



Delay-enhanced coherence of spiral waves in noisy Hodgkin–Huxley neuronal networks

Qingyun Wang^{a,b,*}, Matjaž Perc^c, Zhisheng Duan^a, Guanrong Chen^{a,d}

^a State Key Laboratory for Turbulence and Complex Systems, Department of Mechanics and Aerospace Engineering, College of Engineering, Peking University, Beijing 100871, China

^b School of Statistics and Mathematics, Inner Mongolia Finance and Economics College, Huhhot 010051, China

^c Department of Physics, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška cesta 160, SI-2000 Maribor, Slovenia

^d Department of Electronic Engineering, City University of Hong Kong, Hong Kong SAR, China

ARTICLE INFO

Article history:

Received 16 April 2008

Received in revised form 24 June 2008

Accepted 2 July 2008

Available online 5 July 2008

Communicated by C.R. Doering

PACS:

05.45.-a

05.40.-a

89.75.Kd

Keywords:

Neuronal networks

Delay

Spiral wave

Coherence resonance

ABSTRACT

We study the spatial dynamics of spiral waves in noisy Hodgkin–Huxley neuronal ensembles evoked by different information transmission delays and network topologies. In classical settings of coherence resonance the intensity of noise is fine-tuned so as to optimize the system's response. Here, we keep the noise intensity constant, and instead, vary the length of information transmission delay amongst coupled neurons. We show that there exists an intermediate transmission delay by which the spiral waves are optimally ordered, hence indicating the existence of delay-enhanced coherence of spatial dynamics in the examined system. Additionally, we examine the robustness of this phenomenon as the diffusive interaction topology changes towards the small-world type, and discover that shortcut links amongst distant neurons hinder the emergence of coherent spiral waves irrespective of transmission delay length. Presented results thus provide insights that could facilitate the understanding of information transmission delay on realistic neuronal networks.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Spiral wave dynamics is the subject of ongoing and intense investigations in diverse fields of research ranging from physics and chemistry to biology [1–3]. Especially within real neuronal networks spiral waves are common, and temporal variations of spiral core numbers have been studied extensively [4,5]. To deepen the understanding of mechanisms behind the generation of spiral waves in neuronal systems, several theoretical as well as experimental studies have been conducted, resulting in fascinating new discoveries and insights. In particular, self-maintaining spiral waves have been observed in a non-homogeneous neuronal network with uniform initial conditions, whereas the breakup of outwardly rotating spiral waves has been reported also in settings different from the neuronal dynamics [6–8]. Moreover, the breakup of inwardly rotating spiral waves has been investigated in an oscillatory FitzHugh–Nagumo system near a Hopf bifurcation [9], where it has been shown that the breakup first occurred by regions that are far

away from the core area and then gradually penetrated the whole medium as the diffusion coefficient ratio between the two components of the oscillatory system increased. Two-dimensional lattices of non-homogeneous cardiac cells have also been shown to generate spiral waves due to spatial discreteness and inhomogeneity of the model [10]. Interestingly, it has been argued that the breakup of spiral waves may be an important mechanism by cardiac fibrillation [11], as it was discovered that spatiotemporal patterns of cardiac activity by human seizures have a consistent dynamical evolution by the initialization, development as well as termination of each seizure [12].

Intimately related to the above findings concerning spiral wave formation in non-homogeneous two-dimensional excitable media are studies reporting stochastic and coherence resonance phenomena in dynamically similar excitable systems [13–24]. As noise is an inseparable part of any real-life process, the understanding of its potential impacts is of vital importance. To date, it has become an established and well-accepted fact that biological neurons can exploit the constructive role of noise to extract hindered information and enhance weak stimuli via stochastic resonance [25–27]. Aside from these two rather main-stream phenomena, there exist several related reports on noise-induced order either from chaotic states [28], by means of variations in system size [29,30] and di-

* Corresponding author at: State Key Laboratory for Turbulence and Complex Systems, Department of Mechanics and Aerospace Engineering, College of Engineering, Peking University, Beijing 100871, China. Tel./fax: +86 10 62765037.

E-mail address: nmqingyun@163.com (Q. Wang).

versity [31], or via an enhancement of synchronization in coupled systems [32–34]. Furthermore, order out of noise and the dynamical properties of excitatory events in general have been studied extensively also in non-identical ensembles of systems governed by nonlinear dynamics, such as neurons [35], as well as in small-world neuronal networks [36,37] and ensembles of bistable overdamped oscillators [38]. Following initial advances on isolated dynamical systems, the phenomena of stochastic and coherence resonance have been generalized also to two-dimensional media. In particular, spatiotemporal stochastic resonance has been reported in [39], while spatial coherence resonance has been introduced first near pattern forming instabilities [40] and subsequently also in excitable media [41]. The characteristics of noise-induced patterns have also been investigated in a spatially extended Hodgkin–Huxley (HH) neuronal network in dependence on the coupling strength [42], and it was found that the spatiotemporal dynamics could be enhanced as the connections amongst neurons became stronger. Aside from these examples, the body of recent literature devoted to the study of noise and other stochastic influences on the dynamics of spatially extended systems is huge, so that we found it impossible to select or review here all relevant contributions. The interested reader is pointed towards Ref. [43], while some exemplary studies are also given in [44–50].

