

Spatial decoherence induced by small-world connectivity in excitable media

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New Journal of Physics 7 (2005) 252

Received 19 September 2005

Published 15 December 2005

Online at <http://www.njp.org/>

doi:10.1088/1367-2630/7/1/252

Abstract. We study effects of different network topologies on the noise-induced pattern formation in a two-dimensional model of excitable media with FitzHugh–Nagumo local dynamics. In particular, we show that the introduction of long-range couplings induces decoherence of otherwise coherent noise-induced spatial patterns that can be observed by regular connectivity of spatial units. Importantly, already a small fraction of long-range couplings is sufficient to destroy coherent pattern formation. We argue that the small-world network topology destroys spatial order due to the lack of a precise internal spatial scale, which by regular connectivity is given by the coupling constant and the noise robust excursion time that is characteristic for the local dynamics. Additionally, the importance of spatially versus temporally ordered neural network functioning is discussed.

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1. Introduction

It is a well-established fact that random spatiotemporal perturbations can constructively affect the dynamics of spatially extended systems [1]. In particular, spatiotemporal stochastic resonance has been first reported in [2] for excitable systems, while spatial coherence resonance has been introduced in [3] for systems near pattern-forming instabilities as well as in [4] for excitable media. Other well-known phenomena include noise-induced spiral growth and enhancement of spatiotemporal order [5], noise sustained coherence of space-time clusters and self-organized criticality [6], noise enhanced and induced excitability [7], noise-induced propagation of harmonic signals [8], persistency of noise-induced spatial periodicity [9], as well as noise sustained and controlled synchronization [10]. Furthermore, stochastic [11] and coherence [12] resonance phenomena have also been studied extensively in one-dimensional networks of dynamical systems.

While in the past, the vast majority of scientific research dealing with deterministic or noise-affected dynamics of spatially extended systems was devoted to the study of regular networks, presently the focus is shifting towards networks with variable random connectivity. Since already a small fraction of randomly introduced links between distant vertices largely decreases the typical path length between two arbitrary sites, such networks were termed appropriately as ‘small-world’ networks [13]. Most importantly, small-world networks appear to be excellent for modelling interactions among units of complex systems. Examples range from social networks [14], scientific-collaboration networks [15], food webs [16], computer networks [17], and of immediate importance for the present paper, also to neural networks [13], [18]–[25].

Notably, stochastic [26] and coherence [27] resonance phenomena were already studied in one-dimensional networks with small-world connectivity. In both cases, it was discovered that the introduction of shortcut links between randomly chosen sites increases the global synchrony of the network. In particular, authors in [26, 27] 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 pattern formation in two-dimensional planar networks.

In the present study, we therefore analyse spatial frequency spectra of excitable media in dependence on different levels of additive spatiotemporal noise and variable network topologies. By calculating the average spatial structure function, we show that the introduction of shortcut links between randomly chosen sites blurs the noise-induced spatial periodicity [28] that can be observed by regular, i.e. diffusive, network connectivity. Particularly, our calculations reveal that already a small fraction of randomly introduced shortcut links completely disables coherent noise-induced pattern formation in the studied excitable media. Accordingly, we propose the term ‘spatial decoherence’ to capture the essence of the outlined phenomenon. To explain the observed spatial decoherence, we use arguments recently applied for the explanation of spatial coherence resonance [4], which leads us to the conclusion that small-world-like network topologies with their lack of a precisely defined internal spatial scale, implied by broadened-delta, Poissonian, or even power-law distributions of links per network unit [29], destroy spatial order due to the disruption of the inherent spatial scale of diffusively coupled excitable media given by the coupling constant and the noise robust excursion time [30] that is characteristic for the local dynamics.

