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SPATIAL COHERENCE RESONANCE IN DELAYED HODGKIN–HUXLEY NEURONAL NETWORKS

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We study the phenomenon of spatial coherence resonance (SCR) on Hodgkin–Huxley (HH) neuronal networks that are characterized with information transmission delay. In particular, we examine the ability of additive Gaussian noise to optimally extract a particular spatial frequency of excitatory waves in diffusive and small-world networks on which information transmission amongst directly connected neurons is not instantaneous. On diffusively coupled HH networks, we find that for short delay lengths, there always exists an intermediate noise level by which the noise-induced spatial dynamics is maximally ordered, hence implying the possibility of SCR in the system. Importantly thereby, the noise level warranting optimally ordered excitatory waves increases linearly with the increasing delay time, suggesting that extremely long delays might nevertheless preclude the observation of SCR on diffusive networks. Moreover, we find that the small-world topology introduces another obstacle for the emergence of ordered spatial dynamics out of noise because the magnitude of SCR fades progressively as the fraction of rewired links increases, hence evidencing decoherence of noise-induced spatial dynamics on delayed small-world HH networks. Presented results thus provide insights that could facilitate the understanding of the joint impact of noise and information transmission delay on realistic neuronal networks.

Keywords: Neuronal networks; delay; spatial stochastic resonance.

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1. Introduction

Effects of noise on nonlinear dynamical systems are seldom trivial and often counterintuitive as well as surprising.[1] Although several interesting phenomena have

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already been discovered, this field of research continues to grow at an astonishing rate, especially via fruitful interrelations with other topics of science. Perhaps the most prominent of all phenomena is stochastic resonance (SR),[2–15] which implies that fine-tuned random fluctuations may enhance the response of a nonlinear system to weak periodic driving. Also intriguing is the SR without an external periodic force, whereby noise alone extracts a hidden intrinsic time scale of the dynamics in a resonant manner. The most commonly used term for the latter phenomenon is coherence resonance or autonomous SR.[16–19] Aside from these two rather mainstream phenomena, there exist several related reports on noise-induced order either from chaotic states,[20,21] by means of variations in system size[22] and diversity,[23] or via an enhancement of synchronization in coupled systems.[24–26] Furthermore, order out of noise has been studied extensively also in nonidentical ensembles governed by nonlinear dynamics, such as neurons,[27] as well as in small-world neuronal networks[28] and bistable overdamped oscillators.[29]

Recently, the impact of noise on two-dimensional spatially extended systems has also attracted considerable attention, and several studies were devoted to the exploration of possible effects that have been comprehensively reviewed in Ref. 30, and previously also in Ref. 31. In particular, spatiotemporal SR has been reported in Ref. 32, while spatial coherence resonance (SCR) has been introduced first near pattern forming instabilities[33] and subsequently also in excitable media.[34,35] Noteworthy, some characteristics of noise-induced patterns have also been investigated on a regular Hodgkin–Huxley (HH) neuronal network,[36] and it was found that the order of the firing rate function could be enhanced as the connections amongst neurons became stronger. Moreover, resonance-enhanced signal detection and transduction,[37] the impact of correlated noise on signal processing and neuronal firing,[38,39] as well as the propagation of firing rate in a feed-forward neuronal network,[40] and signal-to-noise ratio (SNR) gain,[41] have been studied closely related to the subject of this work. Aside from these examples related to the study of neuronal systems, 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. 30, while some exemplary studies are also given in Refs. 42–50.