Recently, the body of literature devoted to studying effects of noise on nonlinear, and in particular excitable dynamical systems has been supplemented extensively by the addition of effects of different delay lengths, either in terms of information transmission delay [51] or a delayed inhibitory feedback [52]. It has been shown (see e.g. [51]) that the coherence of noise-induced pulses may exhibit a double resonance outlay that emerges if the delay length is optimally fine-tuned. Furthermore, the phenomenon of stochastic resonance has also been investigated in related systems incorporating time-delay feedback mechanisms [53,54]. However, since information transmission delays are inherent in intra- and inter-neuronal communication because of finite propagation velocities governing the conduction of signals along neuritis as well as delays in the synaptic transmission along chemical synapses [55], it is thus important to understand the dynamics of coupled neuronal ensembles when such temporal delays are not negligible, as was comprehensively exemplified in [56]. Notably, it has been suggested that time delays can facilitate neural synchronization and lead to many interesting and even unexpected phenomena [57,58].

To elaborate on the latter statement and to extend the scope of the subject, we presently study the dynamics of spiral waves in noisy neuronal networks subject to information transmission delay. We employ the realistic Hodgkin–Huxley (HH) [59] model of neuronal dynamics and, in addition to different delay lengths and the classic diffusive coupling, consider also small-world interactions governing the dynamics of the ensemble. More precisely, we examine the impact of different transmission delay lengths on the spiral wave dynamics. We find that, while short transmission delays do enable the existence of spiral waves, their spatial order can be substantially improved if the delay length is fine-tuned. On the other hand, long information transmission delays completely hinder the emergence of spiral waves, thus clearly indicating a resonance-like dependence of the spatial order of spiral waves on the transmission delay length. In particular, we find that there exists an intermediate information transmission delay length by which the spiral waves are optimally ordered in space, hence reporting delay-enhanced coherence of spatial dynamics in the examined system. Importantly, this phenomenon can be observed best on diffusive neuronal networks, whereas the introduction of shortcut links amongst distant units, eventually constituting a small-world topology, progressively hinders coherent spiral wave formation. By employing the circularly averaged spatial structure function [43], we provide conclusive evidences for the delay-enhanced coherence of

spiral waves on diffusively coupled HH neuronal networks, as well as for the small-world induced breakup of spiral waves and related decoherence of spatial dynamics of excitatory events. Interestingly though, the optimal information transmission delay is almost immune to the transition from diffusive to small-world interactions amongst coupled neurons, suggesting that the delay-enhanced coherence is a robust mechanism warranting an enhancement of spatial order by the formation of spiral waves in noisy neuronal environments. These findings can have important practical implementations by various tasks that fall into the domain of neuronal networks (e.g. communication, information processing or computation), where noise and information transmission delays, as well as small-world-like interconnectedness, appear to be universally present.

The Letter is organized as follows. Section 2 is devoted to the description of the HH model and employed networks, whereas Section 3 evidences the phenomenon of delayed-enhanced coherence of spiral waves if the diffusive topology is used. Effects of small-world topology on the delayed-enhanced coherence are presented in Section 4, while the last section summarizes the results.

2. Mathematical model and setup

The spatiotemporal dynamics of studied HH neuronal networks is governed by the following differential equations [59]:

$$C \frac{dV_{i,j}}{dt} = -g_{Na}m_{i,j}^3h_{i,j}(V_{i,j} - V_{Na}) - g_L(V_{i,j} - V_L) - g_Kn_{i,j}^4(V_{i,j} - V_K) + I + D \sum_{k,l} \varepsilon_{i,j,k,l} [V_{k,l}(t - \tau) - V_{ij}] + \sigma \xi_{i,j}(t), \quad (1)$$

$$\frac{dm_{i,j}}{dt} = \alpha_{m_{i,j}}(1 - m_{i,j}) - \beta_{m_{i,j}}m_{i,j}, \quad (2)$$

$$\frac{dh_{i,j}}{dt} = \alpha_{h_{i,j}}(1 - h_{i,j}) - \beta_{h_{i,j}}h_{i,j}, \quad (3)$$

$$\frac{dn_{i,j}}{dt} = \alpha_{n_{i,j}}(1 - n_{i,j}) - \beta_{n_{i,j}}n_{i,j}, \quad (4)$$

where V is the transmembrane voltage in mV, m is the activation and h the inactivation coefficient of sodium conductance, n is the activation coefficient of potassium channels, while the time (t) units are seconds. For a more detailed descriptions of all variables we refer the reader to the original work [59]. The sum in Eq. (1) runs over all lattice sites whereby $\varepsilon_{i,j,k,l} = 1$ if the site (k, l) is coupled to (i, j) and $\varepsilon_{i,j,k,l} = 0$ otherwise. When $\varepsilon_{i,j,k,l} = 1$ only if (k, l) is one of the four nearest neighbors of the focal site (i, j) we obtain a diffusively coupled network of HH neurons each having degree $z = 4$, as depicted in Fig. 1(a). The latter will be used throughout Section 3. However, if a certain fraction $0 < q \ll 1$ of links constituting the diffusively coupled network is randomly rewired, as exemplified in Fig. 1(b), the resulting network is of small-world type [60]. Presently we employ the rewiring procedure described in [61] to preserve the degree of each neuron ($z = 4$), which enables us to focus explicitly on the effect of network topology rather than possible effects originating from different numbers of inputs per neuron. Small-world networks will be used in Section 4. Importantly, we generated each interaction network at the beginning of a particular simulation and kept it fixed the whole time; and moreover, if necessary below results were averaged over 30 different realizations of the interaction network by each q . Quantities σ and τ in Eq. (1) denote the standard deviation of additive uncorrelated Gaussian noise $\xi_{i,j}$, satisfying $\langle \xi_{i,j}(t) \rangle = 0$ and $\langle \xi_{i,j}(t), \xi_{m,n}(t') \rangle = \delta(t - t')\delta_{i,m}\delta_{j,n}$, and the transmission delay, respectively. In order to introduce a noisy background for the dynamics, we set $\sigma = 1.0$ and do not vary this

