Physica A 398 (2014) 243–251

Contents lists available at ScienceDirect

Physica A

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

Cooperative effects of inherent stochasticity and random long-range connections on synchronization and coherence resonance in diffusively coupled calcium oscillators

Maosheng Wang*, Runzhi Sun

Department of Physics, Anhui Normal University, Wuhu 241000, China

HIGHLIGHTS

- Effects of inherent stochasticity on synchronization and coherence resonance in coupled calcium oscillators are studied in the context of chemical Langevin equation.
- Inherent stochasticity and random long-range connections between calcium oscillators can induce/enhance coherence of the system's collective behaviors.
- Random long-range connections can promote the synchronization of the calcium oscillators and induce coherence resonance.

ARTICLE INFO

Article history:
Received 9 October 2013
Received in revised form 12 December 2013
Available online 27 December 2013

Keywords:
Internal noise
Random long-range connection
Chemical Langevin equation
Coherence resonance
Synchronization

ABSTRACT

The cooperative effects of inherent stochasticity and random long-range connections (RLRCs) on synchronization and coherence resonance in networks of calcium oscillators have been investigated. Two different types of collective behaviors, coherence resonance (CR) and synchronization, have been studied numerically in the context of chemical Langevin equations (CLEs). In the CLEs, the reaction steps are all stochastic, including the exchange of calcium ions between adjacent and non-adjacent cells through the gap junctions. The calcium oscillators' synchronization was characterized by the standard deviation of the cytosolic calcium concentrations. Meanwhile, the temporal coherence of the calcium spike train was characterized by the reciprocal coefficient of variance (RCV). Synchronization induced by RLRCs was observed, namely, the exchange of calcium ions between non-adjacent cells can promote the synchronization of the cells. Moreover, it was found that the RCV shows a clear peak when both inherent stochasticity and RLRCs are optimal, indicating the existence of CR. Since inherent stochasticity and RLRCs are two essential ingredients of cellular processes, synchronization and CR are also important for cells' functions. The results reported in this paper are expected to be useful for understanding the dynamics of intercellular calcium signaling processes in vivo.

1. Introduction

During the past three decades, constructive roles of noise in nonlinear systems have been widely studied in many fields [1–4]. The most famous effect of noise is stochastic resonance (SR), which shows the existence of a resonant noise strength at which the response of the system to a periodic force is maximally ordered. The order of the noise-driven system itself was found to have a maximum in the absence of periodic forcing, and this phenomenon was termed as CR [5,6]. Later, the

* Corresponding author. Tel.: +86 13966004997.
E-mail address: maosheng@ustc.edu (M. Wang).

0378-4371/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.physa.2013.12.024

features of the non-monotonic dependence of the system's response on noise have also been used to testify the SR-like phenomena. Recently, SR and CR in spatially extended systems have been intensively studied. Several different kinds of SR-like phenomena have been reported, such as the array-enhanced stochastic resonance [7–9], system-size resonance [10,11], spatiotemporal stochastic resonance and spatial coherence resonance (SCR) [12–17]. Aside from these examples, the effects of complex network connectivity on noise-induced patterns and SCR in excitable media have also been widely studied and the emergences of spatiotemporal stochastic resonance and SCR have been observed. For example, small-world connectivity induced SCR [18,19], time-periodic coupling induced multiple CR in Newman–Watts small-world networks of stochastic Hodgkin–Huxley neurons [20], spatial decoherence induced by small-world connectivity in excitable media [21], optimal network configuration for maximal CR in excitable systems [22], and so on.

Noise is inevitably present in the real world. So far, many kinds of noise have been presented, including Gaussian noise, Gaussian color noise, dichotomous noise, non-Gaussian noise [23,24], among others. Strictly speaking, Gaussian noise is an unbounded noise and there is a positive chance of taking large values [25,26]. However, some experimental results in neuron systems [27] and calcium oscillations in hepatocytes [28] showed that the noise sources in these systems are in general non-Gaussian and their distribution could be bounded [29]. From another point of view, these noises can be divided into two categories, i.e., external noise and internal noise. The external noise comes from the random variations of one or more of externally set control parameters. External noise is usually added to the dynamical equations directly, multiplicatively or additively. But for chemical reactions in small-scale systems, such as the biochemical reaction taking place in the living cell or catalytic reactions happening on nano-scale crystal surfaces, another source of noise, the internal noise, must be taken into account. The internal noise originates from the discrete nature of biochemical events such as transcription, translation, and protein/mRNA decay processes. The internal noise is uncontrollable, which depends on the details of the reaction dynamics as well as the system size. Internal noise induced SR-like phenomena have been intensively studied in many nonlinear systems [30–35].