At present, we would like to extend the subject by building on the fact that information transmission delays are inherent in intra and inter neuronal communication because of both finite propagation velocities by the conduction of signals along neurites as well as delays in the synaptic transmission along chemical synapses.[51] It is thus important to understand the dynamics of coupled neuronal ensembles, either in terms of synchronization or noise-induced phenomena, when such temporal delays are not negligible. For related comprehensive studies we refer to Refs. 52 and 53. Notably, it has been suggested that time delays can facilitate neural synchronization and lead to many interesting and even unexpected phenomena.[54] Rossoni *et al.* showed that two diffusively coupled HH neurons can exhibit different synchronization behavior, including in-phase and anti-phase synchronies, due to the effect

of different time delays.[55] To the best of our knowledge, however, the possibility of SCR in neuronal networks with information transmission delay has not yet been investigated. To fill the gap, we study the phenomenon of SCR on HH[56] neuronal networks that are characterized with information transmission delay. More precisely, we examine the ability of additive temporally and spatially uncorrelated Gaussian noise to extract a particular spatial frequency of excitatory waves in diffusive and small-world networks of HH neurons amongst which the information transmission is not instantaneous. We find that for short delay lengths and diffusive coupling, there always exists an intermediate noise level by which the spatial dynamics is characterized by nicely ordered circular excitatory waves with a well-defined spatial frequency. By employing the average spatial structure function[31] we provide conclusive evidences for the existence of SCR in delayed diffusively coupled HH neuronal networks. However, we also show that as the transmission delay lengthens the optimal level of noise, warranting the most ordered spatial dynamics of excitatory waves, increases in a robust linear fashion as well. This suggests that extremely long delays might ultimately preclude the observation of SCR in diffusive neuronal networks due to the ever-increasing stochastic component. Similarly, as long information transmission delays, we find that the small-world topology[57] also hinders coherent pattern formation out of noise because the magnitude of SCR fades fast as the fraction of rewired links increases. We thus show that delayed HH neuronal networks are not immune to the small-world induced decoherence of noise-induced spatial dynamics. Presented results hence provide insights into the joint impact of noise and information transmission delay on realistic neuronal ensembles, supplementing nicely the existing body of literature devoted to the study of deterministic and stochastic neuronal dynamics on complex networks.[58–66]

The paper is organized as follows. Section 2 is devoted to the description of the HH mathematical model and network topologies presently in use, whereas Sec. 3 presents the main results. In Sec. 4 we summarize the results and outline possible biological implications of our findings.

2. Mathematical Model and Setup

The spatiotemporal dynamics of studied HH neuronal networks is governed by the following differential equations[56]:

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

$$\frac{\mathrm{d}m_{i,j}}{\mathrm{d}t} = \alpha_{m_{i,j}}(1 - m_{i,j}) - \beta_{m_{i,j}}m_{i,j}, \tag{2}$$

$$\frac{\mathrm{d}h_{i,j}}{\mathrm{d}t} = \alpha_{h_{i,j}}(1 - h_{i,j}) - \beta_{h_{i,j}}h_{i,j}\,, \tag{3}$$

$$\frac{\mathrm{d}n_{i,j}}{\mathrm{d}t} = \alpha_{n_{i,j}}(1 - n_{i,j}) - \beta_{n_{i,j}}n_{i,j}\,. \tag{4}$$

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 first in Sec. 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.[57] Presently we employ the rewiring procedure described in Ref. 67 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 towards the end of Sec. 3. Importantly, we generated each small-world network at the beginning of a particular simulation with the precise number of rewired links as constituted by q, and kept the network fixed the whole time. Moreover, for small q, below results were averaged over 30 different realizations of the interaction network. Quantities σ and τ in Eq. (1) are the main control parameters to be varied in this study, denoting the intensity of additive uncorrelated Gaussian noise $\xi_{i,j}$ that satisfies $\langle\xi_{i,j}(t)\rangle = 0$ and $\langle\xi_{i,j}(t),\xi_{m,n}(t')\rangle = \delta(t - t')\delta_{i,m}\delta_{j,n}$, and the information transmission delay, respectively. Furthermore, $D = 0.35$ is the presently employed coupling strength, $i,j = 1,\ldots,N = 128$ is the system size in each direction of the two-dimensional grid with periodic boundary conditions, whilst all other parameter values used throughout the paper are listed in Table 1. Finally, the experimentally determined voltage
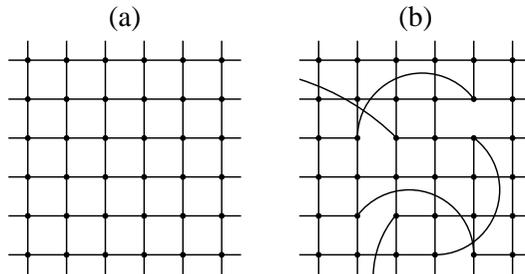

(a)   (b)

Fig. 1.   Examples of considered network topologies. For clarity, only a 6×6 large part 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.