Table 1
Employed parameter values

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

parameter in the following sections. Furthermore, $D = 0.5$ is the presently employed coupling strength, $i, j = 1, \dots, N = 128$ is the system size in each direction of the two-dimensional grid with periodic boundary conditions, whilst all other parameter values used throughout the Letter are listed in Table 1. Finally, the experimentally determined voltage transition rates are given explicitly by the following expressions:

$$\alpha_{m_{i,j}} = \frac{0.1(V_{i,j} + 10)}{1 - \exp\left[-\frac{(V_{i,j} + 40)}{10}\right]}, \quad (5)$$

$$\beta_{m_{i,j}} = 4 \exp\left[-\frac{(V_{i,j} + 65)}{18}\right], \quad (6)$$

$$\alpha_{h_{i,j}} = 0.07 \exp\left[-\frac{(V_{i,j} + 65)}{20}\right], \quad (7)$$

$$\beta_{h_{i,j}} = \left\{ 1 + \exp\left[-\frac{(V_{i,j} + 35)}{10}\right] \right\}^{-1}, \quad (8)$$

$$\alpha_{n_{i,j}} = \frac{0.01(V_{i,j} + 55)}{1 - \exp\left[-\frac{(V_{i,j} + 55)}{10}\right]}, \quad (9)$$

$$\beta_{n_{i,j}} = 0.125 \exp\left[-\frac{(V_{i,j} + 65)}{80}\right]. \quad (10)$$

For a single HH neuron in the absence of noise ($\sigma = 0$), a subcritical Hopf bifurcation occurs at the external current $I_1 = 9.8 \mu\text{A}/\text{cm}^2$. Between $I = I_2 = 6.2 \mu\text{A}/\text{cm}^2$ and I_1 stable oscillatory solutions coexist with stable steady states, whereas for $I < I_2$ excitable steady states are the only stable solutions. As I is increased further and is larger than $I = 155 \mu\text{A}/\text{cm}^2$, the stable limit cycle vanishes via the supercritical Hopf bifurcation. A more detailed bifurcation analysis of the HH neuron was performed in [62]. Here we are interested in the parameter region $I < I_2$, where neurons are unable to fire spontaneously. At present, we set $I = 6.1 \mu\text{A}/\text{cm}^2$ such that each neuron in the network stays at an excitable steady state. Importantly, the employed intensity of noise, equaling $\sigma = 1.0$ throughout this work, is too small to warrant large amplitude excitations as it serves only to provide a noisy background for the dynamics in accordance with real neuronal systems. Moreover, the employed coupling strength $D = 0.5$ also prevents spontaneous firings, and thus in this respect neither σ nor D fulfill any special resonance criteria, but simply warrant steady state excitable behavior with a noisy background upon which the spiral waves can be introduced with appropriate initial conditions [63].

3. Delay-enhanced coherence on diffusive networks

Using suitable initial conditions for spiral wave formation (see e.g. [63]), we first present results obtained on diffusively coupled HH neuronal networks. We start by showing snapshots of $V_{i,j}$ obtained by different values of τ in Fig. 2. The visual examination of the three snapshots reveals rather clearly that as the delay increases the spiral wave formation may become completely impaired [see Fig. 2(c)], yet in the interim, the spirals may become denser and the excitatory fronts somewhat narrower [see Fig. 2(b)] in comparison to the delay-free case [see Fig. 2(a)]. Thus, presented results do attest to the fact that different transmission delay

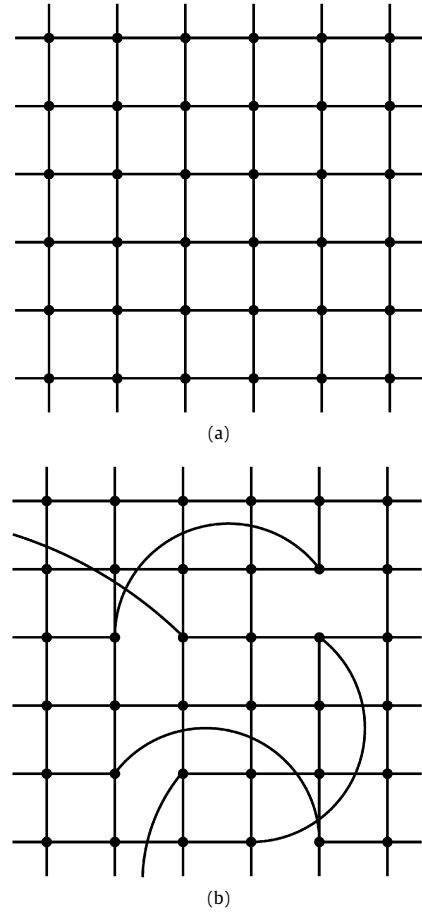


Fig. 1. Examples of considered network topologies. For clarity only a 6×6 excerpt of the whole network is presented in each panel. (a) Diffusively coupled network characterized by $q = 0$. Each vertex is directly connected only to its four nearest neighbors, hence having connectivity $z = 4$. (b) Realization of small-world topology via random rewiring of a certain fraction q of links, constrained only by the requirement that the initial connectivity $z = 4$ of each unit must be preserved.

lengths play a significant role by the spiral wave formation on diffusively coupled HH neuronal networks. However, solely from the visual inspection of the snapshots, it is difficult to deduce whether intermediate values of τ actually succeed in improving the order of the spatial dynamics, and thus whether we can speak of delay-enhanced coherence or not.

