



Effects of small-world connectivity on noise-induced temporal and spatial order in neural media

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Abstract

We present an overview of possible effects of small-world connectivity on noise-induced temporal and spatial order in a two-dimensional network of excitable neural media with FitzHugh–Nagumo local dynamics. Small-world networks are characterized by a given fraction of so-called long-range couplings or shortcut links that connect distant units of the system, while all other units are coupled in a diffusive-like manner. Interestingly, already a small fraction of these long-range couplings can have wide-ranging effects on the temporal as well as spatial noise-induced dynamics of the system. Here we present two main effects. First, we show that the temporal order, characterized by the autocorrelation of a firing-rate function, can be greatly enhanced by the introduction of small-world connectivity, whereby the effect increases with the increasing fraction of introduced shortcut links. Second, we show that the introduction of long-range couplings induces disorder of otherwise ordered, spiral-wave-like, noise-induced patterns that can be observed by exclusive diffusive connectivity of spatial units. Thereby, already a small fraction of shortcut links is sufficient to destroy coherent pattern formation in the media. Although the two results seem contradictory, we provide an explanation considering the inherent scale-free nature of small-world networks, which on one hand, facilitates signal transduction and thus temporal order in the system, whilst on the other hand, disrupts the internal spatial scale of the media thereby hindering the existence of coherent wave-like patterns. Additionally, the importance of spatially versus temporally ordered neural network functioning is discussed.

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1. Introduction

Somewhat in contradiction to the intuitive belief, random perturbations, in conjunction with a weak deterministic stimuli, turned out to possess the ability to induce temporal as well as spatial order in nonlinear dynamical systems [1–3].

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Since often the constructive role of noise depends resonantly on the noise intensity, these effects are known as stochastic resonance phenomena [4–6]. Noteworthy, it has also been discovered that, in temporal systems, the stochastic resonance effect can be amplified by the addition of a second weak external stimuli, whereby this phenomenon was termed appropriately as the amplification or control of stochastic resonance [7–11]. Often, this second signal has a frequency that matches some intrinsic frequency of the system [8,11–14], thus combining stochastic resonance effects with classical resonance.

Remarkably, constructive effects of noise can also be observed in the absence of any additional deterministic inputs, whereby one usually speaks of coherence resonance phenomena [15–23]. Particularly related to the present work are studies evidencing coherence resonance phenomena in two-dimensional networks, i.e., media [22,23], where it has been reported that solely additive spatiotemporal random perturbations can induce coherent patterns with a characteristic spatial frequency in a resonant manner. Presently, we extend these results by considering not just regular diffusively coupled spatial units, but also introduce small-world connectivity [24,25] to the two-dimensional network. Moreover, besides spatial order that can be characterized by a spatial structure function [2], we also analyse temporal order in the media via an autocorrelation of the firing-rate function.

Small-world networks differ from their regular counterparts in that connections are allowed not just between nearby neighbours, as is for example the case in a diffusively coupled system, but also among arbitrary distant randomly chosen units of the network [24,25]. Most importantly, with the increasing fraction of these so-called long-range couplings or shortcut links the typical path length between two arbitrary sites decreases rapidly, which also motivated the name given to such networks. Also very important is the fact that such networks are scale-free [26], meaning that the distribution of number of links pertaining to a particular unit of the network can be described by a simple power-law equation. Thereby, it should be fully appreciated that a power-law distribution, implying a scale-free system, is very much a counterintuitive description of a real-life system. Fascinatingly though, small-world networks appear to be excellent for modelling interactions among units of complex systems, whereby examples range from social networks [27], scientific-collaboration networks [28–30], food webs [31], computer networks [32–34], and of immediate importance for the present paper, also to neural networks [24,35–42].

The present study is, however, not the first to analyse noise-induced phenomena in small-world networks. Notably, stochastic [43] and coherence [44] resonance phenomena were already studied in one-dimensional networks with small-world connectivity. In both cases it has been discovered that the introduction of shortcut links between randomly chosen sites increases the global synchrony of the network. In particular, authors in [43,44] report that the noise-induced temporal order increases with the fraction of randomly introduced long-range couplings. To this day, however, little attention has been devoted to the explicit analysis of effects of small-world connectivity on the noise-induced temporal and spatial order in two-dimensional small-world networks, i.e., small-world media.

The present study is therefore devoted to the analysis of exclusively noise-induced temporal and spatial order in small-world media. In particular, we focus on the transition from the diffusive to small-world connectivity of spatial units to investigate effects of this qualitative change of network topology on temporal as well as spatial noise-induced dynamics of the studied system. As already noted, we quantify the temporal order in the system via an autocorrelation of the firing-rate function, whilst the spatial order is characterized by a spatial structure function derived from the two-dimensional Fourier transform of the media. We obtain two main results. First, in accordance with previous studies analysing one-dimensional small-world networks [43,44], we find that the increasing fraction of shortcut links increases the noise-induced temporal order also in the studied two-dimensional small-world network. Second, the spatial noise-induced pattern formation is, however, disrupted by the introduction of small-world connectivity already at a small fraction of introduced long-range couplings. Although contradictory at first sight, both results can be well explained by taking into account the inherent scale-free nature of small-world networks [26,34], which on one hand facilitates signal transduction among distant system units and thus enhances temporal order, whilst on the other hand, destroys the spatial order due to the disruption of the internal spatial scale of the media.