The excitable media under study is locally modelled by the FitzHugh–Nagumo equations [31] that were derived from the Hodgkin–Huxley model describing the excitable dynamics of

electrical signal transmission along neuron axons [32]. Since recently evidences for small-world connectivity of neurons in neural tissue are accumulating rapidly [13, 19, 20, 22, 25], and stochastic influences are widely acknowledged to be an inseparable part of every real-life process, it is of great interest to study effects of different network topologies on the noise-induced spatial dynamics of such systems.

The paper is structured as follows. Section 2 is devoted to the description of the mathematical model. In section 3, evidence for the spatial decoherence are presented, while in the last section, we summarize the results and outline biological implications of our findings.

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 [31]

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

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

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 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 [1]. The sum in equation (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, 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 connectivity, as described in [13]. For parameter values $a = 0.75$, $b = 0.01$ and $\kappa = 0.05$, the local FitzHugh–Nagumo system is governed by a single excitable steady state $u = v = 0.0$, which is presently used as the initial condition for all lattice sites. In what follows, we will show that non-zero values of p induce decoherence of otherwise coherent noise-evoked spatial structures that can be observed by $p = 0$, thus providing evidence for spatial decoherence in excitable media due to the introduction of small-world connectivity.

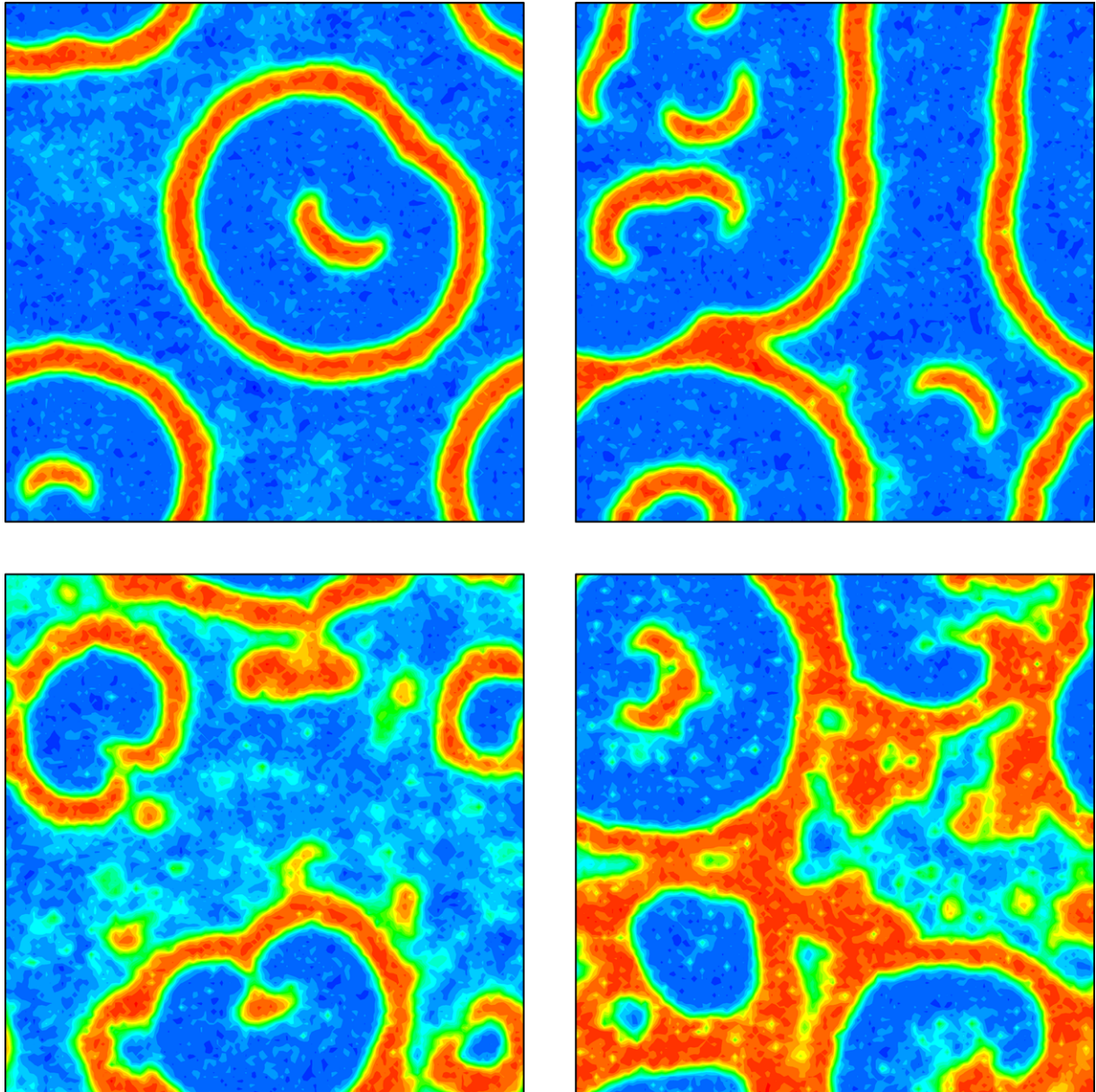


Figure 1. Characteristic snapshots of the spatial profile of u for $p = 0$ (top left), $p = 0.001$ (top right), $p = 0.005$ (bottom left) and $p = 0.01$ (bottom right) at the near optimal noise level $\sigma = 0.15$ and $D = 3.84$. All figures are depicted on a 128×128 square grid with a linear colour profile, red marking 1.0 and blue 0.0 values of u .

3. Spatial decoherence

We start the study by visually inspecting four characteristic spatial profiles of u obtained by various p at a near optimal σ for noise-induced pattern formation in the studied excitable media. Results presented in figure 1 clearly evidence that increasing values of p hinder coherent pattern formation. Importantly, whilst spatial profiles obtained by $p = 0$ and $p = 0.001$ present

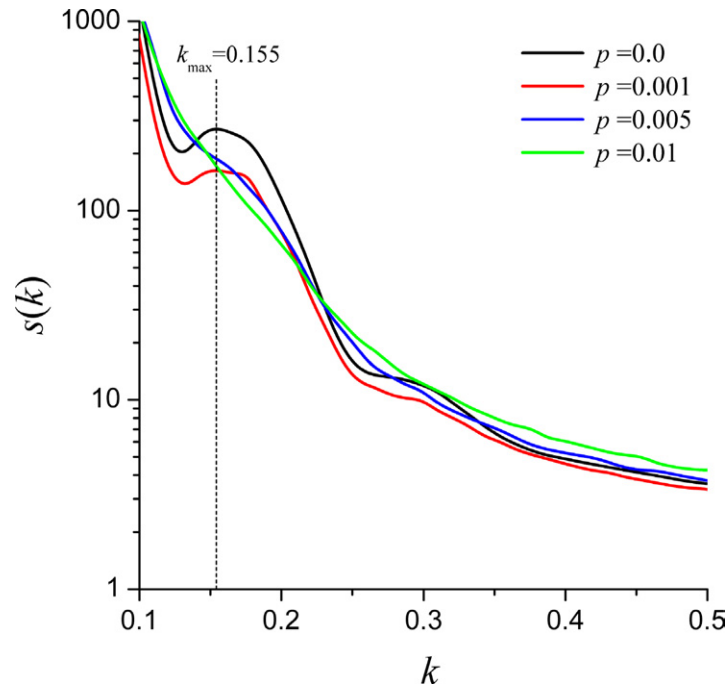


Figure 2. Circular average of the structure function for four different values of p corresponding to the spatial profiles in figure 1.

compelling evidences of noise-induced self-organization in excitable media and qualitatively differ only minutely, substantial spatial decoherence can be visually assessed already at $p = 0.005$. Thus if only 0.5% of all links constituting the planar network are randomly rewired, spatiotemporal noisy perturbations are unable to induce coherent patterns in the media. At $p = 0.01$, the spatial decoherence is pronounced even more profoundly, thus indicating the destructive nature of increasing values of p on the noise-induced spatial dynamics.