In order to quantify the spatial order of spiral waves presented in Fig. 2 more precisely, the spatial structure function of $V_{i,j}$ is introduced as follows:

$$P(k_x, k_y) = \langle H^2(k_x, k_y) \rangle, \quad (11)$$

where $H(k_x, k_y)$ is the two-dimensional Fourier transform of the spatial grid at a particular time t and $\langle \dots \rangle$ is the ensemble average over different temporal realizations. Results obtained via Eq. (11) for the three τ used for the snapshots in Fig. 2 are presented in Fig. 3. If compared with one another, it can be observed that for the intermediate value of τ the spatial structure function is characterized by best-expressed periodic undulations of the surface [see Fig. 3(b)], whereas smaller and larger τ do not evoke such a persuasive response. In particular, while for $\tau = 0.0$ some periodic undulations can still be inferred [see Fig. 3(a)], the latter vanish completely in panel (c) where the length of the transmission delay completely hinders spiral wave formation as exemplified in Fig. 2(c). These results fuel the fact that fine-tuned information transmission delays may indeed warrant optimally ordered spiral waves in noisy diffusively coupled HH networks.

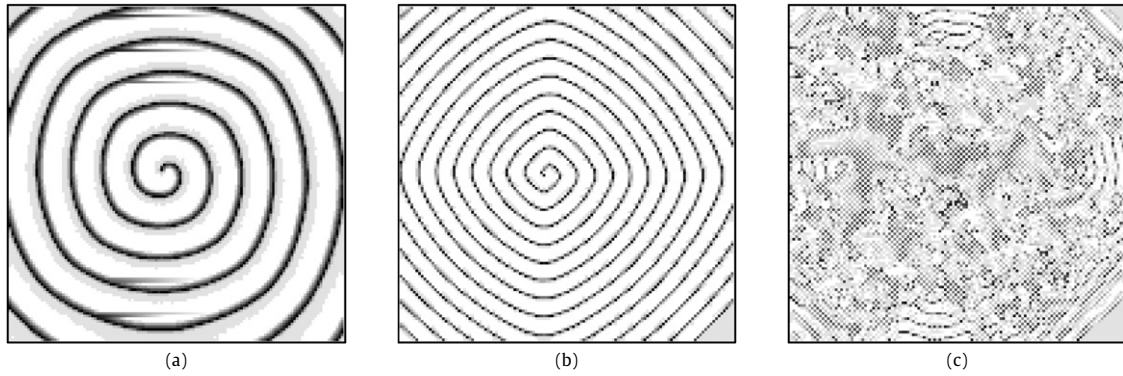


Fig. 2. Spiral wave formation on diffusively coupled HH neuronal networks. All panels depict values of $V_{i,j}$ on a 128×128 square grid at a given time t . The information transmission delay τ is: (a) 0.0, (b) 1.2 and (c) 2.2. Grey scale coloring in all panels is linear, white depicting minimal (-80) and black maximal (40) values of $V_{i,j}$.

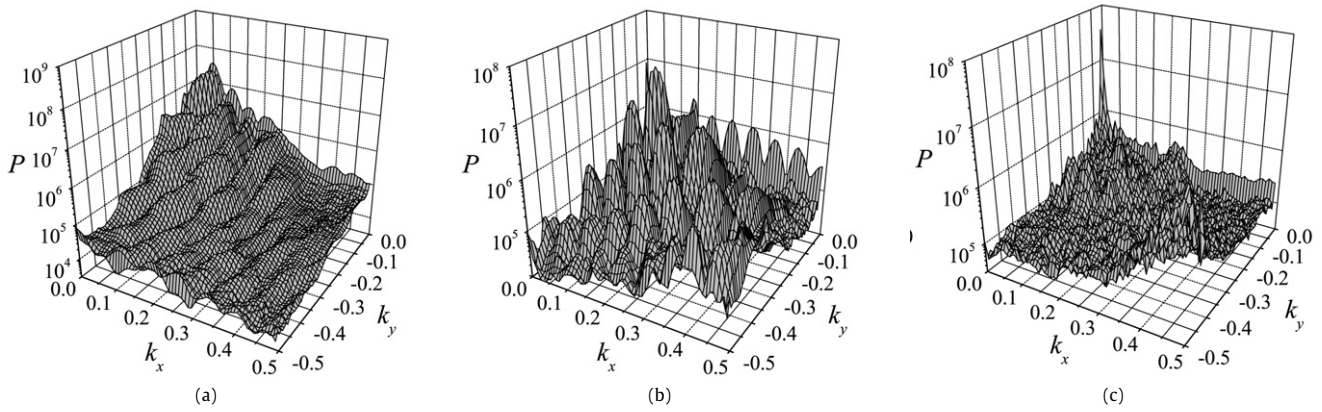


Fig. 3. Spatial structure functions of $V_{i,j}$ obtained for different values of τ : (a) 0.0, (b) 1.2 and (c) 2.2. Note that in all panels only an excerpt of the whole $P(k_x, k_y)$ plane is shown for better clarity.

