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Spatio-temporal patterns in a square-lattice Hodgkin-Huxley neural network

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Abstract. The collective behaviour of a square-lattice Hodgkin-Huxley neural network model with white noise is investigated by numerical methods. It is found that for an intermediate value of noise the Hodgkin-Huxley neurons in the square lattice exhibit an ordered circular structure. However, as the noise level increases, the ordered circular structures are distorted, and eventually totally destroyed. Thereby, the constructive role of appropriately pronounced random perturbations in the studied network is revealed. Furthermore, it is shown that as the diffusive coefficient increases, the typical width of the spatial waves also increases accordingly, which results in a decrease of the number of cycles by a given size of the spatial grid. More interestingly, it is observed that the spatio-temporal coherence resonance is enhanced as the diffusive coefficient is increased. Finally, the dependence of the typical width and the average period of the firing rate function on the diffusive coefficient is studied. Results presented in this paper should prove valuable for the understanding of information processing of neural systems in the presence of noise.

PACS. 05.45.Xt Synchronization; coupled oscillators – 05.40.Ca Noise – 89.75.Kd Patterns

1 Introduction

In their seminal work, Hodgkin and Huxley proposed a mathematical model of neuron functioning described by four nonlinear differential equations, which has become an excellent and established mathematical tool for studying dynamical behaviour of biologically realistic neurons [1]. Thereafter, this model was called the Hodgkin-Huxley (HH) neuron model. In the past decades, much attention was given to the constructive effects of (external or internal) noise on an isolated HH neuron or some coupled ones, where many intriguing nonlinear phenomena have been found [2–6]. Stochastic resonance, which shows that the HH neuron responds to periodic forcing in the presence of noise, can exhibit a resonance-like dependence on the noise intensity [2,3]. Coherence resonance, where spikes of the HH neuron have a maximal regularity in the presence of noise even without external signals, was also reported [4,5]. Noise-induced synchronization including internal and external noise, has been studied for the HH neurons [6,7]. Some effects among those cases have been observed in numerous experiments, and they may be very important in the signal processing in neural systems [8–11]. More interestingly, It was found [12] that the network size, i.e. the number of HH neurons in the network, has an optimal value at which the collective behaviour shows the best performance. However, the nontrivial dependence on the network size could not be found by considering only the response of an individual neuron in the network. Hence, it is speculated that the average output of all neurons plays a critical role in neural information processing. Importantly thus, the study of the HH model still provides several scientific challenges, and new phenomena are yet to be discovered. Therefore, the aforementioned hypotheses are not conclusive today.

It is commonly accepted that a single neuron in the vertebrate cortex connects to more than 10 000 postsynaptic neurons via a synapses-forming complex network [13]. On the other hand, neurons are known to be subjected to several stochastic influences, which arise from many different sources such is the quasi-random release of neurotransmitters by synapses, random switching of ion channels, and most importantly random synaptic inputs from other neurons. Noisy neurons coupled via synapses can carry out highly complex and advanced operations with cognition and reliability [14]. As far as these perspectives are concerned, it is evident that neural tissue combines features of being both noisy and spatially extended. Therefore, a new

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and interesting nonlinear phenomenon, namely the noise-induced pattern formation, has gained much attention in the scientific community.

In the past, array-enhanced coherence resonance has been studied by using an array of coupled FitzHugh-Nagumo neurons [15]. It was shown that the coupling of such elements leads to a significantly stronger coherence as compared to that of a single element and parameter heterogeneity. It was reported that random spatio-temporal perturbations can constructively affect the dynamics of spatially extended systems [16]. For example, spatial coherence resonance has been introduced for systems near pattern-forming instabilities [17] as well as for excitable media [18]. It was shown that there exists an optimal noise intensity at which the inherent spatial periodicity of the media was resonantly pronounced. Effects of small-world connectivity on spatial coherence resonance in excitable media have been studied in [19]. Results show that the introduction of long-range couplings can induce decoherence of noise-induced spatial patterns observed by the regular connectivity of spatial units. Other well-known phenomena include noise enhanced and induced excitability [20], noise-induced propagation in monostable media [21], persistence of noise-induced spatial periodicity [22] as well as noise-induced wave propagation in chemical media [23]. Furthermore, coherence resonance has also been studied in a spatial prisoner's dilemma game [24]. Hence, spatial patterns that propagate through spatially extended systems on random support have become one of the most flourishing and fascinating topics of research in the field of nonlinear science today.

