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Interplay between internal delays and coherent oscillations in delayed coupled noisy excitable systems

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ABSTRACT

Numerical study of variations in coherence of spike trains produced by two stochastically perturbed FitzHugh–Nagumo excitable systems with internal and coupling time-delays is performed. Both, the internal time-delay and the interaction time-delay in some domains of values can substantially increase the coherence but the interplay of the two delays can also lead to quite incoherent spike trains. Numerically observed dependence of the coherence on the delays is qualitatively explained by considering the bifurcations in the system caused by the variations of the values of the internal and the interaction time-lags.

1. Introduction

Excitability is a common property of many physical and biological systems. Although there is no unique definition [1]. Typical examples of the excitable behavior are provided by dynamics of single neurons [2], collection thereof [3] and by laser dynamics [4]. The defining property of the excitability is that 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. Such dynamical behavior is a consequence of the fact that the system is close to the bifurcation transition from stable stationary state attractor to the stable oscillatory dynamics. Proximity of the bifurcation implies that the model non-linear dynamical equations are qualitatively sensitive to small variations of different kinds. Therefore, realistic phenomenological models of excitable systems must include perturbation of different origin which often are capable of producing large qualitative differences. Two kinds of model perturbations are quite common. The first one replaces the complicated and often unknown influences of the system's environment by some type of noise. Influence of noise on typical excitable behavior is multifarious, well studied, and is still a source of novel interesting phenomena [5,6]. The other source of the model perturbations is motivated by quite different time-scales that characterize excitable systems. Internal dynamics of a single excitable unit, for example a single neuron, occurs on a much faster scale than the transport of excitations between the units. This justifies introduction of an explicit time delay in the terms describing the interaction. Influence of interaction delays has also been intensively studied [7,8]. In recent years, joint influence on the excitable behavior of both noise and interaction delays has been quite well analyzed (see the references in [9]) . However, there is yet another quite fundamental difference in the time-scales characteristic of a single excitable unit. This is the difference between the time-scales of the dynamics of the so-called excitatory (fast) and refractory (slow) variables. The first variable changes quite rapidly and is usually identified with a single, well defined and measurable physical characteristic of the system, like for example the membrane potential in the neuronal models. The dynamics of the second, refractory, variable usually only qualitatively corresponds to a collection of unspecified processes with quite slow dynamics, and its role is to complete the model of the excitable behavior. It is plausible that an internal time-delay in the coupling between the excitatory and refractory variable is justified, and furthermore one should expect that such time-delay will have important qualitative influence. In this paper we shall report our observations and analyzes of some dynamical phenomena that occur in typical excitable systems because of the

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interplay of noise, interacting delay and the internal delay. In particular we shall focus on the changes of the coherence properties of spike trains which are introduced in the excitable units by noise, occurring in the noisy excitable unitsdue to the bifurcations caused by variation of the small internal delays.

The structure of the paper is as follows. In the next section we introduce the basic model consisting of a pair of delayed coupled FitzHugh–Nagumo excitable systems with noisy perturbation and internal delays. In the same section we recapitulate properties of two types of the single excitable unit coherent oscillations induced by noise. Influence of the internal time-delay on the coherence of spike trains of a single unit is studied in Section 3. We first provide the numerical evidence for the strong variations in these coherence properties caused by variations of the internal delays and then we provide a qualitative explanation of the observed phenomena based on the analyzes of bifurcations caused by variations of the internal delays. Brief summary of our results is given in the final section.

2. The model

The FitzHugh–Nagumo model is a generic model i.e. simplified version of the Hodgkin–Huxley set of 4 non-linear differential equations which models in a detailed manner activation and deactivation dynamics of a spiking neuron (Hodgkin and Huxley received in the 1963 Nobel Prize in Physiology or Medicine for this work). In the original papers of FitzHugh, this model was called Bonhoeffer–van der Pol oscillator because it contains the well none Van der Pol oscillator as a special case (those equations have also been used in: electrical circuits employing vacuum tubes, seismology to model the two plates in a geological fault, etc.). In 1961 FitzHugh proposed to demonstrate that the Hodgkin–Huxley model belongs to a more general class of systems that exhibit the properties of excitability and oscillations. As a fundamental prototype, the van der Pol oscillator was an example of this class, and FitzHugh therefore used it (after suitable modification). A similar approach was developed independently by Nagumo in 1962.