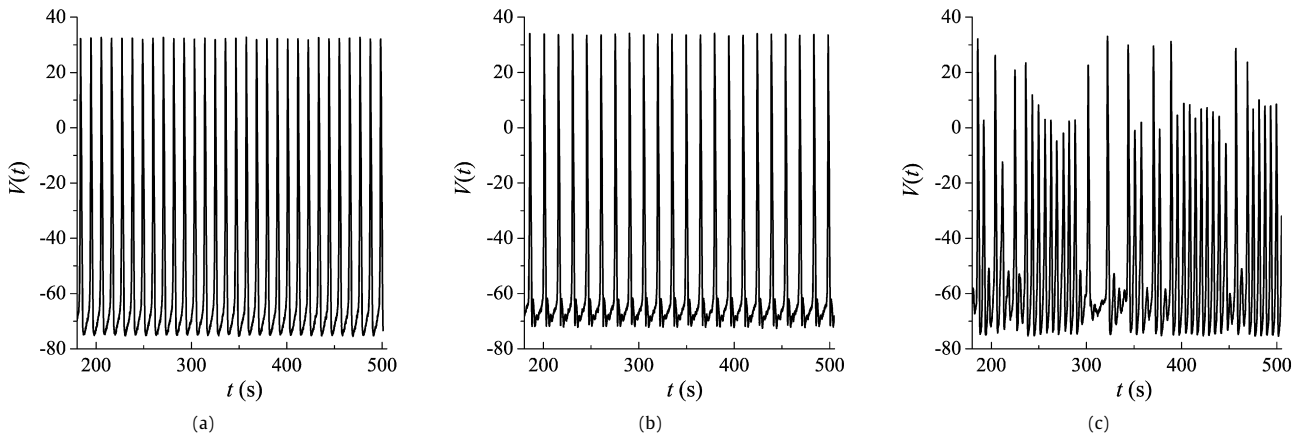


Fig. 4. Temporal courses of $V_{i,j}$ for the neuron $i = j = 32$ and information transmission delays τ : (a) 0.0, (b) 1.2 and (c) 2.2.

In order to support these findings further, we present in Fig. 4 temporal courses of activity of a single neuron forming the diffusively coupled HH network; again for the same values of τ as used in the previous two figures. The temporal course has the advantage that it gives information in continuous time (not just a snapshot), and the obvious disadvantage that it does not capture the whole spatial dynamics but just the temporal dynamics of a single unit. Nevertheless, as the spiral waves for small τ propagate uniformly in space, the back-tracking from the temporal to the spatial dynamics is straightforward. Indeed, there exist good qualitative agreement between the snapshots presented in Fig. 2 and the temporal courses, as both the temporal and the spatial dynamics are either superbly ordered or mostly disordered. For ex-

ample, the lack of an ordered spatial dynamics depicted in Fig. 2(c) is reflected clearly also in the temporal course because the latter is highly irregular as well. It is interesting to note, however, that although the spatial frequency of spiral waves increases with increasing τ [compare Figs. 2(a) and (b) as well as Figs. 4(a) and (b)], the temporal frequency of excitatory events by each particular unit decreases, which implies that the diffusion slows down in comparison to the $\tau = 0.0$ case. This is not surprising as it directly reflects the fact that finite information transmission delays govern the evolution of the system.

Finally, we summon above indications of delay-enhanced coherence of spiral waves by exploiting the outlay of $P(k_x, k_y)$ as proposed by Carrillo et al. [40] to obtain an estimate for the co-

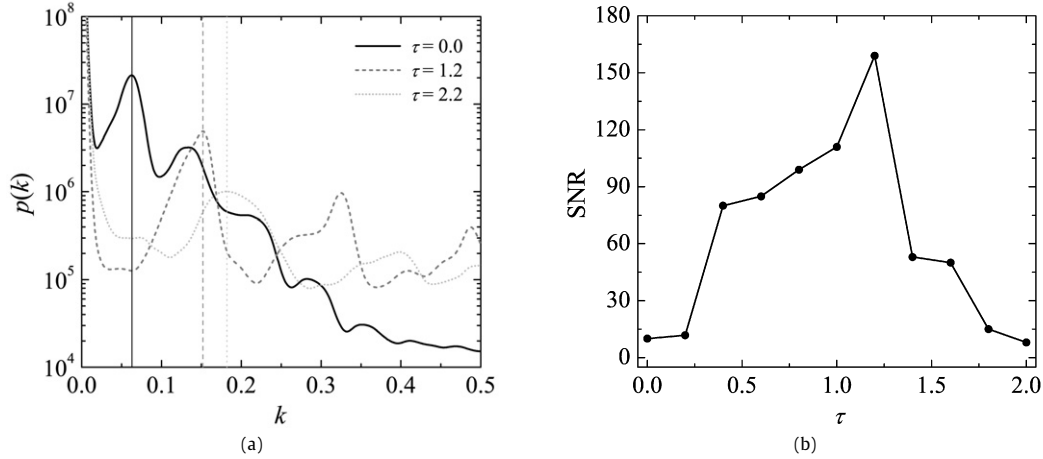


Fig. 5. Evidences for delay-enhanced coherence of spiral waves in diffusively coupled noisy HH neuronal networks. (a) Circular averages $p(k)$ of structure functions $P(k_x, k_y)$ presented in Fig. 3. The vertical lines at $k = k_{\max}$ mark spatial frequencies of spiral waves that are enhanced by given values of τ . (b) Characteristic bell-shaped dependence of the SNR on τ , thus clearly evidencing delay-enhanced coherence in the examined system.

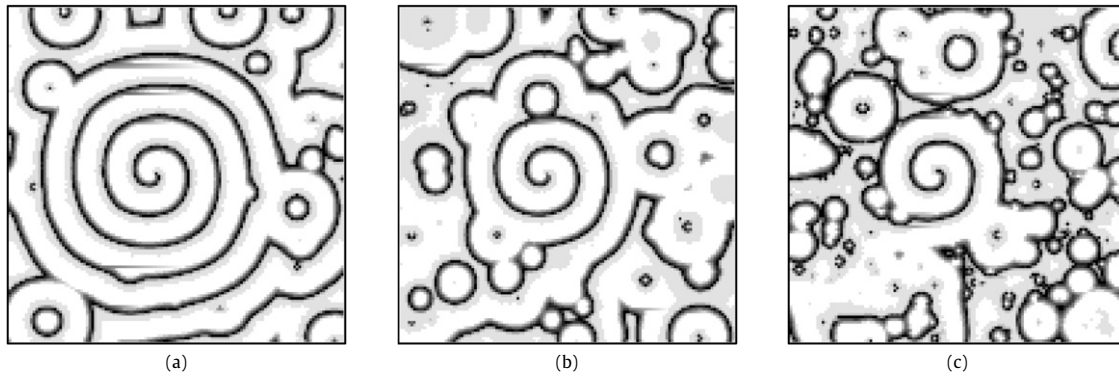


Fig. 6. Spiral wave formation on noisy HH neuronal networks of small-world type with information transmission delay $\tau = 0.2$. The rewiring probability q is: (a) 0.001, (b) 0.003 and (c) 0.005. All panels depict values of $V_{i,j}$ on a 128×128 square grid at a given time t . Grey scale coloring in all panels is linear, white depicting minimal (-80) and black maximal (40) values of $V_{i,j}$.