On the other hand, it is known that neural systems may be coupled into a network and respond to the external noise as a whole. Motivated by many biological network-related applications, an intriguing and significant question arises: How are spatio-temporal patterns in a square-lattice HH neural network affected by noise and different diffusive coefficients? In this paper, spatio-temporal dynamics in a square-lattice HH neural network is studied. It is shown that there exists an intermediate noise level, at which the HH neurons exhibit ordered circular waves, which are destroyed as the noise level becomes high enough. Furthermore, the effect of the diffusive coefficient on the spatio-temporal coherence resonance is investigated. It is found that spatio-temporal coherence resonance increases with the increase of the diffusive coefficient. Finally, the dependence of the firing rate function and the typical width of the spatial waves on the diffusive coefficient is investigated, revealing some characteristic relations between them.

The rest of this paper is organized as follows: in Section 2, a square-lattice neural network comprising HH neurons with nearest-neighbour diffusive coupling is introduced, and some basic dynamics of the HH neuron are described. In Section 3, noise-induced spatial patterns in the network are investigated. The dependence of spatio-temporal patterns on the diffusive coefficient is then presented and discussed in Section 4. Finally, conclusions and discussion are given in Section 5.

2 A square-lattice HH neural network

In neural systems, the so-called electrical synapse is a mechanical and electrically conductive link between two abutting neurons that is formed by proteins known as gap junctions. For this type of coupling, the synaptic current is proportional to the difference of membrane potentials between a neuron and its neighbors. Usually, electrical synapses can increase the speed and coherence of neural activity.

To understand spatio-temporal patterns of neurons coupled by electrical synapses in the presence of noise, we consider an ensemble of HH neurons, which are coupled to their nearest neighbours on a two-dimensional lattice. The dynamics of the spatial-temporal evolution of this ensemble governed by the following differential equations:

$$\begin{aligned}
C\frac{dV_{i,j}}{dt} &= -g_{Na}m_{i,j}^{3}h_{i,j}(V_{i,j}-V_{\mathrm{Na}}) - g_{K}n_{i,j}^{4}(V_{i,j}-V_{K})\\
&\quad -g_{L}(V_{i,j}-V_{L}) + I + D(V_{i-1,j}+V_{i+1,j}\\
&\quad +V_{i,j-1}+V_{i,j+1}-4V_{i,j}) + \sigma\xi_{i,j}(t)\\
\frac{dm_{i,j}}{dt} &= \alpha_{m_{i,j}}(V_{i,j})(1-m_{i,j}) - \beta_{m_{i,j}}(V_{i,j})m_{i,j}\\
\frac{dh_{i,j}}{dt} &= \alpha_{h_{i,j}}(V_{i,j})(1-h_{i,j}) - \beta_{h_{i,j}}(V_{i,j})h_{i,j} \qquad (1)\\
\frac{dn_{i,j}}{dt} &= \alpha_{n_{i,j}}(V_{i,j})(1-n_{i,j}) - \beta_{n_{i,j}}(V_{i,j})n_{i,j},\\
&(i,j=1,\ldots,N)
\end{aligned}$$

where $V_{i,j}$ is the transmembrane potential of the neuron labelled (i,j), of which the temporal evolution is governed by the first differential equation of (1); $m_{i,j}$, $h_{i,j}$, and $n_{i,j}$ are corresponding gating variables (probabilities) characterized by two-state, opening or closing dynamics, as described in the last three equations of (1); I represents the external direct current. σ denotes the level of noise and $\xi_{i,j}$ the Gaussian noise for the (i,j)th neuron with $\langle\xi_{i,j}\rangle = 0$, and $\langle\xi_{i,j}(t)\xi_{m,n}(t')\rangle = \delta(t-t')\delta_{i,m}\delta_{j,n}$; D is the diffusive coefficient. In the present study, periodic boundary condition is used, namely, $V_{0,j} = V_{N,j}$, $V_{N+1,j} = V_{1,j}$, $V_{i,0} = V_{i,N}$, $V_{i,N+1} = V_{i,1}$.