Table 1. Employed parameter values.

Membrane capacitance (μF/cm^2)
$C = 1$

Conductance constants (mS/cm^2)
$g_{Na} = 120$
$g_K = 36$
$g_L = 0.3$

Reversal potentials (mV)
$V_{Na} = 50$
$V_K = -77$
$V_L = -54.4$

transition rates are given explicitly by the following expressions:

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

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

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

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

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

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

For a single HH neuron in the absence of noise ($\sigma = 0$), a subcritical Hopf bifurcation occurs at the external current $I_1 = 9.8\ \mu$A/cm^2. Between $I = I_2 = 6.2\ \mu$A/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 $I = 155\ \mu$A/cm^2, the stable limit cycle vanishes via the supercritical Hopf bifurcation. A more detailed bifurcation analysis of the HH neuron was performed in Refs. 68–71. Here we are interested in the parameter region $I < I_2$, where neurons are unable to fire spontaneously. In order to study explicitly the impact of noise and delay on the spatial dynamics of the system, we set $I = 6.1\ \mu$A/cm^2 so that each neuron stays at the excitable steady state, and

we employ the finite-difference forward-step Heun numerical simulation scheme[31] with a fixed integration step $dt = 0.01$. Noteworthy, the dynamics of deterministic coupled HH neurons has already been studied in Refs. 72–74.

3. Results

We first present results obtained on diffusively coupled HH neuronal networks with delay, starting by showing snapshots of $V_{i,j}$ by different σ in Fig. 2. The visual examination of the three snapshots reveals rather clearly that there exists an intermediate value of σ, at which nicely ordered circular excitatory waves propagate through the spatial domain [Fig. 1(b)]. Smaller or larger values of σ clearly fail to have the same effect, evoking either only small-amplitude deviations from the steady state [Fig. 1(a)] or mostly uncorrelated excitations throughout the spatial grid [Fig. 1(c)], respectively. Noteworthy, all three snapshots feature the spatial dynamics at a given time t and were obtained with the same information transmission delay equaling $\tau = 0.08$. Hence, already with the naked eye, a typical coherence resonance scenario for the spatial dynamics on the studied HH neuronal network can be inferred.

In order to establish and quantify the phenomenon of SCR more rigorously, the spatial structure function of $V_{i,j}$ is introduced as follows:

$$P(k_x, k_y) = \langle H^2(k_x, k_y) \rangle, \tag{11}$$

where $H(k_x, k_y)$ is the two-dimensional Fourier transform of the spatial grid at a particular time t and $\langle \cdots \rangle$ is the ensemble average over noise realizations. The numerical results of $P(k_x, k_y)$ for the three σ used already for the snapshots in Fig. 2 are presented in Fig. 3. Indeed, the results in Fig. 3 fully support our visual assessments, as it can be observed clearly that for small and large noise levels the
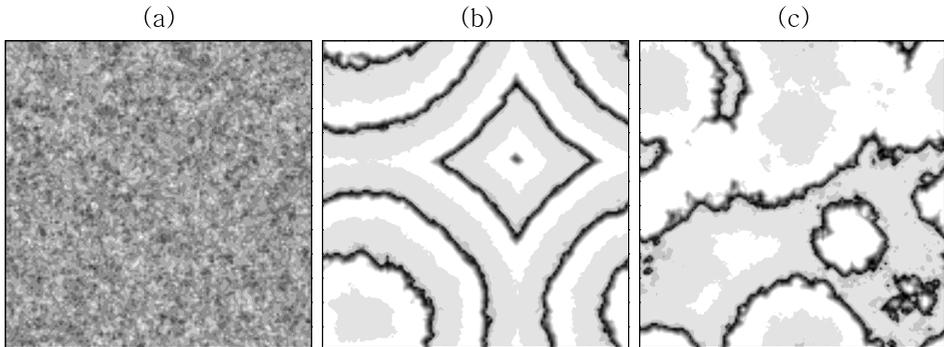
(a)　　　　　　　　　(b)　　　　　　　　　(c)