herence of the spatial dynamics of spiral waves brought about by different τ . In particular, we calculate the circular average of the structure function according to the equation

$$p(k) = \int_{\Omega_k} P(\vec{k}) d\Omega_k, \quad (12)$$

where $\vec{k} = (k_x, k_y)$, and Ω_k is a circular shell of radius $k = |\vec{k}|$. Plots of $p(k)$ are shown in Fig. 5(a) for the three different τ used above. These results evidence more concisely what could be inferred already from outlays of $P(k_x, k_y)$ presented in Fig. 3. In particular, we can establish conclusively that there exist particular spatial frequencies, marked with vertical dashed lines, which are resonantly enhanced by given values of τ . Importantly however, by $\tau = 1.2$ the primary hump (secondary humps are just higher harmonics) is expressed best in comparison to the level of background noise. To quantify the ability of different τ to extract a particular spatial frequency more precisely, we calculate the signal-to-noise ratio (SNR) as the peak height at $k = k_{\max}$ [marked with vertical dashed lines in Fig. 5(a)] normalized with the background fluctuations in the system:

$$\text{SNR} = p(k_{\max})/\bar{p}, \quad (13)$$

where $\bar{p} = [p(k_{\max} - \Delta k_a) + p(k_{\max} + \Delta k_b)]/2$ is an approximation for the level of background fluctuations whereby Δk_a and Δk_b mark the estimated width of the peak around k_{\max} by each particular τ . Variations of SNR in dependence on τ are shown in Fig. 5(b). Indeed, a typical bell-shaped curve characterizes this de-

pendence, thus clearly indicating the possibility of delay-enhanced coherence in noisy diffusively coupled HH neuronal networks. In particular, there exists an optimal finite delay τ by which the spatial dynamics of spiral waves is most coherent, and accordingly the SNR exhibits a maximum, thus suggesting that neuronal ensembles may adjust and optimize their group performance via fine-tuning of the information transmission delay.

4. Decoherence of spiral waves due to small-world interactions

In this section, we examine the impact of small-world topology on the above reported delay-enhanced coherence of spiral waves. For this purpose, we keep the delay constant at $\tau = 0.2$ and first examine characteristic snapshots of $V_{i,j}$ obtained by three different rewiring probabilities q . Snapshots presented in Fig. 6 reveal that the spiral waves become progressively destroyed as q increases. More precisely, circular waves start to appear at random locations on the spatial grid, thereby disrupting the superbly ordered spiral structures that could be observed by diffusive interactions in Figs. 2(a) and (b). The emergence of these additional excitatory cores must be attributed to the introduction of long-range connections amongst distant neurons as they cause firings irrespective of whether the main front has arrived at a particular neuron or not. Such randomly introduced cores can then propagate excitations further via the diffusive route that still dominates the majority of neuronal interactions. Moreover, since larger q introduce more such shortcuts, it is thus understandable that the

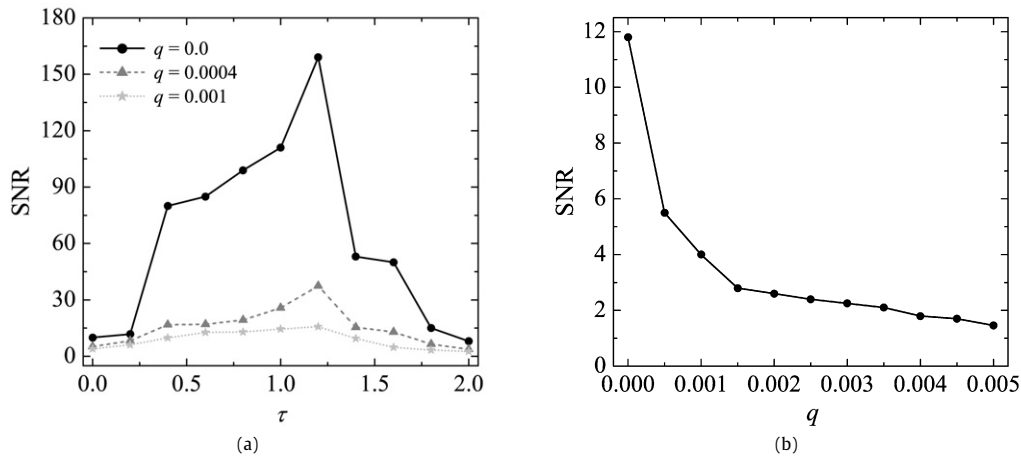


Fig. 7. Decoherence of spiral wave spatial dynamics via the introduction of small-world connectivity amongst noisy HH neurons. (a) Dependence of SNR on τ for different q . Evidently, the maximally attainable peak value of SNR decreases fast as q increases even if the value of τ is fine-tuned. (b) SNR in dependence on q when $\tau = 0.2$. Note that the optimal τ remains unaffected by increasing q , as can be inferred from Fig. 7(a).

number of new cores of excitatory events increases, as can be observed by comparing results presented in the three panels of Fig. 6.