The experimentally determined voltage transition rates are given explicitly by the following expressions:

$$\begin{aligned}
\alpha_{m_{i,j}}(V_{i,j}) &= \frac{0.1(V_{i,j}+10)}{1-\exp[-\frac{(V_{i,j}+40)}{10}]}\\
\beta_{m_{i,j}}(V_{i,j}) &= 4\exp\left[-\frac{(V_{i,j}+65)}{18}\right]\\
\alpha_{h_{i,j}}(V_{i,j}) &= 0.07\exp\left[-\frac{(V_{i,j}+65)}{20}\right]\\
\beta_{h_{i,j}}(V_{i,j}) &= \left\{1+\exp\left[-\frac{(V_{i,j}+35)}{10}\right]\right\}^{-1}\\
\alpha_{n_{i,j}}(V_{i,j}) &= \frac{0.01(V_{i,j}+55)}{1-\exp[-\frac{(V_{i,j}+55)}{10}]}\\
\beta_{n_{i,j}}(V_{i,j}) &= 0.125\exp\left[-\frac{(V_{i,j}+65)}{80}\right]. \qquad (2)
\end{aligned}$$

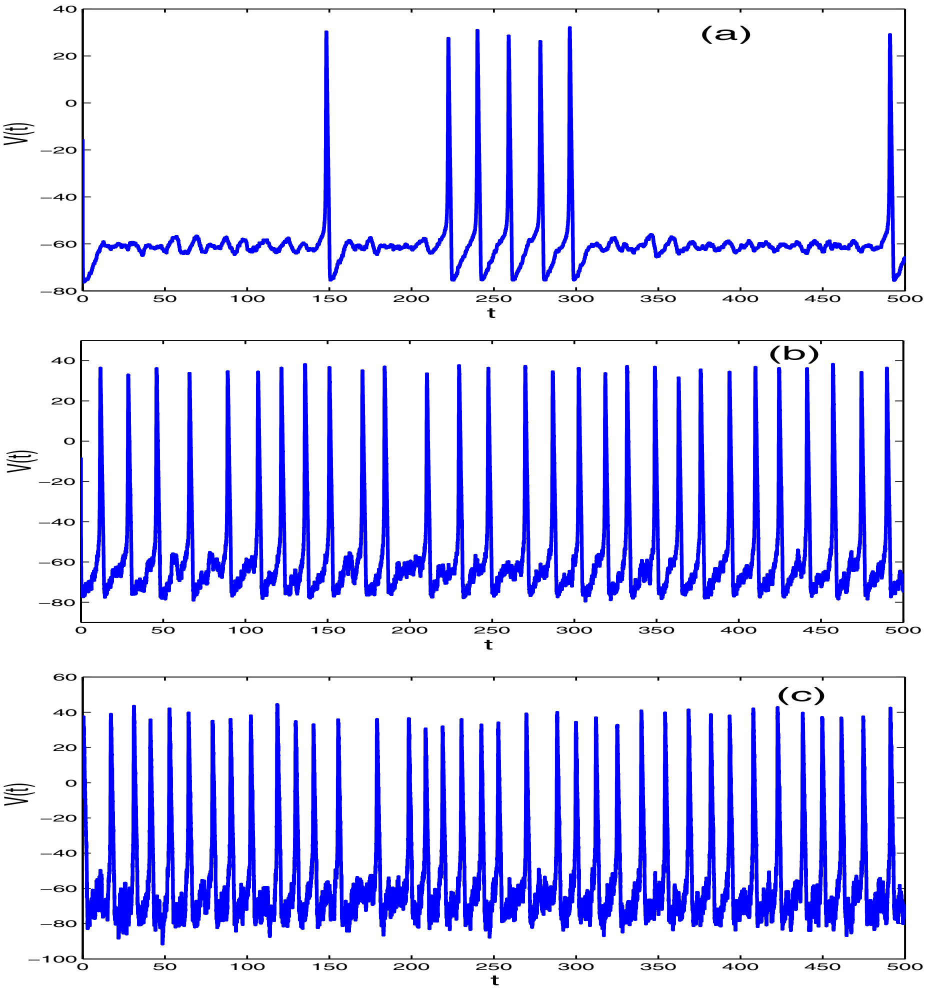

Fig. 1. Time series of an HH neuron at the different noise levels. The noise level σ is: (a) 0.1, (b) 10, (c) 60, respectively.

Table 1. The values of parameters.

