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Spatial coherence resonance in excitable biochemical media induced by internal noise

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Abstract

We show that in a spatially extended excitable medium, presently modelled with diffusively coupled FitzHugh–Nagumo neurons, internal stochasticity is able to extract a characteristic spatial frequency of waves on the spatial grid. Internal noise is introduced via a stochastic simulation method and is the only agent acting on the system. Remarkably, the spatial periodicity is best pronounced at an intermediate level of internal stochasticity. Thus, the reported phenomenon is an observation of internal noise spatial coherence resonance in excitable biochemical media.

Keywords: Excitable biochemical media; Neuronal dynamics; Internal noise; Spatial coherence resonance

1. Introduction

It is a well-known fact that noise can have constructive effects in different nonlinear dynamical systems. It has been shown that a proper amount of noise can resonantly amplify weak signals, which is known as stochastic resonance [1–3]. Fascinatingly, noise can play an ordering role even in the absence of weak deterministic stimuli, whereby the established term describing the phenomenon is coherence resonance [4–7]. Especially in biochemical reaction systems, it is a rather firmly established fact that a certain degree of stochasticity is unavoidable. Therefore, many studies have been performed for a variety of biological processes, where the constructive role of noise has been investigated. It has been shown, that noise can induce stochastic calcium oscillations in a subthreshold system, whereby the best temporal order is obtained by an intermediate intensity of noise [8–11]. Similar studies have also been performed for circadian rhythms [12,13] as well as genetic regulation [14] and neuronal systems [15,16].

Remarkably, noise induced resonance phenomena are not restricted only to the adjustment of temporal dynamics. Several studies are focused also on the spatial or spatiotemporal dynamics of biochemical media [17–19], whereby frequently the impact of noise on the spatiotemporal order is investigated. It has been discovered that noise alone often suffices to induce spatiotemporally ordered behaviour in systems as diverse as optical devices and biochemical media [20,21]. In particular, spatiotemporal stochastic resonance has been first reported in [22] for excitable systems. Moreover, there also exist studies reporting noise-induced spiral growth and enhancement of spatiotemporal order [23–25], noise sustained coherence of space-time clusters and self-organized criticality [26], noise induced excitability [27], noise induced propagation of harmonic signals [28], as well as noise sustained and controlled synchronization [29] in spatially extended systems.

Recently, specifically the spatial dynamics of noise-induced excitatory events in spatially extended systems has been investigated in great detail. Carrillo et al. [30] have shown that, for a nonlinear medium near a pattern-forming instability, there exists an intermediate value of additive spatiotemporal noise for which the peak of the circularly averaged spatial structure function is best resolved, thus marking spatial coherence resonance in the system. Recently, the concept was extended and spatial coherence resonance phenomena have been reported in excitable media [31,32] and in networks with different topologies [33].

Probably the most famous excitable medium, studied in the framework of physiology, is the neuronal network. It has been evidenced, that the consistency of spike generation and signal

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transition in networks of neurons depends on intrinsic noise, which may originate from fluctuations of channel gating, synaptic release, or of background presynaptic activity [34]. The role of noise in neuronal networks, and excitable media in general, has been and still is a vibrant avenue of research, thus yielding many experimental and theoretical studies over the past decade [35]. While real-life biological neurons exhibit extremely complex behavior, neuronal dynamics must be considerably simplified in order to make networks computationally traceable. Therefore, the neuronal medium is presently modelled by FitzHugh–Nagumo equations [36,37], which have been derived from the Hodgkin–Huxley model describing the excitable dynamics of electrical signal transmission along neuron axons [38].

Typically, when studying the spatial dynamics of excitable media, for example that of neuronal networks, the role of different intensities of external additive noise has been investigated [32]. Importantly, we presently extend the ideas of previous authors and investigate the spatial order of excitable media in dependence on internal noise only, which is introduced by using a stochastic simulation method. We demonstrate that internal stochasticity is sufficient to extract a characteristic spatial frequency of excitable media, which is best expressed for an intermediate level of internal noise. The phenomenon is thus an observation of internal noise spatial coherence resonance in excitable media.