Fig. 2.   Spatial pattern formation out of noise on the diffusively coupled HH neuronal network. All panels depict values of $V_{i,j}$ on a 128×128 square grid at a given time t. The noise level σ is: (a) 1.2, (b) 1.5, and (c) 2.1, whereas the employed delay is the same in all three panels, equaling $\tau = 0.08$. Grey scale coloring in all panels is linear, white depicting minimal and black, maximal values of $V_{i,j}$.
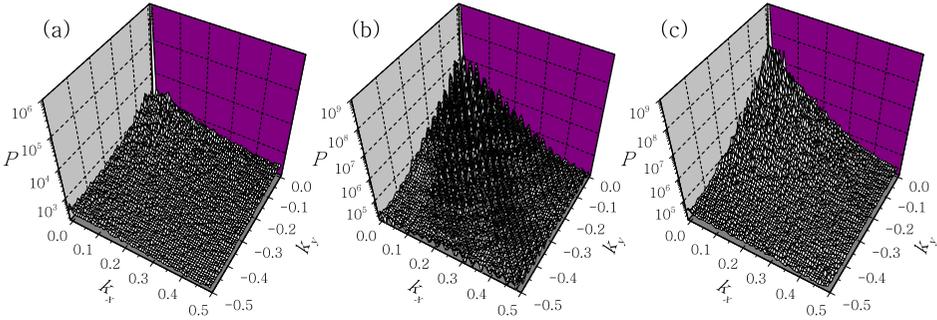
Fig. 3. Spatial structure functions of $V_{i,j}$ obtained for $\tau = 0.08$, whereas the noise level σ is: (a) 1.2, (b) 1.5, and (c) 2.1. For the intermediate value of σ the well-expressed circularly symmetric outlay of $P(k_x, k_y)$ is evident, indicating the existence of a preferred spatial frequency of noise-induced excitatory events in the diffusive HH neuronal network. Note that in all panels only a part of the whole $P(k_x, k_y)$ plane is shown for better clarity.

presented spectra show no particularly expressed spatial frequency. Only for intermediate σ, the spatial structure function develops several well-expressed circularly symmetric rings, indicating the existence of a preferred spatial frequency induced by additive Gaussian noise. Such waterfall-like structures cannot be observed for smaller and larger σ, either because the noisy perturbations are too weak to induce large-amplitude excitations, or because they start to dominate the spatial dynamics, whereby either the characteristic outlay of $P(k_x, k_y)$ vanishes and no preferred spatial frequency can be extracted.

Next, we exploit the circularly symmetric outlay of $P(k_x, k_y)$ as proposed by Carrillo *et al.*[33] to obtain an estimate for the SNR of the spatial dynamics of excitatory events induced by different σ. In particular, we calculate the circular average of the structure function according to the equation

$$p(k) = \int_{\Omega_k} P(\mathbf{k}) \mathrm{d}\Omega_k \,, \tag{12}$$

where $\mathbf{k} = (k_x, k_y)$, and Ω_k is a circular shell of radius $k = |\mathbf{k}|$. Variations of $p(k)$ are shown in Fig. 4(a) for the three different σ corresponding to the values used already in panels of Figs. 2 and 3. Line plots of $p(k)$ show more concisely what could be inferred already from $P(k_x, k_y)$. In particular, we can establish conclusively that there exists a particular spatial frequency, marked with the vertical dashed line at $k = k_{\max}$, which is resonantly enhanced for some intermediate level ($\sigma = 1.5$) of additive Gaussian noise. Moreover, smaller and larger σ fail to yield qualitatively identical results as their circularly averaged spatial structure functions are essentially flat, i.e., lacking any noticeable or preferred spatial frequency.