Membrane capacitance $C = 1$ (μF/cm^2)		
Conductance constants (mS/cm^2)		
$g_{\mathrm{Na}} = 120$,	$g_K = 36$,	$g_L = 0.3$
Reversal potentials (mV)		
$V_{\mathrm{Na}} = 50$,	$V_K = -77$,	$V_L = -54.4$

The values of the parameters that appear in the above equations are listed in Table 1.

For a single HH neuron in the absence of noise ($\sigma = 0$), a limit cycle appears at the external direct current $I = I_1 \approx 6.2$ μA/cm^2 due to a saddle-node bifurcation of a periodic solution. However, the unstable branch of the periodic solution dies out at $I = I_2 \approx 9.8$ μA/cm^2 through an inverse Hopf bifurcation. Thus, when $I < I_1$, the resting state is a globally stable equilibrium point, whereas for $I_1 < I < I_2$ the system has two stable attractors, a fixed point and a limit cycle. A more detailed bifurcation analysis of the HH neuron was presented in [5]. Here, we are interested in the parameter region near the onset of the saddle-node bifurcation of the periodic orbit. In this excitable region, neurons are unable to fire spontaneously in the absence of noise. In all subsequent calculations, we set $I = 6.1$ μA/cm^2 such that each neuron in this network stays at the excitable steady state.

When a single HH neuron, located at the excitable steady state, responds to a suitable intensity of noise, noise-induced spikes can be observed as shown in Figure 1, and the number of the spikes increases in a given time interval as the noise level increases. The stochastic dynamics of the HH neuron near a bifurcation point, stochastic resonance and coherence resonance have been studied extensively before. Results show that there exists an optimal noise level, at which temporal order of the HH neuron is maximal.

3 Spatial patterns of the HH neural network in the presence of noise

In this section, we focus on spatial patterns in the above-described square-lattice HH neural network in the presence of noise. Noise-induced ordered circular structures

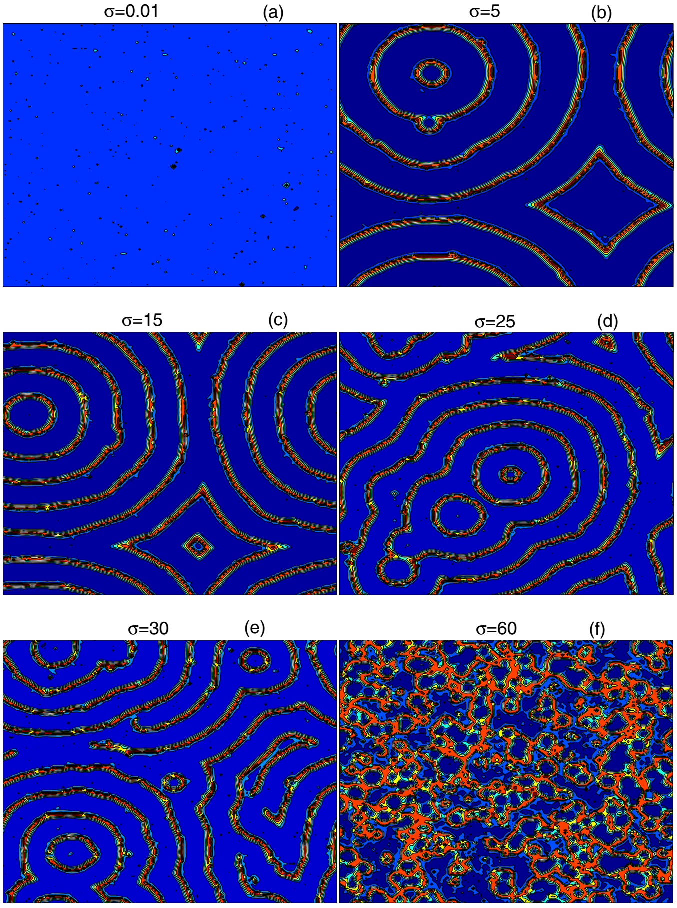

Fig. 2. Spatial pattern formation in the square-lattice HH neural network for different levels of noise. All figures depict values of $V_{i,j}$ on a 128×128 square grid at a given time t. The noise level σ is: (a) 0.01, (b) 5, (c) 15, (d) 25, (e) 30, (f) 60, respectively. Here, the diffusive coefficient is $D = 0.5$.

can be observed at an intermediate noise level, which are destroyed when the noise level becomes high enough. Hence, there exists an intermediate noise level, at which the spatial dynamics exhibits maximal order.