To investigate the effect of small-world connectivity on the spiral wave formation in noisy HH networks more precisely, we conduct the same analysis as in the preceding section. Fig. 7(a) shows how the SNR varies in dependence on τ by different q . Presented results fully support the visual assessment of spatial portraits in Fig. 6, as the maximally attainable peak of SNR decreases continuously as q increases. Albeit importantly, the optimal $\tau = 1.2$ does not change as q increases, thus indicating that the delay-enhanced coherence presented in Section 3 is a robust mechanism warranting an enhancement of spatial order by the formation of spiral waves in noisy neuronal environments. Further supplementing the small-world induced decoherence of spiral waves are results presented in Fig. 7(b), which show that in fact the SNR by $\tau = 0.2$ decreases almost exponentially as q increases. Presented results thus confirm that long-range interactions amongst distant neurons preclude the observation of ordered spatial dynamics on two-dimensional neuronal networks. Moreover, this holds irrespective of delay fine-tuning and spiral wave dynamics governing the spatiotemporal evolution of the presently employed HH mathematical model.

5. Summary

In sum, we study the impact of different lengths of information transmission delay on spiral wave formation in noisy HH neuronal networks. Presented results evidence that the spiral waves become optimally ordered by an intermediate length of the transmission delay, hence evidencing the phenomenon of delay-enhanced coherence of the spatial dynamics of spiral waves. In particular, while short transmission delays warrant considerably ordered spiral waves, the latter can be additionally regularized via fine-tuning of the delay. On the other hand, long transmission delays may completely hinder coherent pattern formation, thus ultimately resulting in a resonant dependence of the order of spatial dynamics on the transmission delay length. In addition, we show that a small fraction of shortcut links amongst distant units still preserves this phenomenon, yet as the small-world topology becomes increasingly pronounced coherent pattern formation is impaired. Indeed, as low as 0.1% of rewired links completely hinder the emergence of ordered spirals, thus indicating that information transmission delays cannot prevent the small-world induced decoherence of spatial dynamics. We demonstrate that the decoherence is truly very fast, as a near exponential decrease of SNR can be observed as q

increases. From the biological aspect, the existence of an optimal finite information transmission delay for coherent spiral wave formation in neuronal networks seems reasonable, since it has been reported [64] that the conduction velocity along axons connecting neurons varies from 20 to 60 m/s. Real-life transmission delays are thus within a range of milliseconds, suggesting that substantially lower or higher values may be preclusive for optimal functioning of neuronal tissue. In the field of neuroscience, where excitability, noise, delay and complex topologies appear to be universally present, the need for additional theoretical as well as experimental studies is substantial, and it is our sincere hope that the present work will be an inspiration for the future.

Acknowledgements

This work was supported by the National Science Foundation of China (Funds Nos. 10702023 and 60674093) and China's Post-Doctoral Science Foundation (Fund No. 20070410022). This work was partially supported also by the National Science Foundation of Inner Mongolia Autonomous Region (Fund No. 2007110020110). Matjaž Perc additionally acknowledges support from the Slovenian Research Agency (Project No. Z1-9629).

References

- [1] A.N. Zaikin, A.M. Zhabotinsky, *Nature (London)* 255 (1970) 535.
- [2] A.T. Winfree, *Science* 175 (1972) 634.
- [3] K.J. Lee, E.C. Cox, R.E. Goldstein, *Phys. Rev. Lett.* 76 (1996) 1174.
- [4] N. Bursac, F. Aguel, L. Tung, *Proc. Natl. Acad. Sci. USA* 101 (2004) 15530.
- [5] S.-M. Hwang, K.-H. Yea, K.J. Lee, *Phys. Rev. Lett.* 92 (2004) 198103.
- [6] M. Bär, M. Hildebrand, M. Eiswirth, M. Falcke, H. Engel, M. Neufeld, *Chaos* 4 (1994) 499.
- [7] S.M. Tobias, E. Knobloch, *Phys. Rev. Lett.* 80 (1998) 4811.
- [8] Q. Ouyang, H.L. Swinney, G. Li, *Phys. Rev. Lett.* 84 (2000) 1047.
- [9] F.G. Xie, D.Z. Xie, J.N. Weiss, *Phys. Rev. E* 74 (2006) 026107.
- [10] O.I. Kanakov, G.V. Osipov, C.-K. Chan, J. Kurths, *Chaos* 17 (2007) 015111.
- [11] J.N. Weiss, H.S. Karagueuzian, Z.L. Qu, P.S. Chen, *Circulation* 99 (1999) 2819.
- [12] S.J. Schiff, T. Sauer, R. Kumar, S.L. Weinstein, *NeuroImage* 28 (2005) 1043.
- [13] W. Horsthemke, R. Lefever, *Noise-Induced Transitions*, Springer, Berlin, 1984.
- [14] P. Häggi, R. Bartussek, in: J. Parisi, S.C. Müller, W. Zimmermann (Eds.), *Nonlinear Physics of Complex Systems*, Springer, New York, 1999.
- [15] R. Benzi, A. Sutera, A. Vulpiani, *J. Phys. A* 14 (1981) L453.
- [16] C. Nicolis, G. Nicolis, *Tellus* 33 (1981) 225.
- [17] A. Neiman, W. Sung, *Phys. Lett. A* 223 (1996) 341.
- [18] S.G. Lee, S. Kim, *Phys. Rev. E* 60 (1999) 826.
- [19] L. Martínez, T. Pérez, C.R. Mirasso, E. Manjarrez, *J. Neurophysiol.* 97 (2007) 4007.
- [20] E. Manjarrez, I. Mendez, L. Martínez, A. Flores, C.R. Mirasso, *Neurosci. Lett.* 415 (2007) 231.
- [21] P. Jung, *Phys. Rep.* 234 (1993) 175.