To quantify the ability of each σ to extract the characteristic spatial frequency of the diffusively coupled HH neuronal network more precisely, we calculate the SNR as the peak height at $k_{\max}$ normalized with the background fluctuations in
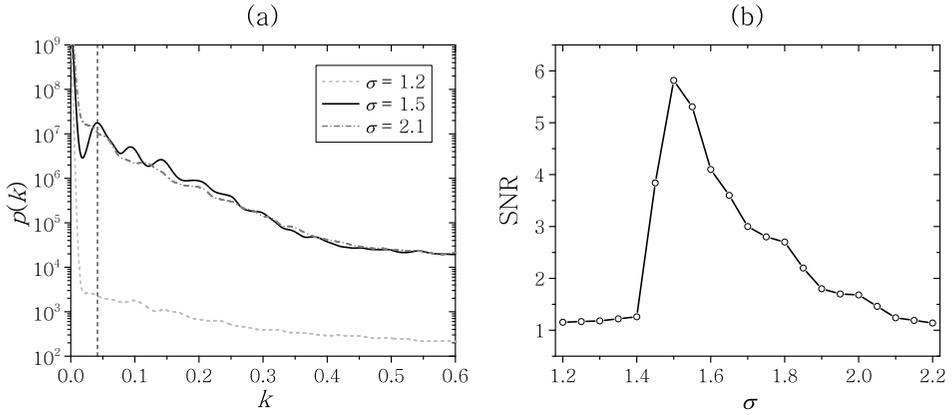
Fig. 4.   Evidences for SCR in diffusively coupled HH neuronal networks with delay. (a) Circular averages $p(k)$ of structure functions $P(k_x, k_y)$ presented in Fig. 3. The vertical dashed line at $k = k_{max}$ marks the spatial frequency of excitatory waves that is resonantly enhanced by an intermediate level of additive Gaussian noise. (b) Characteristic bell-shaped dependence of SNR on σ, clearly evidencing SCR in the examined system. Results in both panels were obtained for $\tau = 0.08$.

the system,

$$\text{SNR} = p(k_{max})/\tilde{p}, \tag{13}$$

where $\tilde{p} = [p(k_{max} - \Delta k_a) + p(k_{max} + \Delta k_b)]/2$ is an approximation for the level of background noise whereby Δk_a and Δk_b mark the estimated width of the peak around k_{max} at the optimal σ. Equation (13) simply gives the spatial counterpart of the measure frequently used for quantifying constructive effects of noise in the temporal domain of dynamical systems. Employing it on the examined system setup yields results presented in Fig. 4(b), showing that the SNR exhibits a typical bell-shaped form in dependence on σ, thus clearly evidencing SCR in the diffusively coupled HH neuronal network with delay. In particular, there exists an optimal level of additive temporally and spatially uncorrelated Gaussian noise, for $\tau = 0.08$ equaling $\sigma = 1.5$, by which the spatial dynamics of noise-induced waves is most coherent and supported by the optimal (minimal) level of stochasticity still warranting their propagation across the spatial grid.