In what follows, a detailed analysis will be presented to explain the variation of spatial patterns as the noise level is changed. Figure 2 shows some typical spatial patterns for different noise levels in a HH neural network of size 128×128 (in this paper, N is always 128). It is observed in Figure 2a that for lower noise levels, neurons don't exhibit large-amplitude spikes, and hence an outstanding spatial structure is absent. On the other hand, for an intermediate noise level, noise-induced patterns emerge in space, which orderly propagate across the spatial grid in form of circular waves as shown in Figures 2b and 2c. It is obvious that spatial patterns of the circular structure are characterized by layers with one smaller cycle being surrounded by other larger one. Furthermore, the number of ordered cycles increases with the increment of the noise level.

However, Figures 2d and 2e show that as the noise level increases further, ordered spatial patterns are distorted by strong noisy perturbations. Fact is that larger intensities of noise induce random firings of individual neurons, which ultimately results in lack of order in the spatial domain. Thus, when the noise level is high enough, ordered circular structures cannot persist and are replaced by disordered random portraits as observed in Figure 2f. In sum, it is shown that there exists an intermediate level of noise at which ordered patterns in the square-lattice HH neurons are resonantly pronounced and ordered. This scenario is characteristic for the solely noise-induced pattern formation, or as introduced in [17,18], the so-called spatial coherence resonance.

4 Dependence of spatio-temporal patterns on the diffusive coefficient

However, since it is impossible to present spatial patterns in continuous time, we try to capture the essence of the resonant dynamics by defining a firing-rate function Π, as follows. For a rough illustration of firing behaviour of a single HH neuron, a neuron is said to be firing when the membrane potential of the neuron V reaches the threshold value $V_{th} = 0$ from below at a given time. If m neurons are fired simultaneously at a given time t, then $\Pi(t,m) = m/N^2$. It is obvious that $\Pi(t,m)$ is a function of time t and space m. This statistical function simply measures the fraction of fired neurons on the lattice at any given time. Clearly, if $\Pi(t,m) = 0$, this means that none of the neurons is perturbed strong enough for V to exceed the threshold V_{th}, while $\Pi(t,m) = 1$ indicates that all neurons are simultaneously in the firing state at the given time t, which constitutes global synchrony and thus corresponds to the most ordered temporal dynamics in this square-lattice HH neural network.

In what follows, we study the effect of the diffusive coefficient on the spatio-temporal patterns in this network in terms of the firing rate function. Results show the enhancement of spatio-temporal coherence resonance as the diffusive coefficient increases. Finally, the average period of the firing rate function and a typical width of the spatial waves are investigated statistically.

4.1 Enhancement of spatio-temporal coherence resonance

It has been demonstrated clearly that spatio-temporal noise plays a significant role by the spatial pattern formation in the square-lattice HH neural network. However, one may wonder how the spatio-temporal patterns in the network depend on the diffusive coefficient. Figures 3a–3c show the characteristic spatial patterns of this network for different diffusive coefficients D. It is observed that as D is increased, the number of cycles in the spatial domain decreases. More interestingly, it is found that the typical width of circular waves becomes larger as D increases. Since a larger D leads to a faster diffusive spread, local excitations can propagate further through space in a given amount of time. Hence, it is understandable that