Although the cooperative effects of external noise and coupling on biological systems have gained considerable attention [36–40], there have been a few discussions about the combined effects of internal noise and coupling in biological systems. For example, internal noise induced spatial patterns and SCR in coupled Höfer calcium oscillators have been reported in Ref. [41]. SCR in FitzHugh–Nagumo neurons induced by internal noise has been studied with Gillespie's τ-leap method [42]. Collective calcium signaling behavior of an array of coupled cells subjected to internal noise have been studied by Hou et al., and two system-size-resonances were observed [43]. In the present work, the interplay of internal noise and coupling in calcium oscillators has been studied numerically in the context of CLEs. It is important to note that the internal noise originates from the discrete nature of biochemical processes, and the coupling via gap junctions is also stochastic events. We found that the synchronization can be enhanced by increasing the number of RLRCs, i.e., synchronization can be improved through coupling. Interestingly, there is an optimal internal noise level at which the calcium spikes' coherence shows a peak, indicating the occurrence of internal noise CR. Moreover, the coherence has a maximum when both inherent stochasticity and RLRCs are optimal. Therefore, the interplay of internal noise and coupling can lead to the best performance of calcium oscillations.

2. Models and equations

2.1. A single calcium oscillation system

Ca^{2+} is one of the important second messengers in the cytosol of living cells. Ca^{2+} Oscillations are important in the control of many cellular processes [41–44]. There are a number of models for intracellular and intercellular calcium oscillations [45]. The model used in the present work was proposed by Höfer and by Gracheva et al. [46–48], which describes the dynamics of calcium in a single cell of rat hepatocytes. According to this model, the calcium signaling in a single cell involves the interplay of calcium fluxes from and into the endoplasmic reticulum (ER) and across the plasma membrane. If the noise is ignored, the dynamical equations of this calcium model can be governed by the following macroscopic kinetics:

$$\begin{aligned}
\frac{dx}{dt} &= \rho\left\{v_0 + v_c\frac{p}{k_0+p} - v_4\frac{x^2}{k_4^2+x^2} + \frac{\alpha k_r(x,p)}{\beta}\left[z-(1+\beta)x\right] - \alpha v_3\frac{x^2}{k_3^2+x^2}\right\}\\
\frac{dz}{dt} &= \rho\left(v_0 + v_c\frac{p}{k_0+p} - v_4\frac{x^2}{k_4^2+x^2}\right)\\
k_r(x,p) &= k_1\left\{\frac{d_2(d_1+p)px}{(d_p+p)(d_a+x)\left[d_2(d_1+p)+x(d_3+p)\right]}\right\}^3 + k_2
\end{aligned} \tag{1}$$

where x and z denote the concentrations of cytosolic Ca^{2+} and the total Ca^{2+} in the cell, respectively. The model parameters are (see Ref. [48] for more details): $\rho = 0.2\,\mathrm{L}\cdot\mu\mathrm{mol}^{-1}$, $\alpha = 2.0\,\mathrm{L}\cdot\mu\mathrm{mol}^{-1}$, $\beta = 0.1\,\mathrm{L}\cdot\mu\mathrm{mol}^{-1}$, $v_0 = 0.2\,\mu\mathrm{mol}\cdot\mathrm{L}^{-1}\cdot\mathrm{s}^{-1}$ describes a calcium leakage from the background, $v_c = 4.0\,\mu\mathrm{mol}\cdot\mathrm{L}^{-1}\cdot\mathrm{s}^{-1}$ denotes the maximum rate of calcium influx induced by IP_3 (inositol 1, 4, 5-trisphosphate), $v_3 = 9.0\,\mu\mathrm{mol}\cdot\mathrm{L}^{-1}\cdot\mathrm{s}^{-1}$ denotes the maximum rate of ER uptake calcium from the cytosol, and $v_4 = 9.0\,\mu\mathrm{mol}\cdot\mathrm{L}^{-1}\cdot\mathrm{s}^{-1}$ is the maximum rate of calcium efflux through the plasma membrane. The values of the other parameters are $k_0 = 4.0\,\mu\mathrm{mol}\cdot\mathrm{L}^{-1}$, $k_1 = 40.0\,\mathrm{s}^{-1}$, $k_2 = 0.02\,\mathrm{s}^{-1}$, $k_3 = 0.12\,\mu\mathrm{mol}\cdot\mathrm{L}^{-1}$, $k_4 = 0.12\,\mu\mathrm{mol}\cdot\mathrm{L}^{-1}$,