To enable a quantitative analysis of the observed phenomenon outlined in figure 1, we calculate the structure function of the system according to the equation

$$S(k_x, k_y) = \langle H^2(k_x, k_y) \rangle, \quad (5)$$

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 by calculating the circular average of $S(k_x, k_y)$ according to the equation

$$s(k) = \int_{\Omega_k} S(\vec{k}) d\Omega_k, \quad (6)$$

where $\vec{k} = (k_x, k_y)$, and Ω_k is a circular shell of radius $k = |\vec{k}|$. Figure 2 shows four $s(k)$ obtained for the same values of p and σ as used in figure 1. In accordance with results published recently [4], it can be observed that for $p = 0$ as well as $p = 0.001$ there exists a particular spatial frequency, marked with the thin dashed line at $k = k_{\max}$, that is greatly enhanced for some intermediate σ . On the other hand, the fingerprint of spatial coherence reduces substantially for $p = 0.005$

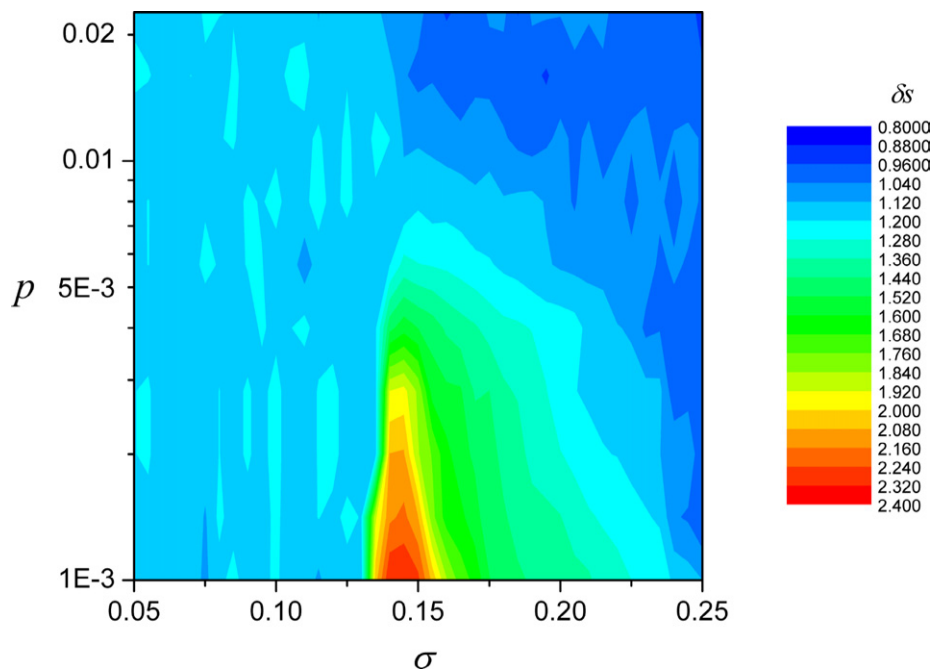


Figure 3. Spatial decoherence in the studied excitable media. The colour map displays δs in dependence on σ and p . Whilst the optimal σ required to induce the most coherent response remains largely unaffected by p , the maximally attainable spatial coherence decreases rapidly with the increasing fraction of long-range couplings.

(note that the peak at $k = k_{\max}$ is barely visible), whilst it disappears completely for $p = 0.01$. Thus, results presented in figure 2 fully support above visually assessed findings, implying the fact that increasing values of p induce decoherence of noise-induced spatial patterns.