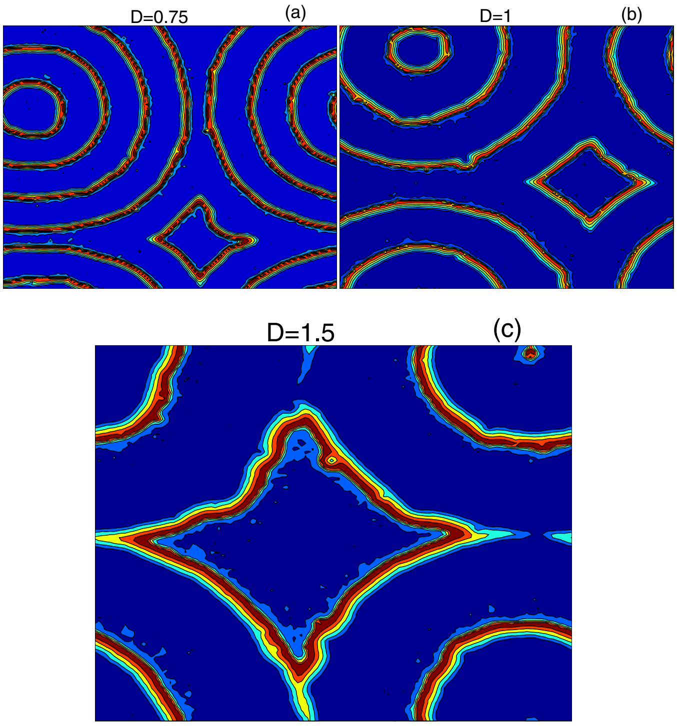

Fig. 3. Spatial pattern formation in the square-lattice HH neural network for different diffusive coefficients. All figures depict the values of $V_{(i,j)}$ on a 128×128 square grid at a given time t. The diffusive coefficient D is: (a) 0.75, (b) 1, (c) 1.5, respectively. Here, the noise level is $\sigma = 25$.

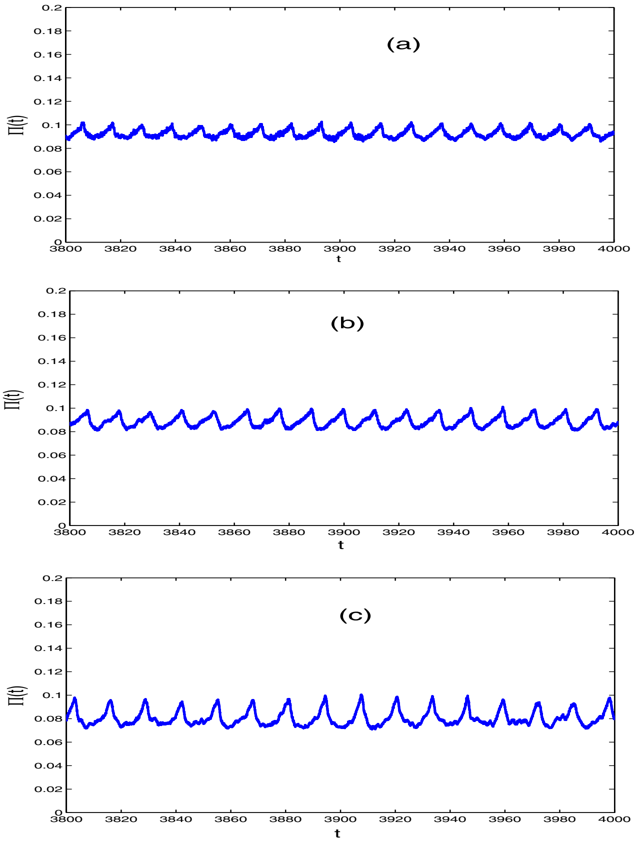

Fig. 4. The corresponding firing-rate functions of Figure 3.

the characteristic width of the spatial waves increases as D increases.

Intuitively, it is not clear why the spatio-temporal coherence resonance increases or decreases when the diffusive coefficient increases as a result of two opposite effects, one associated with the decrease of the number of cycles and the other with the increase of width. However, a basic property of the firing rate function may guide us to understand this phenomenon very well. It is observed in Figure 4 that the fluctuation amplitude of the firing rate function becomes large as D is increased, which implies the enhancement of the spatio-temporal coherence resonance. To further explain this, Figure 5a shows the power spectrum density of the firing rate function for different diffusive coefficients at the noise level $\sigma = 25$. It is obvious that the highest peak of the power spectrum density exhibits an increase as the diffusive coefficient increases.

To quantitatively characterize the coherence of the spatio-temporal motion, we employ the time series of the firing rate function, whose amplitude and temporal coherence reflect the spatial and temporal coherence in the lattice, respectively, to define a spatio-temporal coherence quantity [25],

$$\beta = H\frac{\omega_p}{\Delta\omega}, \tag{3}$$

where ω_p is the frequency of the main peak in the spectrum of Π, H is the peak height mainly depending on the amplitude of Π, and $\Delta\omega$ is the half-width of the peak, reflecting the temporal randomness of Π. In Figure 5b, β is shown as a function of the diffusive coefficient D for the noise level $\sigma = 25$. It is observed that the coherence quantity β is increases as the diffusive coefficient becomes larger, which implies the enhancement of the spatio-temporal coherence resonance.

