



NOISE-INDUCED SPATIAL STRUCTURES IN EXCITABLE MEDIA

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The paper considers the formation of coherent structures in a population of excitable systems driven by noise. We focus on two effects. (i) A one-dimensional lattice with at least one inhomogeneous unit demonstrates noise-induced excitation waves. The degree of coherence in such a spatial structure can be enhanced by tuning the noise intensity. (ii) A random distribution of the parameters responsible for the excitatory properties and the interaction strength leads to self-organization in the form of cluster synchronization.

1. Introduction

Together with self-sustained oscillators, excitable units serve as an important paradigm in the study of nonlinear dynamic phenomena. To understand electrical signaling in cells, it is helpful to divide all cell types into two groups: excitable cells and nonexcitable cells. Many cells maintain a stable equilibrium potential. For some of these, if a current is applied to the cell for a short period of time, the potential returns *directly* to its equilibrium value after the applied current has been removed. Such cells are called nonexcitable. Typical examples are the epithelial cells that line the walls of the gut. However, there are other cells for which, if the applied current is sufficiently strong, the membrane potential goes through a *large excursion*, called an action potential, before eventually returning to rest. Such cells are called excitable. Excitable cells include cardiac cells, smooth and skeleton muscle cells, secretory cells, and most neurons.

The underlying excitability determines, for example, the propagation of an action potential along the axon of a nerve, the reverberating cortical depression waves in the brain cortex [1], waves in muscle tissue (particularly the heart muscle: in their two- and three-dimensional manifestations these excitable waves are intimately related to the problem of atrial flutter and fibrillation [2]), or waves in colonies of microorganisms [3]. In this context, a number of interesting problems arise for experimental and numerical investigations of excitable media. Both the response of a single excitable functional unit and the overall dynamics of an ensemble of such units to an external stimulus are now well understood [3-5].

Noise is inevitably present in all natural oscillators. The positive (that is creative), ordering role of noise was recently demonstrated for a wide range of natural systems, including systems of physical, chemical, and biological origin. The phenomena of stochastic resonance, noise-induced transitions, and stochastic synchronization have been observed experimentally in various biological systems [6, 7]. Our topic here is the

phenomenon of coherence resonance that is induced *purely by noise without an external signal* [8-10]. At a certain noise amplitude the regularity of the noise-induced dynamics is maximal. This is witnessed by a well-pronounced peak in the Fourier power spectrum and by a ring-like structure of probability density distribution in the phase space of the system. Recently, Postnov *et al.* [11-13] described synchronization mechanisms of coupled coherence resonance oscillators.

Cooperative dynamics of an ensemble of interacting self-sustained systems manifests itself in the form of synchronization phenomena and wave propagation. Clustering, i.e. the formation of groups of functional units with similar properties (amplitudes, phases or frequencies) is an important phenomenon which is assumed, for instance, to underlie perception and the processing of information by the brain [14]. The problem of clustering was formulated and analyzed in a general context within the framework of phase equations [15], self-sustained periodic oscillators [16], chaotic dynamical networks [17], or of a chain of bistable elements [18]. Vadivasova *et al.* [19] showed that cluster synchronization is structurally stable to small fluctuations.

In the present paper we focus on the questions: what are the types of noise-induced ordering that can be observed in ensembles of *stochastic* excitable systems? What are the common, respectively the specific properties of chains of coupled excitable and self-sustained systems? With this aim we investigate the generation and propagation of excitable waves caused by the presence of an inhomogeneous element with a low excitation threshold. Then we analyze cluster formation caused by the random distribution of excitation parameters and coupling strengths.

2. Model and Method

Let us take FitzHugh-Nagumo model as the unit in an array. Being originally suggested for the description of nerve pulses [20], this model is commonly applied to describe excitable dynamics in different fields ranging from chemical reactions to biological processes.

With x and y being a fast and a slow variable, respectively, the model reads

$$\begin{aligned} \varepsilon dx/dt &= x_j - x_j^3/3 - y_j + g_j(x_{j+1} + x_{j-1} - 2x_j), \\ dy_j/dt &= x_j + a_j + D\xi_j(t), \quad j = 1, \dots, N. \end{aligned} \quad (1)$$

Here, j numbers the excitable unit in the chain, and $\varepsilon=0.01$ is the small time-scale ratio of the two variables. The parameter a governs the character of the solutions and is responsible for the excitatory properties of the individual dynamics, and g denotes the coupling strength. Each functional unit is subjected to stochastic forcing by Gaussian white noise $\xi_j(t)$ which is statistically independent in space and with zero mean value, i.e. $\langle \xi_j(t)\xi_j(t') \rangle = \delta_{ij}\delta(t-t')$ and $\langle \xi_j(t) \rangle = 0$. We use free boundaries and random initial conditions.

With noise, an excitable system generates a random sequence of pulses, i.e. firing events, whose properties can be described by Eq. (1). We characterize the process via the distribution of the time intervals between pulses, the periodicity of their occurrence, and the mean frequency. The mean frequency of noise-induced oscillations in the j -th element is defined as $\langle f_j \rangle = 1/\langle \tau_j \rangle$, where $\langle \tau_j \rangle$ is the time averaged pulse duration specified as the sum of the activation time needed to excite the system from the stable fixed point and the excursion time needed to return from the excited state.