The excitable media under study is locally modelled by the FitzHugh–Nagumo equations [45,46] that were derived from the Hodgkin–Huxley model describing the excitable dynamics of electrical signal transmission along neuron axons [47]. Since recently evidences for small-world connectivity of neurons in neural tissue are accumulating rapidly [24,36,37,42], and stochastic influences are widely acknowledged to be an inseparable part of every real-life process, the present study is strongly motivated also from the biomedical point of view.

The paper is structured as follows. Section 2 is devoted to the description of the mathematical model. In Section 3 general aspects of noise-induced temporal and spatial dynamics of neural media for different network connectivities are presented, whilst Sections 4 and 5 feature a detailed analysis of temporal and spatial order, respectively. Finally, in the last section we summarize the results and outline biomedical implications of our findings.

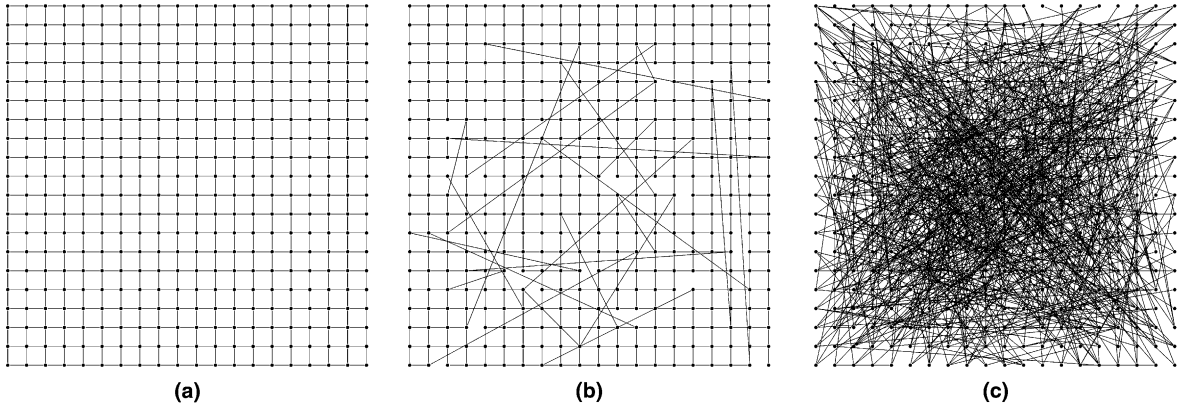


Fig. 1. Schematic presentation of various network connectivities of the studied two-dimensional media for different fractions p of randomly rewired links. (a) Regular diffusive connectivity given by $p = 0$. (b) Small-world connectivity given by $p = 0.05$. (c) Completely random connectivity given by $p = 1$.

2. Mathematical model

The studied mathematical model takes the form

$$\frac{du_{ij}}{dt} = f(u_{ij}, v_{ij}) + D \sum_{kl} \varepsilon_{ijkl} (u_{kl} - u_{ij}) + \xi_{ij}, \quad (1)$$

$$\frac{dv_{ij}}{dt} = g(u_{ij}, v_{ij}), \quad (2)$$

whereby the dynamics of each individual unit is described by the FitzHugh–Nagumo equations [45,46]

$$f(u_{ij}, v_{ij}) = \frac{1}{\kappa} u_{ij} (1 - u_{ij}) \left(u_{ij} - \frac{v_{ij} + b}{a} \right), \quad (3)$$

$$g(u_{ij}, v_{ij}) = u_{ij} - v_{ij}. \quad (4)$$

The membrane potential $u_{ij}(t)$ and time-dependent conductance of potassium channels $v_{ij}(t)$ are considered as dimensionless two-dimensional scalar fields on a $n \times n$ square lattice with no-flux or periodic boundary conditions, whereby the local dynamics of u is much faster ($\kappa \ll 1$) than that of v . Moreover, ξ_{ij} is additive spatiotemporal Gaussian noise with zero mean, white in space and time, and variance σ^2 [2]. The sum in Eq. (1) runs over all lattice sites, whereby $\varepsilon_{ijkl} = 1$ if the site (k, l) is coupled to (i, j) , whilst otherwise $\varepsilon_{ijkl} = 0$. If the fraction of randomly introduced shortcuts, i.e., rewired links, p equals zero, $\varepsilon_{ijkl} = 1$ only if (k, l) indexes one of the four nearest neighbours of site (i, j) . Thereby, we obtain a diffusively coupled regular spatial network of excitable units as presented schematically in Fig. 1(a), whereby the coupling coefficient D equals the diffusion constant. If $p > 0$, however, the corresponding fraction of links is randomly rewired, i.e., indexes k and l are shuffled for a given fraction p of randomly chosen sites (i, j) , keeping $\varepsilon_{ijkl} = 1$ to form a spatial network with small-world or completely random connectivity, as presented in Fig. 1(b) and (c) for $p = 0.05$ and $p = 1$, respectively. For parameter values $a = 0.75$, $b = 0.01$, $\kappa = 0.05$, and $D = 3.84$ each FitzHugh–Nagumo unit is governed by a single excitable steady state $u = v = 0.0$, which is presently used as the initial condition for all lattice sites. Thus, without the addition of noise ($\sigma = 0$), the medium remains strictly quiescent regardless of p . Large-enough non-zero σ , however, locally evoke spiking behaviour, whereby the value of variable u varies between 0.0 (quiescent state) and 1.0 (excited state). In the following section, we present possible effects of random spatiotemporal perturbations on the temporal as well as spatial dynamics of the studied system for various σ and p .