4.2 Characteristics of the firing rate function and spatial waves

In particular, we found in Figure 7a that the average period of the firing rate function increases as the diffusive coefficient is increased. Moreover, it is observed that there exists an approximate linear relation between the average period of the firing rate function and the diffusive coefficient. Numerical results are in good accordance with the linear function $\langle T\rangle = 2.652D + 9.158$. The mechanism of variation of the average period can be understood as follows: larger D not only constitute faster diffusive spread, which results in wider waves, but can also make local excitations tend to die out more quickly. Thus, most neurons in this network cannot leave their steady states for firing until a stronger stimulus is accumulated, which results in an enhancement of the average period. Moreover, since a nonlinear selection of threshold-crossing events in excitable systems is absent, it is understandable that the dependence of the average period on the diffusive coefficient obeys to a linear relation.

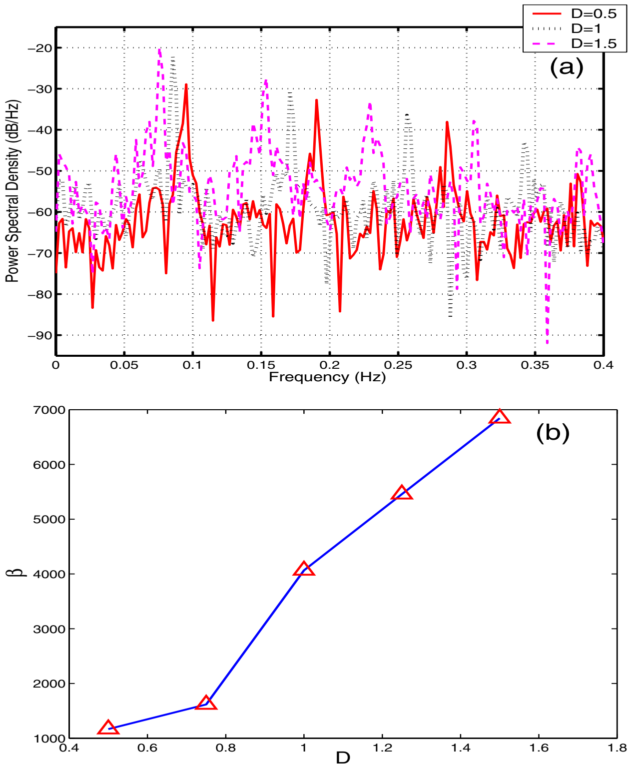

Fig. 5. (a) Variations of the power spectrum density for different diffusive coefficients. (b) The coherence quantity β vs. the diffusive coefficient D.

It was remarked in [26] that the typical width of a particular circular wave in the square-lattice Rulkov-map neural network could be estimated in terms of the statistical relation: $W = \sqrt{\tau D}$. Here, $\tau \propto n_e =$ constant and n_e is the excursion time, which was given by the width of spikes depicted in the temporal plots of Figure 1. Figure 6 shows an estimation of the typical width of a particular circular wave. Dependence of W on D is shown in Figure 7b, with $\tau \approx 5.9820$. It is evident that the values obtained here are in excellent agreement with the predicted square-root function, which reflects a fixed excursion time n_e, characteristic for excitable systems, thus shedding light on the noise-induced pattern formation in the presently studied spatially extended system.

5 Conclusions and discussion

Spatio-temporal patterns in a square-lattice HH neural network with nearest diffusive coupling have been studied. Results show that there exist ordered circular waves with a layered structure in this network at an intermediate noise level. As the noise level increases, the ordered circular waves become deformed, and finally transform into random patterns. The characteristics of noise-induced patterns have also been investigated in dependence on the diffusive coefficient. It is found that the spatio-temporal coherence resonance characterized by the coherence quantity β is increased as the diffusive coefficient increases.