To quantify the ability of each particular σ to extract the inherent spatial scale of the media at a given p more precisely, we calculate the quantity $\delta s = s(k_{\max})/\tilde{s}$, where $\tilde{s} = [s(k_{\max} - \Delta k_a) + s(k_{\max} + \Delta k_b)]/2$ is an approximation for the level of background fluctuations in the system, whereby 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 . Results are presented in figure 3. It is evident that for $p < 0.005$ there always exists an optimal level of additive spatiotemporal noise for which the peak of the circularly averaged structure function is best resolved, thus indicating the existence of spatial coherence resonance in the studied excitable media, as reported previously in [4]. For $p > 0.005$, however, the fingerprint of spatial coherence resonance disappears rapidly. The flat resonance curves for $p > 0.005$ thus evidence complete spatial decoherence of noise-induced patterns, brought about by the introduction of shortcut links in the excitable media.

In order to shed light on the observed phenomenon, we first briefly recapture results recently published in [4]. There it was argued that the noise-robust excursion time that is characteristic for the local dynamics of excitable units [30], together with the spread rate proportional to \sqrt{D} with which excitations percolate through the media, constitute an inherent spatial scale that can be resonantly enhanced by additive random spatiotemporal perturbations, thus enabling spatial coherence resonance in the system [4].

Presently, we argue that the spatial decoherence sets in due to the disruption of the afore-described inherent spatial scale of the excitable media. In particular, while the excursion time of individual space units remains unaltered by the introduction of long-range couplings, the spread rate of excitations is indirectly very much affected by increasing values of p . This is a direct consequence of the fact that the introduction of shortcut links decreases the typical path length between two arbitrary sites in comparison to a regular diffusively coupled network. Thus, while the spread rate of excitations is still proportional to \sqrt{D} , the typical path length between two arbitrary grid units decreases dramatically, which in turn has the same effect as if D would increase. Therefore, in a small-world network, a locally induced excitation can reach much more distant sites than it would normally do, facilitating noise-induced synchronization of distinct network units [26, 27], or assuring fast response abilities of the system [18]. 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 networks with small-world and random topologies lack a precisely defined internal spatial scale, which is implied by broadened-delta, Poissonian, or even power-law distributions of links per network unit that characterize them [29]. 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. Note that roughly similar effects would be obtained if D would vary randomly from grid unit to unit. Either way the well-defined inherent spatial scale existing for the regular diffusively coupled network is lacking. Ultimately, this leads to spatial decoherence of noise-induced spatial patterns already at very small values of p , as emphasized throughout this work.

4. Summary and discussion

In summary, we show that the small-world connectivity of units forming a two-dimensional spatial grid hinders noise-induced coherent pattern formation in the studied excitable media. This so-called spatial decoherence is attributed to the inherent long-range couplings of small-world networks, which effectively disrupt the internal spatial scale of the media already at small p .

Interestingly, at first sight our results appear to be somewhat in contradiction with previous studies analysing effects of small-world connectivity on deterministic [18, 23] as well as noise-induced dynamics in complex networks [26, 27]. In particular, while long-range couplings were found to have a favourable effect on the temporal noise-induced coherence of neural networks [27], we presently report otherwise for the spatial system dynamics. These results are of course not contradictive but 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 [33] as well as long-range random [19, 20], neural tissue thus presents an environment in which both, temporally as well as spatially ordered information transfer and storage are feasible, 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 [34]. 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 [35], while diffusively coupled areas enabling coherent spatial patterns might be the actual data storage facilities of the brain. 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.

Finally, it is important to note that in neural tissue each axon can have synaptic connections with several distant neurons. Thus, despite the fact that the above-used method for constructing small-world networks yields some units that have connections not just to a single but also to several distant vertices, care should be exercised when interpreting above findings in terms of functionality of real-life neural networks. Although it is reasonable to expect that intentionally produced hubs in an otherwise regularly coupled network will have qualitatively the same impact on the spatial dynamics as the small-world connectivity were hubs are introduced by chance, additional detailed studies regarding function-follow-form [36] are necessary to clarify the importance of different structural physiological properties of neural networks.

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