3. Noise-induced temporal and spatial dynamics

We start the study by visually inspecting noise-induced temporal and spatial dynamics of the system for three different σ and exclusively regular diffusive coupling of network units given by $p = 0$ (see Fig. 1(a)). To envision the spatial

dynamics of the system, we present characteristic snapshots of the spatial profile of u for different σ , as presented in the upper row of Fig. 2. Furthermore, since it is impossible to present several such snapshots in continuous time, we capture the essence of temporal dynamics by presenting time traces of a firing-rate function Π , which simply measures the fraction of spatial units that have values of variable u above a certain threshold $u_{\text{th}} = 0.5$ at any given time t . If $\Pi = 0$ this means that none of the spatial elements is perturbed strongly enough for u to exceed u_{th} , whilst $\Pi = 1$ indicates that all spatial units are simultaneously in the excitable state, which constitutes global synchrony and thus corresponds to the most ordered temporal dynamics of the media. Firing-rate functions corresponding to the presented spatial profiles are shown in the bottom row of Fig. 2.

By inspecting the presented spatial profiles in the upper row of Fig. 2, it becomes instantly obvious that there indeed exist an intermediate value of σ , for which coherent pattern formation in the media is resonantly pronounced, yielding well-ordered spiral waves in the spatial profile of u (see Fig. 2(b)). On the other hand, smaller σ are unable to excite the system strong enough to evoke any particular spatial dynamics in the media, whilst for larger σ the pattern formation becomes violent so that the spatial profile again lacks any visible structure or order. The same scenario applies for the noise-induced temporal dynamics given by Π , as presented in the bottom row of Fig. 2. Thereby, it should be noted that by regular diffusive connectivity of the network, as is presently the case, it is impossible to achieve complete global synchronization ($\Pi = 1$) of all spatial units. Thus, although by $\sigma = 0.16$ the firing-rate function Π varies near-periodically in time, indicating some extended of noise-induced temporal order in the system, its maximum value $\Pi \approx 0.4$ indicates the fact that at most only 40% of all spatial units can be simultaneously driven to the excitable state.

Next, we analyse the noise-induced temporal and spatial dynamics of the system also for $p > 0$. Thus, we switch our attention from regular diffusively coupled to small-world coupled networks, as schematically presented in Fig. 1(b). Obtained results are shown in Fig. 3. It can be observed immediately that we obtain a qualitative shift in the temporal as well as spatial dynamics of the system, in particular for the intermediate values of σ (compare Figs. 2(b) and 3(b)). While small and large values of σ have a similar impact both on the temporal as well as spatial dynamics of the system as by $p = 0$, the intermediate values of σ are no longer able to induce coherent pattern formation in the spatial domain, but instead ensure nearly perfect ($\Pi \approx 1$) global synchrony, i.e., temporal order, in the system. Moreover, similarly as by $p = 0$, Π varies periodically in time, which is additionally stressed by the insert in the spatial profile of Fig. 3(b) that

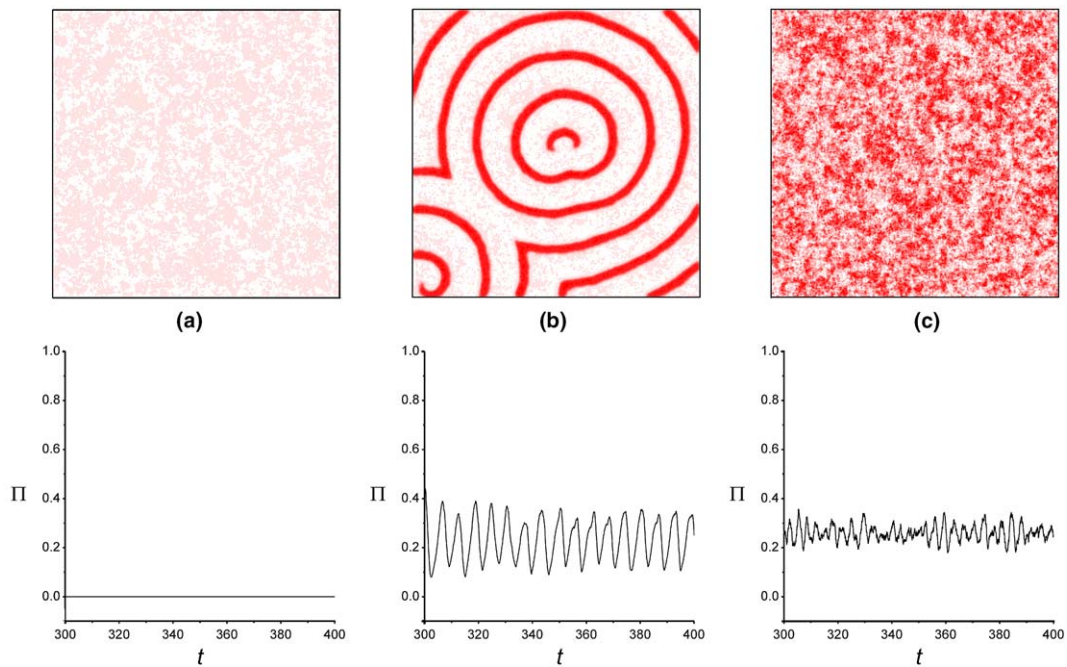


Fig. 2. Noise-induced temporal (bottom row) and spatial (upper row) dynamics in the exclusively diffusively coupled ($p = 0$) media for various noise levels: (a) $\sigma = 0.1$, (b) $\sigma = 0.16$, (c) $\sigma = 0.9$. Spatial profiles are depicted on a 256×256 square grid with a linear colour profile, red marking 1.0 and white 0.0 values of u . (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