Having conclusively established the possibility of SCR on diffusively coupled HH neuronal networks with delay, it remains of interest to examine the impacts of different delay lengths τ on the above-reported phenomenon. Note that all so far presented results were obtained by using $\tau = 0.08$. First, we examine how different τ affect the characteristic bell-shaped dependence of SNR on σ. As can be inferred from Fig. 5(a), the resonant outlay remains preserved over a broad span of τ, albeit the peak value of SNR moves to even larger σ as τ increases. Normally, such a trend would dictate a steady decrease in the maximally attainable peak values of SNR as τ increases as well, simply because the level of background fluctuations needed
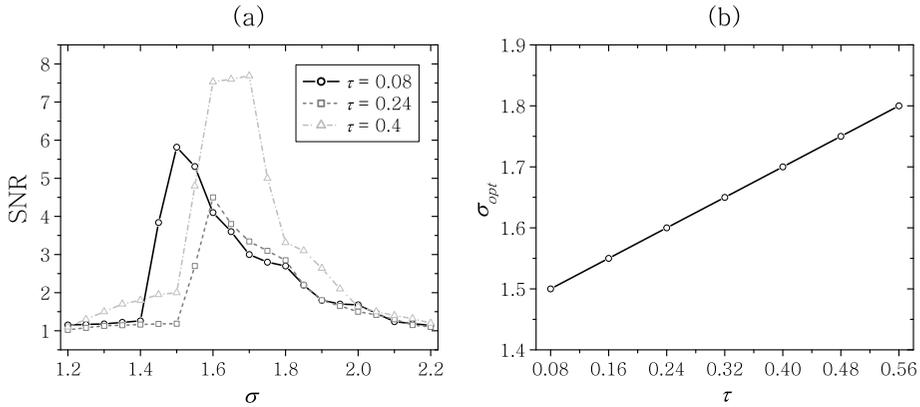
Fig. 5. Effects of different information transmission delays τ on SCR in diffusively coupled HH neuronal networks. (a) SNR in dependence on σ for different τ. (b) Dependence of the optimal noise level σ_{opt}, warranting the peak value of SNR in panel (a), on τ.

to sustain coherent pattern formation increases. However, since the increase of the optimal noise level σ_{opt} increases only linearly with τ, as depicted in Fig. 5(b), we found it impossible to extract a clear trend of peak SNR values in dependence on τ [note that peak values of SNR in Fig. 5(a) fluctuate heavily and irregularly in dependence on τ]. Arguably, a larger span of τ values would need to be covered to numerically extract this information, yet computer resources readily available to us preclude analyses for even longer transmission delays. Nevertheless, due to the robust linear increase of σ_{opt} in dependence on τ depicted in Fig. 5(b), we conclude that the eventual complete collapse of ordered spatial dynamics out of noise in diffusively coupled HH neuronal networks is inevitable if the information transmission delay is long enough. This directly implies that the SCR cannot be observed if τ exceeds a critical length. Moreover, the linear increase of σ_{opt} in dependence on τ indicates that the phase transition towards complete disorder may be smooth, albeit additional studied on large-scale computer networks will be necessary to clarify this assertion conclusively.

Finally, it remains of interest to examine the impact of small-world topology on the phenomenon of SCR reported so far only for diffusively coupled HH neuronal networks with delay. For this purpose we set $q > 0$ and follow the same procedures as exemplified above. Figure 6(a) features SNR curves in dependence on σ by different q and a fixed value of τ. First of all, it is clear that the introduction of shortcuts amongst distant neurons hinders coherent pattern formation out of noise as the maximally attainable peak values of SNR decrease fast as q increases. However, the optimal σ warranting peak SNR values seems not to be affected, remaining constant at $\sigma_{\mathrm{opt}} = 1.7$ irrespective of q, as noted with the dashed vertical line. This suggests that the decoherence of noise-induced spatial dynamics is exclusively due to the introduction of interaction randomness. Indeed, since we consider regular
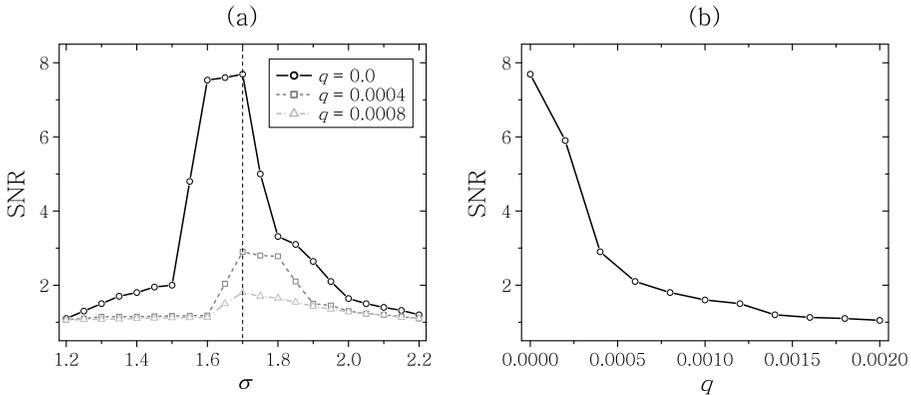
Fig. 6.   Decoherence of noise-induced spatial dynamics on small-world HH neuronal networks characterized with information transmission delay equaling $\tau = 0.4$. (a) SNR in dependence on σ for different q. Evidently, the maximally attainable peak value of SNR decreases fast as q increases, while σ_{opt} remains unchanged (marked with the vertical dashed line). (b) Peak values of SNR, occurring at $\sigma_{opt} = 1.7$ in panel (a), in dependence on q.