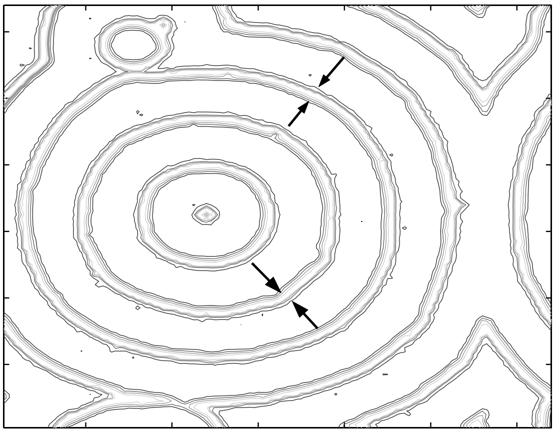

Fig. 6. Explanation of the typical width of waves. Arrows indicate the typical width of the waves, which can be seen to be constant.

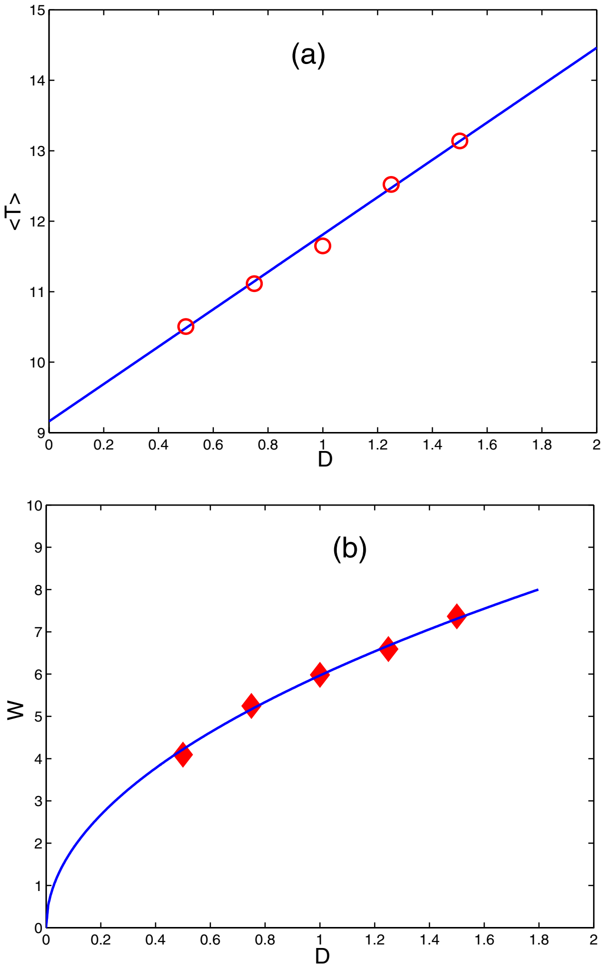

Fig. 7. (a) Dependence of the average period on the diffusive coefficient; circles denote the evaluated average period, while the curve is the fitting $\langle T\rangle = 2.652D{+}9.158$. (b) Dependence of the width of the wave on the diffusive coefficient; diamonds denote the evaluated typical width of the waves, while the curve is the predicted $W = \sqrt{\tau D}$ dependence for $\tau = 5.9820$. Here, the noise level is $\sigma = 25$.

Moreover, the average period of the firing rate function exhibits good linear curve-fitting. Furthermore, by studying the dependence of the typical width of emergent circular waves on various diffusive coefficient values D, it is found that the typical wave width W increases with the square root of D, thereby confirming the explanation given in reference [26].

Several past studies have shown that higher central nervous systems can actually utilize noise to enhance sensory information. For example, it enhances the human tactile sensation, the human visual perception, and the animal feeding behaviour [9]. We have adopted a more realistic biological Hodgkin-Huxely neuron model to study spatial patterns, so as to get better insight into the information processing function of the central nervous system in the presence of noise. Our results show that spatially extended HH neuron models can collectively respond to external noise in the form of ordered circular waves at an intermediate noise level. This is closely related to the existence of resonance, confirmed by recent studies in the human brain [8–11]. Nowadays, many humans live in an environment that is full of stochastic influences and unpredictability. Therefore, it is important to study how noise affects the functioning of neural systems. Only by this can the concept of noise-enhanced sensation be further developed into techniques and devices so as to help stroke patients and those with muscle and joint injuries in rehabilitating activities. Hence, it is extremely important to provide deeper insight into how stochastic fluctuations might affect neural functioning. Results in this paper may provide a better understanding of the generation of spatio-temporal patterns in such neural systems.

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