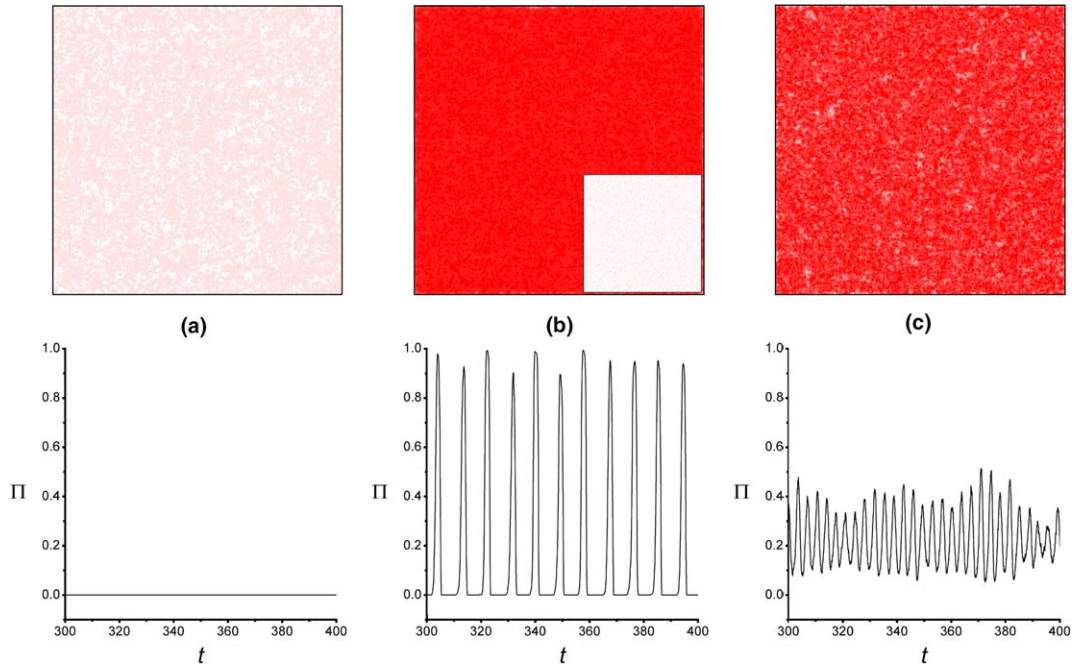


Fig. 3. Noise-induced temporal (bottom row) and spatial (upper row) dynamics in the small-world coupled ($p = 0.1$) media for various noise levels: (a) $\sigma = 0.15$, (b) $\sigma = 0.25$, (c) $\sigma = 1.0$. Spatial profiles are depicted on a 256×256 square grid with a linear colour profile, red marking 1.0 and white 0.0 values of u . The inset in (b) features the spatial profile of u when $\Pi \approx 0$, whereas the main frame corresponds to $\Pi \approx 1$. (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

features the u -field at a different time t when $\Pi \approx 0$, as opposed to the main frame which corresponds to $\Pi \approx 1$, indicating the fact that for $p > 0$ either none or all units can be excited simultaneously at any given time.

Taken together, visually inspected results presented so far lead us to the conclusion that regular diffusively coupled two-dimensional networks facilitate noise-induced coherent pattern formation by a reasonably well-expressed global synchrony and regularity of excitatory events, i.e., temporal order, in the system (see Fig. 2(b)). On the other hand, the introduction of shortcut links, i.e., small-world connectivity, enhances the temporal order, whereby the regularity and wave-like appearance of spatial patterns in the media is completely destroyed (see Fig. 3(b)). Both these conclusions can be additionally strengthened by inspecting the temporal evolution of the spatial profile of diffusively coupled media with embedded small-world clusters, as presented in Fig. 4. It is evident that, at an appropriate $\sigma = 0.16$, diffusively coupled areas enable coherent wave-formation and propagation in the media (similarly as in Fig. 2(b)), whilst small-world clusters (marked with small quadratic frames in Fig. 4) enable either none or all units to be excited simultaneously at any given time (as in Fig. 3(b)), thus facilitating synchronization and temporal regularity of excitatory events in the system. To make these visually assessed findings quantitative, we devote the next two sections to the more precise mathematical quantification of effects of small-world connectivity on the temporal as well as spatial noise-induced dynamics of the system.

