



White noise-induced spiral waves and multiple spatial coherence resonances in a neuronal network with type I excitability[☆]

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ABSTRACT

White noise-induced pattern formation is studied in a network composed of Morris–Lecar neuronal models with type I excitability and with initial values higher than that of the resting potential. The appearance and disappearance of spiral waves, as well as the transitions between spiral wave patterns with different kinds of complexity characterized by the normalized spatial autocorrelation function, enable changes in the order of the network so as to exhibit a scenario with two or more locally maximal peaks, as can be clearly seen in the signal to noise ratio curves, as the noise intensity is adjusted from small to large in a wide range. A possible physical mechanism of the multiple resonances based on the dynamics of type I excitability and initial values is provided. The potential biological significance of the noise-induced spiral waves is discussed.

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1. Introduction

Since the introduction of the concept of stochastic resonance (SR) [1], a positive role of noise has become an important issue in physics and related interdisciplinary studies. A nonlinear system is regarded as displaying SR when its response to both a weak periodic forcing and noise becomes maximally ordered at a resonant noise intensity [2–7]. The maximally ordered state is usually detected by the appearance of a single peak in the curve of signal to noise ratio (SNR) with respect to the noise intensity. The order of a noise-driven system can also exhibit a maximum with respect to the noise intensity, showing the effect of coherence resonance (CR) [8–11] in the absence of an external periodic signal. The classically defined SR phenomenon with one maximally ordered state has been extended to multiple SRs with two or more 'local' peaks in the SNR curve in simulation with a single neuronal model [12–14], suggesting that there exist multiple chances for a neuron to take advantage of the benefits of noise. Both SR and CR effects have been observed in experimentation in diverse nonlinear biological system including nerve systems [4,6,7,15–23]. Such experimental and theoretical results imply that the nervous system may take advantage of the benefits of noises, including internal thermal fluctuations and external noisy inputs [23,24], both of which are inevitable in the real world, to detect and process weak signals.

SR or CR effects result from the interplay between noise and the neuronal system's dynamics. The type of neuronal excitability, which corresponds to specific bifurcation dynamics from resting to oscillation, is the most relevant dynamical characteristics [25]. Neurons can be driven to generate excitations by input signals, including noise, when their dynamics

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are around an equilibrium point very near a bifurcation evolving to oscillations [9,18,21,22,26]. About 60 years ago, Hodgkin discovered that different neurons manifest very different transition processes from resting to oscillation in response to a constant input [27]. The excitability of the neurons starting to oscillate at an arbitrarily low frequency were characterized as type I, and those starting at a specific non-zero frequency as type II. About 20 years ago, bifurcation dynamics corresponding to type I and type II excitabilities were elucidated to be a saddle–node bifurcation and a Hopf bifurcation, respectively [28]. Recently, type I and II excitabilities, especially type I excitability, have attracted increasing attention in both biological experiments and theoretical models [29–40]: for example, the pyramidal neurons in rat somatosensory cortex [32], hippocampus [22,37], visual cortex [38] and other neurons including those in electrosensory lateral line lobe of an electric fish *Apteronotus leptorhynchus* [30], in mesencephalic V of the Sprague Dawley rat [40] and an experimental neural pacemaker [21]. Because of their different bifurcation dynamics, type I neurons manifest responses to the driven signals or noise in a way very different to that of type II neurons [29–36]. They generate distinct phase resetting curves [35,36], excitation frequencies, resonance curves [38], interspike interval (ISI) histogram distributions [18,21,22,26] and coefficients of variability (CV) of ISI series [35]. These different responses to noise or external stimulations indicate that type I and type II neurons may interact with input signals and noise in very different ways, and thus may generate distinct SR or CR phenomena.

Progress in studies on the effects of noise in the nervous system shows a shift from single neuronal systems to spatially extended excitable media [41–62]. Spatiotemporal SR, spatiotemporal CR, and spatial CR in excitable media induced by various noisy signals, including white noise and correlated noise resembling synaptic inputs, have been widely discovered and defined by means of the appearance of a single peak in the SNR curve. A series of important spatiotemporal dynamic behaviors, including synchronization, spiral waves, spatial periodicity, and temporal order, have been identified to emerge due to driven noise [10,11,44–51]. Since different collective dynamic behaviors may underpin different states of the brain function, these recent results imply a more important role of noise in the functioning of the spatially extended human brain [23,24]. For example, networks composed of neurons with type I excitability display a higher degree of synchrony than those with type II excitability [52–55].

Recently, both phenomena and mechanisms of spatial coherence resonance in excitable systems or networks have been studied [10,45,60,61]. In addition to one-peak resonances, double-peak resonances were observed from a single cell in a network stimulated by Gaussian white noise [56,57], and multi-peak resonances have been simulated in a network with time delay [63]. Multiple ‘local’ maxima in an SNR curve have also been observed in a network driven by an artificial stochastic signal [58,59]. Such observations imply a possible way of applying artificial signals to induce the emergence of multiple spatially ordered states in neuronal networks. Since the artificial signal employed in the study is still very different from white noise or correlation noise, extension of the concept of SR to include multiple spatial coherence resonances still needs firm evidence, similar to fluctuations in real nervous systems [23,24]. Recently, single neurons in visual cortex slices were identified to be with type I excitability [38], and spiral waves were observed in a visual cortex [63–67]. The spatiotemporal behaviors of a network composed of neurons with type I excitability should be studied to understand the possible mechanism of the observed experimental spiral waves.

The present study employs a network model composed of neurons with type I excitability and initial values higher than that of the resting potential to explore whether white noise is able to induce spiral waves and multiple spatial CRs. By adjusting the noise intensity, we observed the formation of spiral waves with different spatial structural patterns and clear evidence of emergence of multiple spatial CRs.

The rest of this paper is organized as follows. Section 2 presents the Morris–Lecar (ML) model and the type I excitability. Section 3 describes the network model composed of ML neurons and noise-induced spiral waves with different structural patterns in the network. Section 4 studies the multiple spatial coherence resonances. Section 5 discusses a relationship between spatial frequencies corresponding to spatial coherence resonances and the coupling strength of the network. A possible physical mechanism of the multiple spatial coherence resonances, based on the dynamics of type I excitability and initial values, is provided in Section 6. Section 7 summarizes the paper with some discussion.

2. Type I excitability in the ML model

The ML neuronal model [21,26,58,59,68,69], a well-known conductance-based neuronal model frequently employed to study type I and type II excitability, is described as follows:

$$\frac{dV}{dt} = \frac{1}{C} (-g_l(V - v_l) - g_{Ca}m_\infty(V - v_{Ca}) - g_k\omega(V - v_k) + I) \quad (1)$$

$$\frac{d\omega}{dt} = \lambda_\omega(\omega_\infty - \omega), \quad (2)$$

where V and ω represent the membrane potential and the recovery variable, respectively; I is the background current, whereas t is time; v_k , v_{Ca} , and v_l are, respectively, the reversal potential of potassium, calcium, and leakage current; g_k , g_{Ca} , and g_l are the corresponding maximal conductance, respectively; and C is the membrane capacitance. The units of potential, current, time, conductance, and capacitance are mV, $\mu\text{A}/\text{cm}^2$, ms, $\mu\text{S}/\text{cm}^2$, and $\mu\text{F}/\text{cm}^2$, respectively, in which the functions

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