Commun Nonlinear Sci Numer Simulat 19 (2014) 3202–3219

Contents lists available at ScienceDirect

Commun Nonlinear Sci Numer Simulat

journal homepage: www.elsevier.com/locate/cnsns

Stability, coherent spiking and synchronization in noisy excitable systems with coupling and internal delays

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ARTICLE INFO

Article history:
Received 7 November 2013
Received in revised form 11 February 2014
Accepted 17 February 2014
Available online 26 February 2014

Keywords:
Time-delay
Noise
Coherent spiking

ABSTRACT

We study the onset and the adjustment of different oscillatory modes in a system of excitable units subjected to two forms of noise and delays cast as external or internal according to whether they are associated with inter- or intra-unit activity. Conditions for stability of a single unit are derived in case of the linearized perturbed system, whereas the interplay of noise and internal delay in shaping the oscillatory motion is analyzed by the method of statistical linearization. It is demonstrated that the internal delay, as well as its coaction with external noise, drive the unit away from the bifurcation controlled by the excitability parameter. For the pair of interacting units, it is shown that the external/internal character of noise primarily influences frequency synchronization and the competition between the noise-induced and delay-driven oscillatory modes, while coherence of firing and phase synchronization substantially depend on internal delay. Some of the important effects include: (i) loss of frequency synchronization under external noise; (ii) existence of characteristic regimes of entrainment, where under variation of coupling delay, the optimized unit (noise intensity fixed at resonant value) may be controlled by the adjustable unit (variable noise) and vice versa, or both units may become adjusted to coupling delay; (iii) phase synchronization achieved both for noise-induced and delay-driven modes.

1. Introduction

Generation of different oscillatory modes and their mutual adjustment constitute the basic paradigm behind the local and cooperative dynamics in a wide variety of biological and inorganic systems. Modeling complex multi-scale systems often consists in singling out the components showing typical and well controllable behavior into a few selected degrees of freedom, whereas their interactions incorporate explicit time-delays and different forms of noise. The stochastic component is intended to approximate variations within the embedding environment, as well as the fluctuations due to processes taking place at smaller spatial and temporal scales. The delays typically emerge due to complexity of interactions. In particular, the origin of delay between a sending and a receiving element may be linked to (i) intrinsic times of signal generation in the sending element, (ii) the finite propagation velocity of signals, and (iii) the latency in signal processing of the receiving element [1]. By their characteristic spatial and time-scales, the delays and sources of noise can naturally be associated with the

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http://dx.doi.org/10.1016/j.cnsns.2014.02.022
1007-5704/

degrees of freedom pertaining to a single unit ("internal" noise and delays) or those related to the interactions between the units ("external/interaction" noise and delays).

The existence of multiple noises and delays, together with the vast separation of characteristic time scales of the underlying processes, are inevitable features accompanying the modeling of many different biological systems. While the mere presence of these ingredients may be though of as universal, the prevalence of one type of noise/delay over the other in regard to impact on the system dynamics is an individual feature of any particular system. For instance, the external (synaptic) noise is the dominant factor in the evolution of neuronal systems [2], whereas the internal (biochemical) noise, arising due to small numbers of reactants' molecules [3], is likely the most prominent form of noise for the dynamics of gene expression regulatory networks [4,5]. Nonetheless, in neuronal systems the conduction delays of type (ii) are manifested more strongly than the delays of type (iii), while in gene networks the coupling delays of types (i) and (iii) occur naturally due to multistage synthesis of the reactants and the complex kinetics of intercellular signaling [5,6]. Regarding the photosynthesis and the related photo-respiration cycle, it has been indicated that the primary stochastic component comes from biochemical noise due to small numbers of reacting molecules [7], whereas the delay may be associated with the multistage assembly of reactants, the processes one would expect to naturally involve memory effects. Notably, there is ample evidence that in many biological systems noise and delay, alone or combined, play a significant role. Apart from the well known impact of these ingredients on neuronal systems [8–12], it has also been found that noise substantially affects the gene expression [13–15]. Also, the delayed negative feedback loops induce oscillations in gene transcription networks [16,6], whereas the interplay of randomness and delay has been demonstrated to accelerate signaling in genetic pathways [17,18,6]. As for photosynthesis, it has been suggested that the optimal amount of noise may enhance efficiency of energy transfer at certain stages of the process [19].

In this paper, the aim is to study in detail the interplay of internal and interaction delays and noise on formation and adjustment of oscillatory modes. This issue is especially intricate if the system is not made up of autonomous oscillators, but rather of excitable units [20]. Excitability rests on the point that equilibrium is poised close to a bifurcation toward periodic activity, whereby a unit may produce oscillations under permanent perturbation. If additional ingredients, such as delays, lead to coexistence of equilibrium and certain oscillatory states, then it becomes interesting to examine how excitability feature is modified due to multistability. Note that the body of work referring to models involving coaction of noise and delays is significantly less compared to those where either of them acts alone. Reluctance to consider nonlinear stochastic models with delays is mainly caused by the fact that the underlying systems of nonlinear stochastic delay-differential equations (*SDDEs*) are rarely tractable analytically [21,22].

The research here is focused on interaction of stochastic excitable units, whose dynamics is influenced by the coupling and intrinsic delays. We consider a pair of Fitzhugh–Nagumo (*FHN*) elements, which may be viewed as a basic motif of some complex network. While two distinct forms of perturbation are included as additive noise within the fast and slow subsystems, the model also features two types of delays, one incorporated into the coupling terms and the other related to the recovery mechanism of individual units. Our main goal is to study the particular roles and the co-effects of internal and interaction noise and delays on stability of equilibrium and the onset of different oscillatory modes, further examining regularity of spiking and certain forms of coordinated behavior cast within the framework of stochastic synchronization. Note that the combined effects of two types of noise on a single unit have been considered in [23,24], whereas synchronization of interacting stochastic units in the absence of coupling delays has been analyzed in [25,26]. On the other hand, the results on bifurcations and stability of exact synchronization in the unperturbed system admitting interaction delays have been reported in [27]. Compared to these studies, the novel points here concern (i) the presence of internal delays in each unit, (ii) application of several analytical techniques on the underlying model, including calculation of the stability conditions for the linearized system under perturbation and the method of statistical linearization, as well as (iii) putting emphasis on the competition between the noise-induced and delay-driven oscillatory modes, especially in terms of how it is reflected on the frequency and phase synchronization between the units.

The paper is organized as follows. Section 2 concerns the details of the model, specifying the background and the role of the introduced stochastic terms and delays. Section 3 provides the analysis on stability of a single unit. Apart from considering the local and global bifurcations controlled by intrinsic delay in the deterministic system, we derive the appropriate Fokker–Planck equation and determine stability conditions for the first two moments of the linearized system under perturbation. Method of statistical linearization is applied to study how coaction of noise and delay affects the unit's oscillatory motion. In Section 4, a pair of interacting units is approached by performing bifurcation analysis for the noiseless case, which demonstrates the prevalence of bistable regimes, either between equilibrium and the oscillatory states or between the different oscillation modes. Section 5 contains numerical results, intended to gain insight into the competition between the delay- and noise-driven modes. The issues of spiking coherence and stochastic synchronization are systematically examined under variation of delays, while letting the noise amplitudes take values below, about and above the resonant ones. Concluding remarks are provided in Section 6.

2. Details of the applied model

We consider a couple of identical excitable elements subjected to two types of noise and delay. In its most general form, the model dynamics is given by