small-world networks warranting an equal number of inputs ($z = 4$) to each coupled neuron, the fact that σ_{opt} does not depend on q can be elegantly justified. Turning back to the decoherence of spatial dynamics, results in Fig. 6(a) evidence clearly that the phenomenon of SCR fades continuously as q increases, disappearing almost completely already by $q = 0.0008$. We exploit this fact further in Fig. 6(b), where SNRs obtained by σ_{opt} are plotted in dependence on q. Clearly, the peak values of SNR decrease continuously as q increases, thus evidencing the decoherence of noise-induced spatial dynamics due to the introduction of small-world topology in HH neuronal networks with delay. Remarkably, in contrast with the rather subtle impact of different information transmission delays on the peak values of SNR [see Fig. 5(a)], a near-exponential decrease can be observed in dependence on q. Noteworthy, we have made the same investigations also for other delay lengths, and qualitatively identical results have been obtained. We thus show that delayed HH neuronal networks are not immune to the small-world induced decoherence of noise-induced spatial dynamics, and that indeed random long-range connections amongst distant neurons are extremely effective in disrupting ordered excitatory waves out of noise.

4. Summary

In sum, we show that additive temporally and spatially uncorrelated Gaussian noise is able to resonantly extract a characteristic spatial frequency of excitatory waves on HH neuronal networks even if short delays of information transmission are introduced, hence providing conclusive evidence for SCR in the examined system. However, long delays as well as random shortcuts amongst distant neurons, constituting the small-world interaction topology, hinder coherent pattern forma-

tion out of noise, thus weakening or even completely hindering the observation of SCR. While increasing delay lengths act only linearly (i.e., slowly) on the distortion of noise-induced patterns, the decoherence is much more rapid in dependence on the fraction of shortcut links where a near-exponential decrease of the maximally attainable SNR can be observed as q increases. The linear dependence in the former case currently precludes the accumulation of numerical evidences that would support complete delay-induced decoherence of noise-induced spatial dynamics within computer resources readily available to us. Nevertheless, the robust linear increase of the optimal noise level needed to evoke ordered excitatory waves strongly implies the eventual complete collapse of ordered spatial dynamics out of noise due to the increasing stochastic component.

It has recently been suggested that long-range connections among neurons might yield a faster recall of stored memories due to the distinctive property of small-world environments to link seemingly unrelated events only by a few intermediate steps.[75] On the other hand, diffusively coupled areas might be the actual memory holders in the brain, enabling efficient data encoding through coherent spatial patterns. Thus, while small-world connectivity facilitating temporally ordered behavior appears to be important for information retrieval as well as short term memory,[76,77] diffusively coupled areas enabling coherent spatial patterns might be the actual data storage facilities of the brain. Our current work provides interesting insights in this respect in that, although ordered spatial patterns out of noise seem impossible in the presence of small-world topology and long information transmission delays, the importance of such physiological properties may lay elsewhere, and indeed, additional detailed studies regarding function-follow-form[78–82] are necessary to clarify the importance of different structural attributes of neural networks and their constitutive units. Thus, especially in the field of neuroscience where excitability, noise, 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.

Acknowledgments

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