + \sqrt{2D}dW_i, \quad (1)$$

where b, I, c, D and $\epsilon \ll 1$ are parameters. Single uncoupled unit in Eq. (1) represent one of the common ways of writing the famous FitzHugh-Nagumo (FN) model [6] of the excitable behavior. For certain parameter values, like $b=1.05$, $I=0$ to be used throughout this work, each single isolated unit has stable stationary solution (x_0, y_0) such that small departures from (x_0, y_0) might lead to large and long lasting excursions away from (x_0, y_0) which nevertheless end up on the stable state (x_0, y_0) . The type of excitable behavior epitomized by the FN model is called type II [6] and is characterized by destabilization of the stationary state via the Hopf bifurcation.

The terms $\sqrt{2D}dW_i$ represent stochastic increments of independent Wiener processes, i.e., dW_i satisfy: $E(dW_i) = 0$, $E(dW_i dW_j) = \delta_{i,j} dt$, where $E(\cdot)$ denotes the expectation over many realizations of the stochastic process.

Each of $i=1, 2, \dots, N$ units in Eq. (1) is coupled with each other unit and with itself. The model (1) with instantaneous electrical synapses was used in [5] to study the effect of SSCR. Therefore, in Eq. (1) we use the electrical coupling with the time lag $\tau > 0$. The time lag τ and the coupling strength c are, for simplicity, equal for all pairs of neurons.

III. PHENOMENOLOGY OF SSCR WITH THE INTERACTION TIME DELAY

The parameters in Eq. (1) are such that for $\tau=0$ each of the neurons, and the total system, are excitable, i.e., the stationary state is stable but small deviation from the stationary state might lead to large transient values of x_i . This is why small noisy fluctuations can result in a series of spikes with large x_i amplitude of each unit which resemble oscillatory behavior. In general, the spikes in each of the neurons appear

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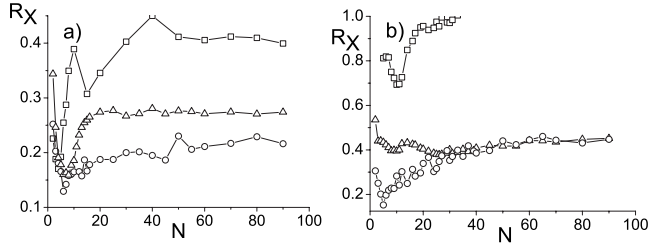


FIG. 1. Illustrates dependence of the jitter R on N for fixed $D = 0.001$ (a) and $D = 0.003$ (b), and for time lags in (a) $\tau = 0$ (triangles), $\tau = 0.2$ (boxes) and $\tau = 7$ (circles); and in (b) $\tau = 0$ (triangles), $\tau = 0.08$ (boxes) and $\tau = 2.7$ (circles). Other parameters are $b = 1.05$, $c = 0.1$.

with an irregular distribution of the interspike intervals, and spiking of different units is not synchronized. The dynamics of the collective variables $X(t) = \sum_i^N x_i / N$ and $Y(t) = \sum_i^N y_i / N$ is in general given by a stochastically distributed sequence of spikes, with different duration, and small fluctuations. However, for some combination of the parameter values the interspike intervals and the spike duration of the collective variables appear quite regular, and the dynamics resembles coherent oscillations with the well defined frequency. The level of coherence of the collective dynamics can be measured by various parameters. We shall use the jitter, defined as the standard deviation of the distribution of interspike intervals $T_{X,Y}$ normalized to its average

$$R_X = \frac{\sqrt{\langle T_X^2 \rangle - \langle T_X \rangle^2}}{\langle T_X \rangle}, \quad R_Y = \frac{\sqrt{\langle T_Y^2 \rangle - \langle T_Y \rangle^2}}{\langle T_Y \rangle}. \quad (2)$$

Smaller values of $R_{X,Y}$ signify more coherent dynamics. In the numerical calculations, it is considered that X or Y experiences a spike if it is larger than some value, in our case: for example $X > X_0 = 1$. The value of R_X is quite independent of X_0 . In our numerical integration we have used the Runge-Kutta fourth order routine for the deterministic part of Eq. (1) 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 computations performed using ready made programs for solving SDDE's available within the XPP package [10]. Values of $R_X(N)$ that are presented in what follows [Figs. 1(a) and 1(b)] represent values that have been obtained with a single typical sample path. The sample path was taken sufficiently long so that increasing it did not change the values of $R_X(N)$ on the scale of Figs. 1(a) and 1(b).