2. Mathematical model

As already mentioned above, local units of the excitable medium under study are governed by the FitzHugh–Nagumo equations [36,37]

$$\frac{du}{dt} = f(u,v) = \frac{1}{\varepsilon}u(1-u)\left(u - \frac{v+b}{a}\right), \tag{1}$$

$$\frac{dv}{dt} = g(u,v) = u - v. \tag{2}$$

Individual units are arranged on the $L \times L$ ($i, j \in [1, L]$) square lattice with no-flux boundary conditions, whereby the

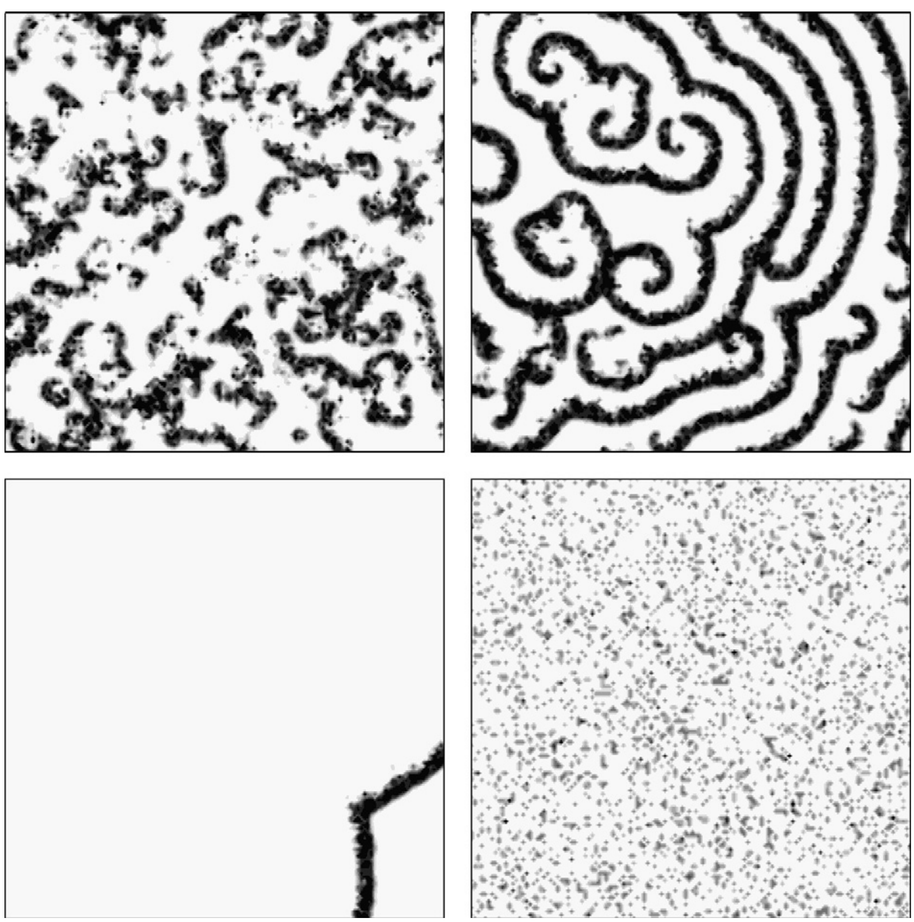

Fig. 1. Characteristic snapshots of the spatial profile of $u_{i,j}$ for χ=(80; 180; 220; 240) increasing from the top left towards the bottom right panel. All snapshots are depicted on square grids of linear size L=128. The colour mapping is linear, white depicting 0.0 and black 1.0 values of $u_{i,j}$. For χ=240 the colour scale extends from 0.0 to 0.01 in order to reveal small-amplitude fluctuations around the excitable steady state of each unit. Evidently, only for χ=180 the spatial domain is characterized by periodic excitatory waves, whereas for χ=80 the excitations are randomly scattered. For χ=220 the level of internal stochasticity is too low to induce periodic waves; only isolated and uncorrelated waves can be noticed, which disappear completely if χ is increased further.