4. Temporal order

To quantify the temporal order in the media more precisely, we calculate the autocorrelation of the firing-rate function Π according to the equation:

$$C(\tau) = \langle \Pi(t)\Pi(t + \tau) \rangle. \quad (5)$$

As is well known, if Π is a periodic function of t than $C(\tau)$ is also periodic to the same extended, whereby if τ equals some predominant oscillations period of Π the autocorrelation has a local maximum at that same τ . Thus, $C(\tau)$ is a comprehensive mathematical quantity for evaluating the temporal order of the studied system. In particular, higher maxima and a periodic profile of $C(\tau)$ indicate a high level of temporal regularity of excitatory events, whilst small-amplitude irregular

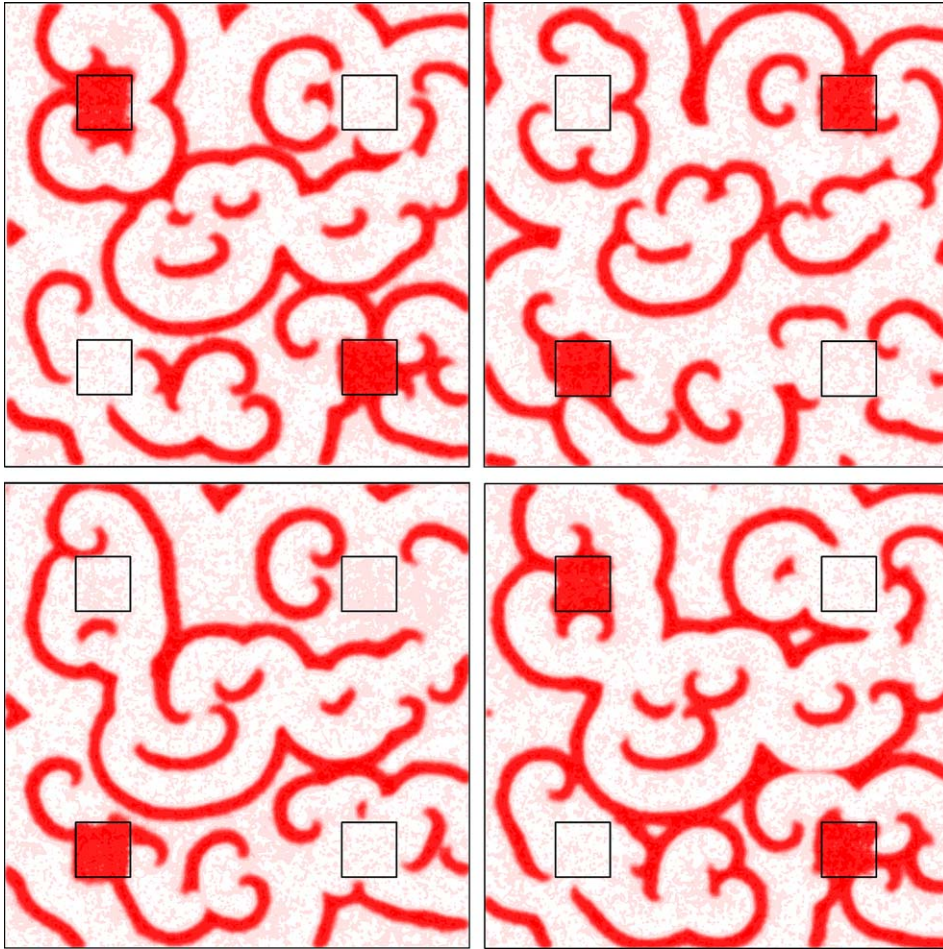


Fig. 4. Noise-induced spatial dynamics in the diffusively coupled media ($p = 0$) with four embedded 30×30 small-world clusters characterized by $p = 0.2$. All spatial profiles are depicted on a 256×256 square grid with a linear colour profile, red marking 1.0 and white 0.0 values of u , whereby the time increases from the top left towards the bottom right picture. (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

oscillations indicate temporal disorder in the system. By inspecting results presented in Fig. 5, it can be captured at a glance that the small-world connectivity (Fig. 5(c) and (d)), in comparison to the regular diffusive coupling of spatial units (Fig. 5(a) and (b)), clearly enhances the temporal order and global synchronization of excitatory events in the system. In particular, for the intermediate σ at $p = 0.1$ (Fig. 5(c)), $C(\tau)$ is characterized by spiky and highly periodic oscillations, which slowly fade in amplitude as τ increases. On the other hand, for $p = 0$ (Fig. 5(a) and (b)) $C(\tau)$ is a small-amplitude faintly periodic function, indicating a low degree of temporal order in the system. For both $p = 0$ and $p = 0.1$, larger than intermediate noise-levels clearly destroy temporal order in the system, whereby it should be noted that the small-world connectivity enables considerable regularity and synchronization of excitatory events even for large σ (see Fig. 5(d)).

Finally, it remains of interest to encompass all above-findings regarding effects of small-world connectivity on the temporal order in a single quantity. To this purpose, we calculate the characteristic correlation time τ_c according to the formal equation:

$$\tau_c = \int_0^{\infty} C^2(t) dt. \quad (6)$$

Notably, the same quantity for quantifying noise-induced temporal order in a single excitable system was also used by Pikovsky and Kurths [18]. Results for various σ and p are presented in Fig. 6. It is evident that there exist a particular σ for each p where the noise-induced temporal order in the media is resonantly pronounced, which is indicated by the