Common types of excitable behavior are of two different varieties, usually called type I and type II [1]. Other types are possible in principle but they would correspond to bifurcations of codimension two or higher, and therefore typically do not occur. Type II excitability is characterized by the Hopf bifurcation of the equilibrium into stable oscillatory dynamics. Most common elementary model of this type of excitability is provided by the FitzHugh–Nagumo dynamical equations [1]:

$$\begin{aligned}\epsilon\, dx_i &= f(x,y)\,dt = (x - x^3/3 - y)\,dt\\ dy_i &= g(x,y)\,dt = (x+a)\,dt, \quad i = 1,2,\end{aligned} \tag{1}$$

where x and y are the fast excitatory and slow refractory variables respectively, and ϵ is a small parameter, here set to $\epsilon = 10^{-2}$ which guaranties the time scale difference between $x(t)$ and $y(t)$. Physical interpretation of the x and y variable is of no importance (since this is a generic model, we keep time in arbitrary units for simplicity), as the equations are never used to model a particular system but the phenomenon of (type II) excitability which occurs in many different systems. In neuronal models x is usually related to the cell membrane potential of a single neuron, but could also represent a collective variable of a network of neurons exhibiting the excitable dynamics and y is representing combined forces that tend to return the state of the axonal membrane to rest. The parameter a is the bifurcation parameter. For $|a| > 1$ the system (1) is excitable and for $|a| < 1$ the stationary state is unstable and there exist a stable limit cycle. In this paper a is fixed to $a = 1.05$.

The first modification of Eq. (1) models various, unspecified influences of the environment on the single excitable unit. For example, there are many different sources of noise which produce qualitative influence on real neuron dynamics [10]. Some are due to random synaptic inputs from other neurons, random switching of ion channels and stochastic release of neurotransmitters in synapses. The random process can be modeled by the additive white noise terms in the first and second equations of the system (1):

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

where $dW_{1,2}$ 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 two noise terms can produce series of spikes in the x variable which for certain values of the noise intensity 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 [11]. The effect is traditionally called coherence resonance [6], but we shall use term stochastic coherence (SC) [12] in order to emphasize the noisy origin of the coherent oscillations. SC occurs only when the parameter a is close to the 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 SC. It has been studied in detail for example in [13], 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 [13], and thus the coherent oscillations resemble the well known effect of the stochastic resonance [14,15]. 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 [16].

The variable y has no direct interpretation, and stands for group of processes that realize the recovery of the x variable to its stable quiescent value. Due to the difference in the x and y time scales it is justified to allow a perturbation of Eq. (1) such that the y value in the first equation is replaced by the value of y at some instant of time slightly before t, i.e. to replace $y(t)$ by $y(t-\tau_{in})$, where t_{in} is small compared to the characteristic time-scale set by the refractory period. This is the second modification to be introduced in Eq. (1).

Interaction between the excitable systems depends on particular physical models that they represent. The most elementary interaction is represented by the difference between the x values of the interacting units. In the neuronal modeling, this type of interneuronal interaction is called the electric synapses. As was pointed in the Introduction the difference in the internal dynamics time-scale and the interaction time-scale justifies the assumption that the interaction should take the form of the difference between the x (t) variable of the one unit and x at the shifted time i.e. $x(t-\tau_{ex})$ of the second unit. Therefore, a pair of identical type II excitable noisy systems with the internal delays and delayed interaction is described by the following stochastic delay-differential equations:

$$\begin{aligned}\epsilon\, dx &= f(x_i(t), y_i(t-\tau_{in}))\,dt + c(x_i(t) - x_j(t-\tau_{ex})) + \sqrt{\epsilon}\sqrt{2D_1^i}\,dW_1^i\\ dy &= g(x_i(t), y_i(t))\,dt + \sqrt{2D_2}\,dW_2^i,\end{aligned} \tag{3}$$

Values of the excitability parameter a, and the internal delays τ_{in} in the two units will always be equal, and denoted by the same symbols. The refractory period of a single isolated unit for $a = 1.05$ is roughly $T_{ref} \approx 1.4$. Values of time lags will be in the range of: $0 < t_{in} \leq 0.2$ for internal time lag, and $0 < t_{ex} \leq 1.3$ for the interaction time lag, and will always be smaller than T_{ref} (small or large