spatial extension is modelled by an additional diffusive flux of the form $D\nabla^2 u_{i,j}$ that is added to the differential equation describing changes of variable u:

$$\frac{du_{i,j}}{dt} = f\left(u_{i,j}, v_{i,j}\right) + D\nabla^2 u_{i,j}, \tag{3}$$

$$\frac{dv_{i,j}}{dt} = g\left(u_{i,j}, v_{i,j}\right). \tag{4}$$

The membrane potential $u_{i,j}(t)$ and time-dependent conductance of potassium channels $v_{i,j}(t)$ are considered as dimensionless two-dimensional scalar fields, whereby the local dynamics of u is much faster than that of v ($\varepsilon \ll 1$). The Laplacian $D\nabla^2 u_{i,j}$, D effectively being the diffusion coefficient, is integrated into the numerical scheme via a first-order numerical approximation $D(u_{i-1,j}+u_{i+1,j}+u_{i,j-1}+u_{i,j+1}-4u_{i,j})$, so that the connection between nearest-neighbour units is established. For parameter values $a=1.05$, $b=0.01$ and $\varepsilon=0.05$, each FitzHugh–Nagumo neuron is described by a single excitable steady state $u=v=0.0$. Small perturbations of the excitable steady state evoke nontrivial spike-like behaviour, which can induce various waveforms in the spatial domain of the spatially extended system [39]. Thus, without taking into account internal stochasticity, which governs the neuronal dynamics, the medium would remain forever quiescent.

To simulate the neuronal dynamics stochastically, we use Gillespie's τ-leap method [40], which is an approximation of the exact stochastic simulation method [41], but is computationally less expensive. The occurring reaction probabilities correspond to the reaction mechanism governed by the deterministic Eqs. (3) and (4). In accordance with reaction probabilities, a discrete change of membrane potential and conductance of potassium channels of the form k_x/χ is performed at each iteration, where k_x is proportional to the flux of the corresponding reactant during time τ and χ is the system size. Such an approach has already been used in the literature for simulating various biological processes [9–11,14,42,43]. Importantly, χ directly determines the level of internal fluctuations to which the medium is exposed. Internal noise is most noticeable for small system sizes and it vanishes in the thermodynamic limit given by $\chi \to \infty$(theoretically), which induces deterministic steady state solutions in the dynamics of each individual unit and ultimately results in a quiescent medium.

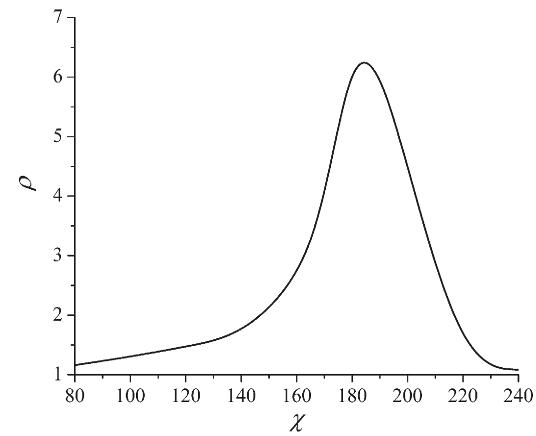

Fig. 3. Internal noise spatial coherence resonance in the studied medium. Signal-to-noise ratio ρ has a clear maximum in dependence on the level of internal stochasticity χ.

In Fig. 1, characteristic snapshots of the spatial grid for four different system sizes χ are presented. It can be noticed nicely that there exists an intermediate system size for which the noise-induced spatial dynamics of the medium is maximally ordered. If χ is small, the excitations are randomly scattered and in case of a large system size, fluctuations are too small to provoke large-amplitude excitations. Only an optimally pronounced level of internal noise is able to induce coherent spatial waves throughout the medium. At this point, we emphasize once more that the studied spatial dynamics is induced solely by internal noise. In what follows, we will show that there exists an optimal system size χ for which a particular spatial frequency of waves is resonantly enhanced, thus providing conclusive evidences for internal noise spatial coherence resonance in excitable media.