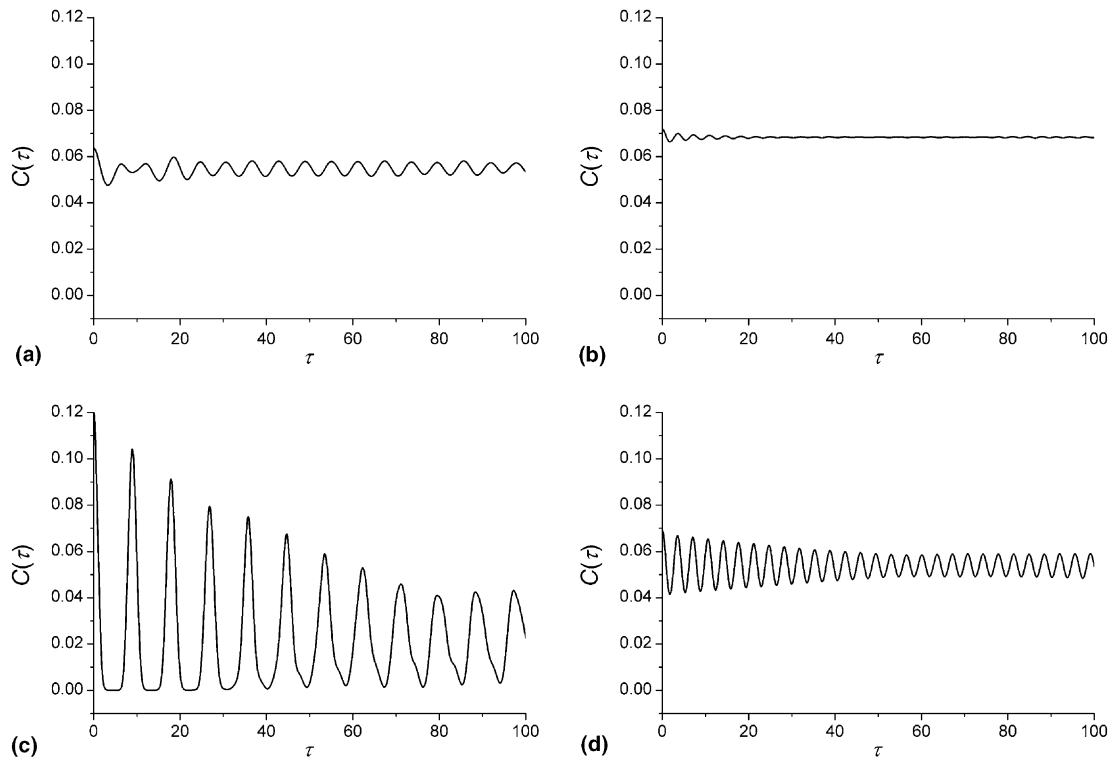


Fig. 5. Autocorrelation of the firing-rate function for different σ and p . (a) $C(\tau)$ corresponding to Π in Fig. 2(b). (b) $C(\tau)$ corresponding to Π in Fig. 2(c). (c) $C(\tau)$ corresponding to Π in Fig. 3(b). (d) $C(\tau)$ corresponding to Π in Fig. 3(c).

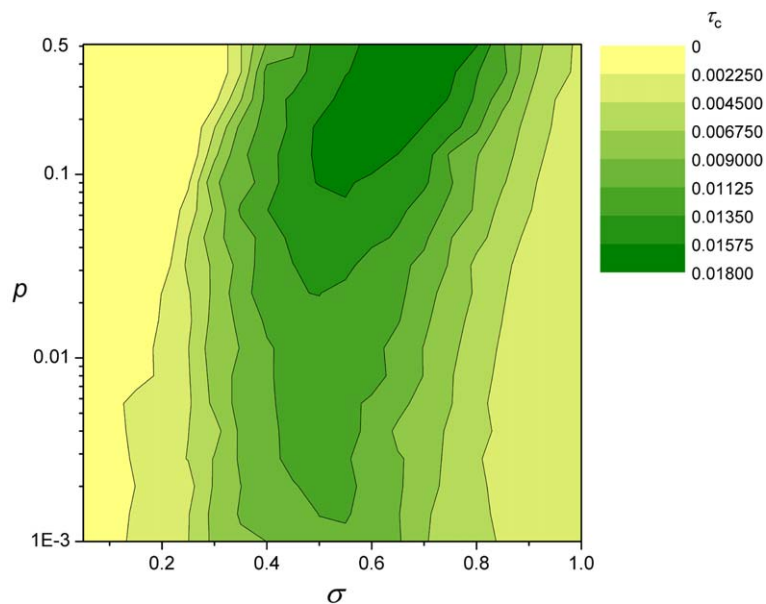


Fig. 6. Effects of small-world connectivity on the temporal order in the studied neural media. It is evident that the maximally attainable temporal coherence, quantified by the characteristic correlation time τ_c , increases with the increasing fraction of shortcut links p .

existence of a maximal τ_c . Clearly, however, the maximally attainable temporal coherence of excitatory events that can be induced by additive random spatiotemporal perturbations increases with increasing values of p . In conjunction with above-presented results, we thus provide ample evidence that the introduction of small-world connectivity, i.e., shortcut links between distant spatial units, facilitates global synchronization of excitatory events and thus temporal order in the studied neural media.

Since the introduction of small-world connectivity largely decreases the average path length between two arbitrary spatial units of the system [24,25], the above concluding statement regarding the effect of shortcut links on the temporal order in the studied media is not surprising. In particular, shorter path lengths between arbitrary sites imply directly that the information in such a network is transmitted much more efficiently than in a regularly coupled lattice. In our case, the information to be transmitted is the excitation of a single neuron to its neighbours. Thus, it is only natural to see locally induced excitations propagate instantly through the media at larger p , thereby facilitating global synchronization and overall temporal order in the system.