The effect of the interaction time delay on the coherence properties of the time series $X(t)$ is induced by the fact that nonzero time lag influences the stability of the stationary state and the synchronization of spiking. Figures 1(a) and 1(b) illustrate the influence of nonzero time delay on the coherence of $X(t)$ for two fixed values of noise and for different values of the system size N . Similar curves are obtained for other fixed small values of noise intensity. All curves on Figs. 1(a) and 1(b), illustrating the functions $R_X(N)$ for fixed noise level and for different fixed time lag τ , do have clear minima $R_{min}(D, \tau)$ at some $N_c(D, \tau)$. As is indi-

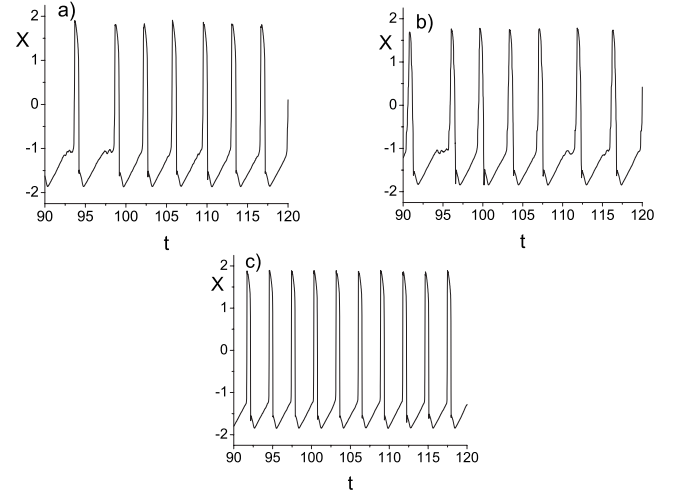


FIG. 2. Segments of the time series $X(t)$ for $D = 0.003$, $c = 0.1$, $b = 1.05$ and for (a) $\tau = 0$, $N = 6$; (b) $\tau = 0.08$, $N = 6$ and (c) $\tau = 2.7$, $N = 6$. In each case N correspond to the minima of the curves on Fig. 1(b), i.e., to the maximal coherence for fixed τ .

ated, the value of N corresponding to the maximal coherence and the level of coherence R depend on the time lag τ (and on the noise level D). However, the dependence of $R_{min}(D, \tau)$ on τ is not monotonic. Increasing small values of τ tends to decrease of the coherence for all N and specially for $N_c(D, \tau)$. On the other hand, for τ larger than some value the increase of τ implies better coherence, i.e., small values of $R(N)$ and in particular smaller R_{min} . Furthermore, the time delay shifts the position of the maximal coherence $N_c(D, \tau)$ toward smaller N . In Figs. 2(a)–2(c) we illustrate segments of the time series $X(t)$ for the values of N corresponding to the maximal coherence for three pairs of D, τ values indicated in Fig. 3(a). An explanation of the nonmonotonic dependence of $R_{X,Y}$ on τ is provided by studying the bifurcations of the collective dynamics induced by the time delay τ .