- [22] L. Gammaitoni, P. Hänggi, P. Jung, F. Marchesoni, *Rev. Mod. Phys.* 70 (1998) 223.
- [23] A.S. Pikovsky, J. Kurths, *Phys. Rev. Lett.* 78 (1997) 775.
- [24] S. Zhong, H.W. Xin, *Chem. Phys. Lett.* 333 (2001) 133.
- [25] G. Mato, *Phys. Rev. E* 59 (1999) 3339.
- [26] M.J. Chacron, B. Lindner, A. Longtin, *Phys. Rev. Lett.* 92 (2004) 080601.
- [27] B. Doiron, B. Lindner, A. Longtin, L. Maler, J. Bastian, *Phys. Rev. Lett.* 93 (2004) 048101.
- [28] L. Zhu, Y.-C. Lai, Z. Liu, A. Raghun, *Phys. Rev. E* 66 (2002) 015204.
- [29] A. Pikovsky, A. Zaikin, M.A. de la Casa, *Phys. Rev. Lett.* 88 (2002) 050601.
- [30] B. von Haefen, G. Izús, H.S. Wio, *Phys. Rev. E* 72 (2005) 021101.
- [31] C.J. Tessone, C.R. Mirasso, R. Toral, J.D. Gunton, *Phys. Rev. Lett.* 97 (2006) 194101.
- [32] C. Zhou, J. Kurths, *Phys. Rev. E* 65 (2002) 040101.
- [33] C.S. Zhou, J. Kurths, *Chaos* 13 (2003) 401.
- [34] C.S. Zhou, J. Kurths, E. Allaria, S. Boccaletti, R. Meucci, F.T. Arecchi, *Phys. Rev. E* 67 (2003) 015205.
- [35] C.S. Zhou, J. Kurths, B. Hu, *Phys. Rev. Lett.* 87 (2001) 098101.
- [36] O. Kwon, H.-T. Moon, *Phys. Lett. A* 298 (2002) 319.
- [37] A. Roxin, H. Riecke, S.A. Solla, *Phys. Rev. Lett.* 92 (2004) 198101.
- [38] Z. Gao, B. Hu, G. Hu, *Phys. Rev. E* 65 (2001) 016209.
- [39] P. Jung, G. Mayer-Kress, *Phys. Rev. Lett.* 74 (1995) 2130.
- [40] O. Carrillo, M.A. Santos, J. García-Ojalvo, J.M. Sancho, *Europhys. Lett.* 65 (2004) 452.
- [41] M. Perc, *Phys. Rev. E* 72 (2005) 016207.
- [42] Q.Y. Wang, Q.S. Lu, G.R. Chen, *Eur. Phys. J. B* 12 (2006) 255.
- [43] J. García-Ojalvo, J.M. Sancho, *Noise in Spatially Extended Systems*, Springer, New York, 1999.
- [44] J. Wang, *Chem. Phys. Lett.* 339 (2001) 357.
- [45] H.S. Wio, S. Bouzat, B. von Haefen, in: *Proceedings of the 21st IUPAP International Conference on Statistical Physics, STATPHYS21*, A. Robledo, M. Barbosa (Eds.) *Physica A* 306 (2002) 140.
- [46] E. Ullner, A.A. Zaikin, J. García-Ojalvo, J. Kurths, *Phys. Rev. Lett.* 91 (2003) 180601.
- [47] M.R. Roussel, J. Wang, *J. Chem. Phys.* 120 (2004) 8079.
- [48] C.S. Zhou, J. Kurths, *New J. Phys.* 7 (2005) 18.
- [49] O. Nekhamkina, M. Sheintuch, *Phys. Rev. E* 75 (2007) 056210.
- [50] H.S. Wio, R.R. Deza, *Eur. Phys. J. Special Topics* 146 (2007) 111.
- [51] G.C. Sethia, J. Kurths, A. Sen, *Phys. Lett. A* 364 (2007) 227.
- [52] B. Lindner, B. Doiron, A. Longtin, *Phys. Rev. E* 72 (2005) 061919.
- [53] R. Zhu, Q.S. Li, *Phys. Lett. A* 292 (2001) 58.
- [54] T. Kanamaru, Y. Okabe, *Biosystems* 58 (2000) 101.
- [55] E.R. Kandel, J.H. Schwartz, T.M. Jessell, *Principles of Neural Science*, Elsevier, Amsterdam, 1991.
- [56] A. Roxin, N. Brunel, D. Hansel, *Phys. Rev. Lett.* 94 (2005) 238103.
- [57] Q.Y. Wang, Q.S. Lu, *Chin. Phys. Lett.* 3 (2005) 543.
- [58] E. Rossoni, Y.H. Chen, M.Z. Ding, J.F. Feng, *Phys. Rev. E* 71 (2005) 061904.
- [59] A.L. Hodgkin, A.F. Huxley, *J. Physiol.* 117 (1952) 500.
- [60] D.J. Watts, S.H. Strogatz, *Nature (London)* 393 (1998) 440.
- [61] G. Szabó, A. Szolnoki, R. Izsák, *J. Phys. A: Math. Gen.* 37 (2004) 2599.
- [62] S.T. Wang, F. Liu, W. Wang, Y.G. Yu, *Phys. Rev. E* 69 (2004) 011909.
- [63] J. Ma, H.P. Ying, Z.S. Pu, *Chin. Phys. Lett.* 22 (2005) 1065.
- [64] T.M. Sainz, C. Masoller, H.A. Braun, M.T. Huber, *Phys. Rev. E* 70 (2004) 031904.