5. Spatial order

Following the detailed analysis of temporal order, this section is devoted to the mathematical quantification of spatial order in the studied media. To this purpose, we calculate the structure function of the system according to the equation

$$S(k_x, k_y) = \langle H^2(k_x, k_y) \rangle, \tag{7}$$

where $H(k_x, k_y)$ is the spatial Fourier transform of the u -field at a particular t and $\langle \dots \rangle$ is the ensemble average over noise realizations. Moreover, we exploit the circular symmetry of the structure function (see Fig. 7) by calculating the circular average of $S(k_x, k_y)$ according to the equation

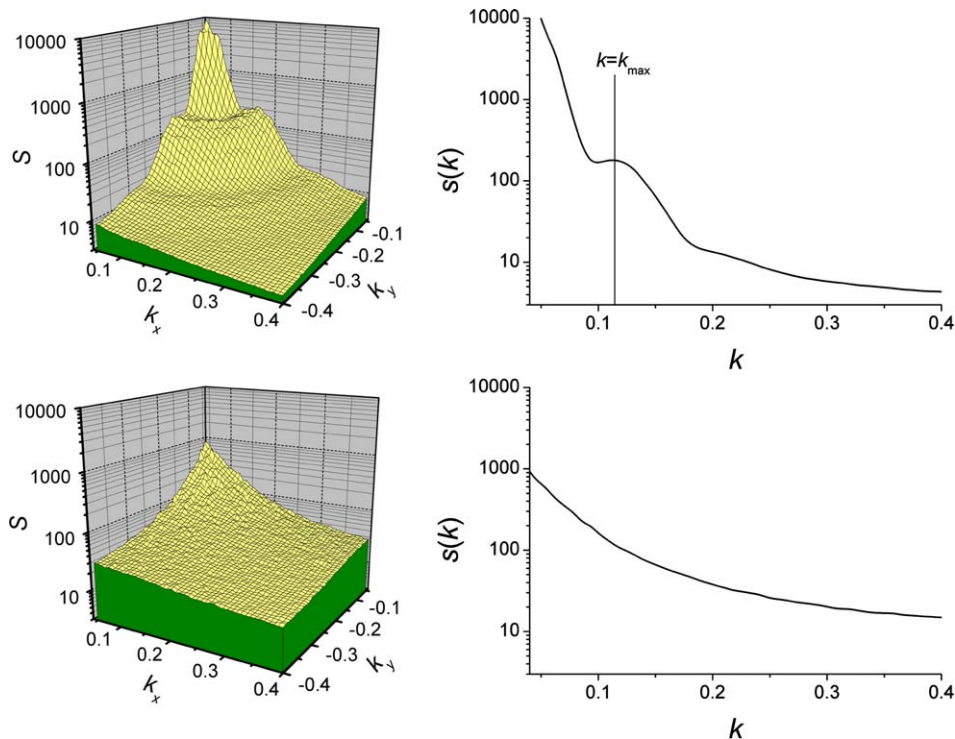


Fig. 7. Spatial structure function S and the circularly averaged spatial structure function $s(k)$ in dependence on p for the near-optimal σ . The upper row corresponds to the spatial profile of u presented in Fig. 2(b) ($p = 0$), whilst the bottom row pertains to Fig. 3(b) ($p = 0.1$).

$$s(k) = \int_{\Omega_k} S(\vec{k}) d\Omega_k, \tag{8}$$

where $\vec{k} = (k_x, k_y)$, and Ω_k is a circular shell of radius $k = |\vec{k}|$. Results presented in Fig. 7 show $S(k_x, k_y)$ and $s(k)$ for the near-optimal σ at $p = 0$ and $p = 0.1$ in the upper and bottom row, respectively. It is evident that for $p = 0$ there exist a particular spatial frequency, marked with the vertical line at $k = k_{\max}$, that is resonantly pronounced for some intermediate value of σ [48]. This is the fingerprint of spatial coherence resonance, recently reported in [23,49], and is a clear indicator for the existence of a well-defined noise-evoked characteristic spatial periodicity in the exclusively diffusive coupled ($p = 0$) excitable neural media. On the other hand, for $p = 0.1$ the circularly averaged structure function is completely flat, indicating the fact that no particular spatial periodicity can be induced by random spatiotemporal perturbations if shortcut links are introduced to the two-dimensional network. Thus, results presented in Fig. 7 fully support above visually assessed findings (compare the upper row of Figs. 2(b) and 3(b)), confirming the disordering effect of long-range couplings on the spatial order in neural media.

As by the analysis of temporal order, it remains of interest to encompass all above-findings regarding effects of small-world connectivity on the spatial order in a single quantity. To quantify the ability of each particular σ to extract the spatial order in the media at a given p more precisely, we calculate the quantity $\delta s = s(k_{\max})/\bar{s}$, where $\bar{s} = (s(k_{\max} - \Delta k_a) + s(k_{\max} + \Delta k_b))/2$ is an approximation for the level of background fluctuations in the system, whereas Δk_a and Δk_b mark the estimated width of the peak around k_{\max} at the optimal σ . Thus, δs measures the normalized height of the peak at k_{\max} for each particular σ and p , thereby unambiguously determining the spatial order in the system. Noteworthy, a similar measure for quantifying effects of noise on the spatial order of spatially extended systems was also used in [22,23]. Results for various σ and p are presented in Fig. 8. It is evident that, unlike by the analysis of temporal order presented in Fig. 6, the small-world connectivity destroys spatial order in the media, i.e., the maximally attainable δs decreases, already at very small fractions of introduced shortcut links. In particular, less than 1% of long-range couplings suffices to completely hinder coherent pattern formation in the system. Conclusively, presented results clearly evidence that the introduction of small-world connectivity vastly impairs spatial order in the studied neural media.