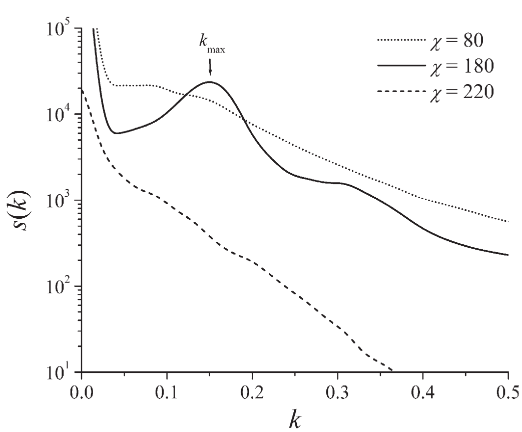

Fig. 2. Circular average of the structure function $s(k)$ for different system sizes χ.

3. Spatial dynamics

To quantify effects of different levels of internal noise on the spatial dynamics of the studied medium we calculate the structure function according to the equation

$$P\left(k_x, k_y\right) = \langle H^2\left(k_x, k_y\right)\rangle, \tag{5}$$

where $H(k_x, k_y)$ is the spatial Fourier transform of the $u_{i,j}$ field at a particular time t and $\langle\ldots\rangle$ is the ensemble average over different temporal realizations of the spatial grid. To study results obtained according to Eq. (5) more precisely, we exploit the circular symmetry of $P(k_x, k_y)$ as proposed in [30]. In particular, we calculate the circular average of the structure function according to the equation

$$s(k) = \int_{\Omega_k} P\left(\vec{k}\right) \mathrm{d}\Omega_k, \tag{6}$$

where $\vec{k}=(k_x,k_y)$, and Ω_k is a circular shell of radius $k=|\vec{k}|$. Fig. 2 shows results for various χ. It is evident that there indeed exists a particular spatial frequency $k=k_{\max}$ that is resonantly enhanced for a particular system size χ, defining an intermediate level of internal stochasticity to which the medium is exposed.

To quantify the ability of a particular system size to extract the characteristic spatial periodicity of waves in the medium more precisely, we calculate the signal-to-noise ratio ρ as the peak height at $k_{\max}$ normalized with the level of fluctuations existing in the system. This is the spatial counterpart of the measure frequently used for quantifying constructive effects of noise in the temporal domain of dynamical systems, whereas a similar measure for quantifying effects of noise on the spatial dynamics of spatially extended systems was also used in [30]. Fig. 3 shows how ρ varies with χ. It is evident that there exists an optimal intensity of internal noise for which the peak of the circularly averaged structure function is best resolved, thereby indicating the existence of internal noise spatial coherence resonance in the studied medium.

To shed light on the above-reported internal noise spatial coherence resonance, we first briefly summarize findings obtained when studying spatial coherence resonance in excitable media [31]. It has been argued that, since individual excitable units have a noise robust characteristic firing time t_f [6], additive spatiotemporal noisy perturbations are able to extract a characteristic spatial frequency of waves in a resonant manner so that $k_{\max} \propto 1/\sqrt{t_f D}$. Presently, each excitable unit may be activated by an appropriate level of internal stochasticity, which is an innate property of constitutive units of the medium and can have a conceptually identical impact on the spatial dynamics thus warranting the observation of internal noise spatial coherence resonance.

4. Discussion

We show that internal stochasticity is able to extract a characteristic spatial frequency of excitable media in a resonant manner. The phenomenon is an observation of internal noise spatial coherence resonance, since the induced characteristic spatial frequency is a consequence of internal stochasticity only, *i.e.* no additional deterministic inputs or external noise have been applied.

The presented results can be generalized also to other excitable media and might have important biological implications, since it is known, that excitability is ubiquitous in various biological systems [35]. Furthermore, especially in biochemical systems the presence of internal noise is widespread due to finite and relatively small numbers of reacting molecules, which are involved in different biological processes (see *e.g.* [44,45]). In the future, it would also be interesting to study effects of different topologies of the ensemble on the internal noise induced waves, as for example scale-free [46] or small-world [47] networks, which have already proved vital by the spatial dynamics of excitable media driven by external noise [33]. Due to conceptual similarities of effects of internal and external noise, however, it is reasonable to expect that the destructive effect reported in [33] will prevail also in the presently employed system set-up.

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