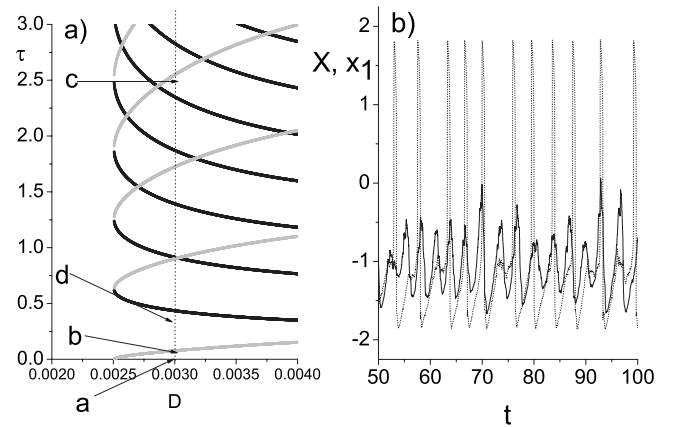


FIG. 3. (a) Bifurcation curves $\tau_{c-,j}^j, j = 0, 1, 2, \dots$ (gray) and $\tau_{c+,j}^j, j = 1, 2, \dots$. Labels a, b, and c indicate parameter values used in Figs. 2 and 2(a)–2(c), and the label d indicate the parameter value for Fig. 3(b). (b) Time series $X(t)$ (full) and $x_1(t)$ (dotted) for the parameters in $X(t)$ amplitude death domain: $D = 0.003$, $\tau = 0.25$. Other parameters are $b = 1.05$, $c = 0.1$.

IV. AMPLITUDE DEATH OF THE COLLECTIVE OSCILLATIONS

Time-delay induced amplitude death is an important phenomenon which occur in delay coupled oscillators [7,11,12], and consist in a replacement of stable oscillations by a stable stationary state, which is induced by the inverse Hopf bifurcation for some value of the time delay. When the time lag is near the bifurcation values, corresponding to the lower and the upper boundary of the τ -domain for the amplitude death, the oscillations of the system have much smaller amplitudes, which approach zero as the amplitude death parameter domain is approached. Consider now a relaxation oscillator which can display delay induced amplitude death but with added stochastic fluctuations. The effect of fluctuations is negligible when the oscillations have large amplitudes. However, as the parameter domain of the amplitude death is approached the regular oscillations amplitude becomes smaller and the fluctuations become more important. Thus, coherence of the oscillations is decreasing or increasing when the system is approaching or advancing away from the parameter domain corresponding to the amplitude death.

The type of dynamics of the collective variables $X(t), Y(t)$ can be predicted by a simple mean-field approximation of the system [Eq. (1)] which we have recently developed [13]. Using the standard assumptions of the mean-field approach but applied to systems with delayed interaction the following simple system of only two ordinary delay-differential equations was obtained as the approximation of the exact system [Eq. (1)] of SDDE,

$$\begin{aligned} \epsilon \frac{dX(t)}{dt} &= X(t) - X(t)^3/3 - \frac{X(t)}{2} \{1 - c - X(t)^2 \\ &\quad + \sqrt{[c - 1 + X^2(t)]^2 + 4D}\} - Y(t) + c[X(t - \tau) - X(t)], \\ \frac{dY(t)}{dt} &= X(t) + b. \end{aligned} \quad (3)$$

The phenomenon of delay induced amplitude death for small D and c of $X(t), Y(t)$ can be quantitatively studied by an analysis of the bifurcations that occur in the approximate system [Eq. (3)]. The corresponding bifurcation formulas have been obtained in [13], and the general formulas will not be reproduced here. In Fig. 3(a) we reproduce the curves of direct and inverse Hopf bifurcations for the values of the parameters that are relevant for our present analysis, and can be used to explain the dependence of the coherence $R_{X,Y}$ on τ for fixed D and arbitrary N . For sufficiently large N , the bifurcations of the $X(t), Y(t)$ dynamics of the exact system are not only qualitatively the same as for the approximate system but even the quantitative values of the parameters corresponding to the bifurcation points, and the parameter domains of different stability, are well predicted by the approximate system. For example, the bifurcation curves of the approximate system predict that for the parameters D, τ in the domain between the curves $\tau_{c,-}^0, \tau_{c,+}^1$ the stationary state should be stable. The exact dynamics of $X(t), Y(t)$ for D, τ in the specified domain and for $N=95$ is illustrated in Fig. 3(b). We see that there is no large spikes of $X(t)$, the dynamics is

that of subthreshold stochastic fluctuations. It is interesting to observe that the local variables $x_i(t), y_i(t)$ nevertheless can display oscillatory dynamics [Fig. 3(b)]. On the other hand, for quite small N , like those that correspond to the maximal coherence in Figs. 1(a) and 1(b), the agreement between the quantitative values of the parameters that correspond to the qualitative change of the exact dynamics and the bifurcations of the approximate systems are not as good as they are for larger N . Nevertheless, there is a domain of D, τ values with small D and relatively small but nonzero τ interval, which is relatively near the domain of the amplitude death and the neighboring bifurcations of the approximate system, such that the exact dynamics of $X(t), Y(t)$ is not dominated by large amplitude oscillations but by the stochastic fluctuations, as if the stationary state is stochastically stable. For small N such small fluctuations can occasionally induce a large amplitude spike, but they appear quite irregularly. As N is increased the qualitative bifurcations and the bifurcation values of the parameters predicted by the approximate system become more relevant for the exact system global dynamics.