In order to provide an explanation for the reported destructive influence of small-world connectivity on the spatial order in neural media, we first briefly summarize recent findings regarding noise-induced spatial periodicity in excitable media [23,48]. There it was argued that the noise-robust excursion time that is characteristic for the local dynamics of excitable units [18], together with the spread rate proportional to \sqrt{D} with which excitations propagate through the

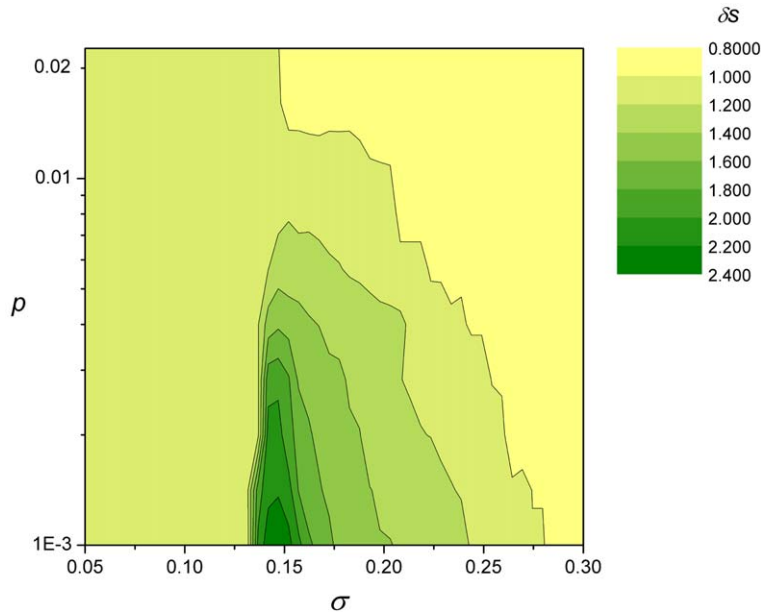


Fig. 8. Effects of small-world connectivity on the spatial order in the studied neural media. It is evident that the maximally attainable spatial coherence, quantified by the normalized peak height of the circularly averaged spatial structure function, decreases rapidly with the increasing fraction of shortcut links p .

media, constitute an inherent spatial scale, i.e., spatial periodicity, that can be resonantly enhanced by additive random spatiotemporal perturbations, thus enabling spatial coherence resonance in the system [23,48]. Here we argue that the introduction of small-world connectivity disrupts this inherent spatial scale of the media since it indirectly affects the spread rate D with which local excitations propagate through the two-dimensional network. As already argued, fact is that shortcut links decrease the typical path length between two arbitrary sites, thereby facilitating temporal order in the system (see Fig. 6). On the other hand, the decreased typical path length implies that local excitations can reach more distant spatial units in a given time than they would normally do in case of a regular diffusive coupling. This in turn has the same effect as if D would increase. Importantly, however, the typical path length between two arbitrary sites decreases only on average, meaning that there does not exist an exact path length defining the distance between all possible pairs of sites. Note that small-world systems were found to be scale-free [26,34]. Thus, due to the introduced small-world connectivity a given local excitation can, during the excursion time, propagate to the most distant site or just to its nearest neighbour. Therefore, the well-defined inherent spatial scale existing for the regular diffusively coupled network is lacking, which ultimately induces spatial disorder, as evidenced succinctly in Fig. 8.

6. Summary and discussion

In summary, we show that the small-world connectivity of spatial units forming a two-dimensional grid facilitates global synchronization of excitatory events and thus temporal order in the system, whilst on the other hand hinders coherent pattern formation thereby impairing spatial order. The constructive effect of small-world connectivity on the temporal order is argued to originate from the effective shortening of typical path lengths between arbitrary spatial units [24,25], which facilitates information transduction among distant parts of the network, while the disordering effect on the spatial scale is attributed to the scale-free nature of small-world networks [26,34] that effectively disrupts the internal spatial scale of the media already at small p .

While at first sight our results might appear somewhat contradictory, we emphasize that they merely stress the fact that the temporal and spatial network dynamics is governed by different mechanisms, which suggests that both might have separate importance for the functioning of neural tissue. Since couplings among neurons were found to be diffusively regular [50] as well as long-range random [36,37], neural tissue thus presents an environment in which both temporally as well as spatially ordered information transfer and storage are feasible, possibly each fulfilling a distinctive task.

Recently, it has 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 [51]. On the other hand, diffusively coupled areas might be the actual memory holders in the brain, enabling efficient data encoding through coherent spatial patterns. In summary, small-world connectivity facilitating temporally ordered behaviour appears to be important for information retrieval as well as short term memory [52,53], while diffusively coupled areas enabling coherent spatial patterns might be the actual data storage facilities of the brain.

Moreover, since it has been discovered that excitable systems guarantee robust signal propagation through the neural tissue in a substantially noisy environment [54], and studies evidencing the constructive role of stochastic influences on the functioning of the human brain have recently been mounting [55–59], it would be very interesting to elucidate if above reported theoretical results are readily attainable also experimentally. Our work thus provides interesting aspects on the importance of temporally and spatially ordered functioning of neural networks, while hopefully providing also some possibilities for future research work, especially in the field of neuroscience, where excitability, noise, and small-world connectivity in spatially extended systems appear to be universally present.

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