Consider the bifurcation diagram of the approximate system [Eq. (3)] in the (D, τ) plane for fixed arbitrary positive c , like in Fig. 3(a). For the parameters D and τ to the left and to the right of the bifurcation curves and below the bifurcation curves the stationary state of the approximate systems is unstable for any τ . For D in the area below the bifurcation curves the stability of the stationary state is changed when the bifurcation curves are crossed. Crossing of τ_{c-}^j [gray on Fig. 3(a)] from below implies decrease of the number of unstable directions, and upon crossing τ_{c-}^j from below the number of unstable directions is increased. For example, the area between the curves τ_{c-}^0 and τ_{c+}^1 , corresponds to the amplitude death, the stationary state is stabilized by the time delay.

Bifurcation curves of the approximate system suggest the following qualitative properties of dynamics of the global variables of the exact system. As pointed out, for relatively small N like those that correspond to the minima of the coherence curves of Figs. 1(a) and 1(b), the predictions of the exact global dynamics must be considered only as qualitative and approximate, but for large N the approximation of the stability regions in the parameter domains become even quantitatively correct. For the parameters D and τ to the left and to the right of the bifurcation curves the stochastic fluctuations and the coupling induce more or less stochastic sequence of spikes in the exact system. For τ, D below the values on the bifurcation curve τ_{c-}^0 the global variables also display oscillatorylike dynamics. As τ is increased, for fixed other parameters like D on Fig. 3(a), the curve τ_{c-}^0 is approached from below, the oscillation amplitudes decrease, the statistical fluctuations become dominant and the coherence is in general decreased. Above the curve τ_{c-}^0 and below τ_{c+}^1 the stationary state of the system is stochastically stable and the oscillatory behavior is unstable. Stochastic fluctuations constantly attempt to move the system away from the stationary state but the stationary state is stabilized by the appropriate time delay and constantly attracts back the system. As τ is further increased beyond the curve τ_{c+}^1 the stationary state becomes unstable and a stable limit cycle is

created around it. However, the size of the limit cycle is proportional to the distance from the bifurcation curve τ_{c+}^1 on the lower side and from the bifurcation curve τ_{c-}^1 on the upper side. The system for the parameters between these two curves oscillates but with a relatively small amplitude. Such dynamics must be considered as subthreshold oscillations.

As τ is increased, there are such D values that the number of τ_{c+}^j curves crossed by the vertical with constant D becomes larger than the number of the crossed τ_{c-}^j [point c on Fig. 3(a)]. The oscillatory dynamics is then stable for all larger τ . Furthermore, for sufficiently large τ the amplitude of the (stochastically) stable limit cycle can be large enough so that the dynamics on it can be considered as spiking. For such τ the fluctuations become negligible and the coherence is again increased.

V. SUMMARY

We have studied the influence of interaction time delay in a system of all-to-all coupled excitable neurons which display the system size coherence of noise-induced oscillations.

It is observed that the coherence of spiking dynamics of the global variables has nonmonotonic dependence on the interaction delay, and that time delay tends to shift N that corresponds to the maximal coherence toward smaller values. The nonmonotonic dependence of coherence on τ is related to the occurrence of the domain of time lags for which the oscillations of the global variable are replaced by small fluctuations around the stable stationary state, i.e., to the phenomenon of delay induced amplitude death of the global variables. We have no explanation for the observed time delay induced shift of N that corresponds to the maximal coherence. Mean-field approximate equations are used to quantitatively study the Hopf bifurcations which are responsible for the amplitude death in the approximate model and suggest the type of dynamics of global variables of the exact system.

ACKNOWLEDGMENTS

This work is partly supported by the Serbian Ministry of Science Contract No. 141003, and partly by Abdus Salam ICTP, Trieste, Italy.

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