In order to quantitatively characterize the effect of coherence resonance, different methods can be used, including the signal-to-noise ratio [8, 9] and a properly defined entropy-like measure [13]. In this paper, we calculate the regularity of an individual unit as [10]:

$$R_j = \langle \tau_j \rangle / [\text{Var}(\tau_j)]^{1/2}. \quad (2)$$

Overall dynamics of the whole array is described by the regularity averaged over all functional units $R_i = \bar{R}_j$.

3. Wave structures

In the deterministic case, due to the local coupling between neighboring elements, excitation waves can propagate through the medium. In the one-dimensional lattice, such waves propagate without any decrement of their amplitude and velocity until they reach the boundary of the medium. Note, that excitable systems are characterized by both excitability and refractoriness. That is, after the system has responded to a superthreshold stimulus with a large excursion from rest, there is a period of refractoriness during which no subsequent response can be evoked followed by a period of recovery during which excitability is gradually rebuilt. Once excitability is restored, another wave of excitation can be evoked. The wave velocity is the higher the stronger the coupling and the lower the excitation threshold of the individual functional units. Moreover, it strongly depends on the time allowed for recovery of excitability.

With noise added to each system, the formation and propagation of excitation waves are changed. Random excitation can happen in any element at any time. This element then becomes the center of a wave propagating to both sides. The propagation stops as soon as it reaches the array boundary or an element in the excitatory (or refractory) state. Depending on the relation between the mean frequency of noise-induced firings and the wave velocity, the wave can pass a shorter or longer distance along the array before it disappears in a collision with another wave propagating in the opposite direction.

For identical units and equal noise intensity, the above process is completely unpredictable. In this paper we investigate the case when the one-dimensional lattice of excitable systems contains an inhomogeneous element with lower excitation threshold. This element is more frequently excited by noise and becomes the center of wave propagation. In our simulations, the inhomogeneous unit with $a_1=1.01$ is located at the beginning of a chain ($j=1$). For $j=2, \dots, 100$, the excitation parameter is fixed at $a_j=1.05$.

Fig. 1 presents the spatio-temporal pattern of noise-induced waves in the system (1) for weak noise ($D=0.0002$). Black dots represent the firing state. The gray arrow indicates a center of wave birth. The black arrow points at an event of wave suppression after collision with another wave. One can observe how a wave is annihilated when it reaches elements in the refractory state.

In spite of a large number of excitation and annihilation points, the cooperative spatiotemporal dynamics looks fairly regular (Fig. 2, a). In this case, wave propagation precedes the mean time between noise-induced firings for any (except the first) unit in an array. As a result, spatiotemporal structures in the form of excitation waves running in different directions can be observed. Along such waves each element operates in a more

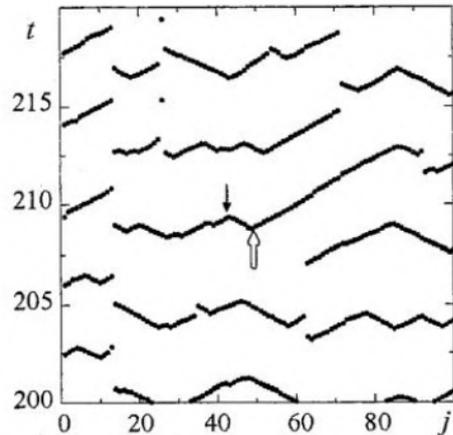


Fig. 1. Spatiotemporal pattern for $D=0.0002$ and $g=0.015$. Black dots indicate firing events. Appearance (gray arrow) and annihilation (black arrow) as well as interruption of excitation waves are clearly observed

regular way than it would be possible for the same noise intensity, but without spatial communications. For strong interaction and weak noise, the first unit becomes the single excitation center and waves propagate without annihilation for long distances. With stronger noise as well as with weaker coupling, the structure is changed. Increasing noise leads to interruption of wave fronts (Fig. 2, *b*). This is related both to effects of refractoriness and to an instantaneously increase of the excitation threshold caused by noise. Subsequent waves can not cause firings. Figs 2, *b*, *c*, and *d* illustrate how wave fronts are interrupted more and more frequently with decreasing coupling strength. Thus, the regime in Fig. 2, *a* in spite of wave fronts consisting of combinations of oppositely-propagating waves, is seen to be more regular than the structures in Fig. 2, *b*, *c*, and *d*.

To characterize the observed structures, we introduce a causality principle for firing events in two neighboring units if their phases overlap in time (Fig. 3). Let us call a group consisting of L paired elements a mutually-conditioned discharge. Obviously, large (in average) values of L correspond to a well-pronounced spatial structure. Hereafter the spatial regularity can be defined as the ratio between the mean length of the mutually-conditioned discharge and its maximal value $L=N$ (i.e. the length of the chain):

$$R_s = \langle L \rangle / N. \quad (3)$$

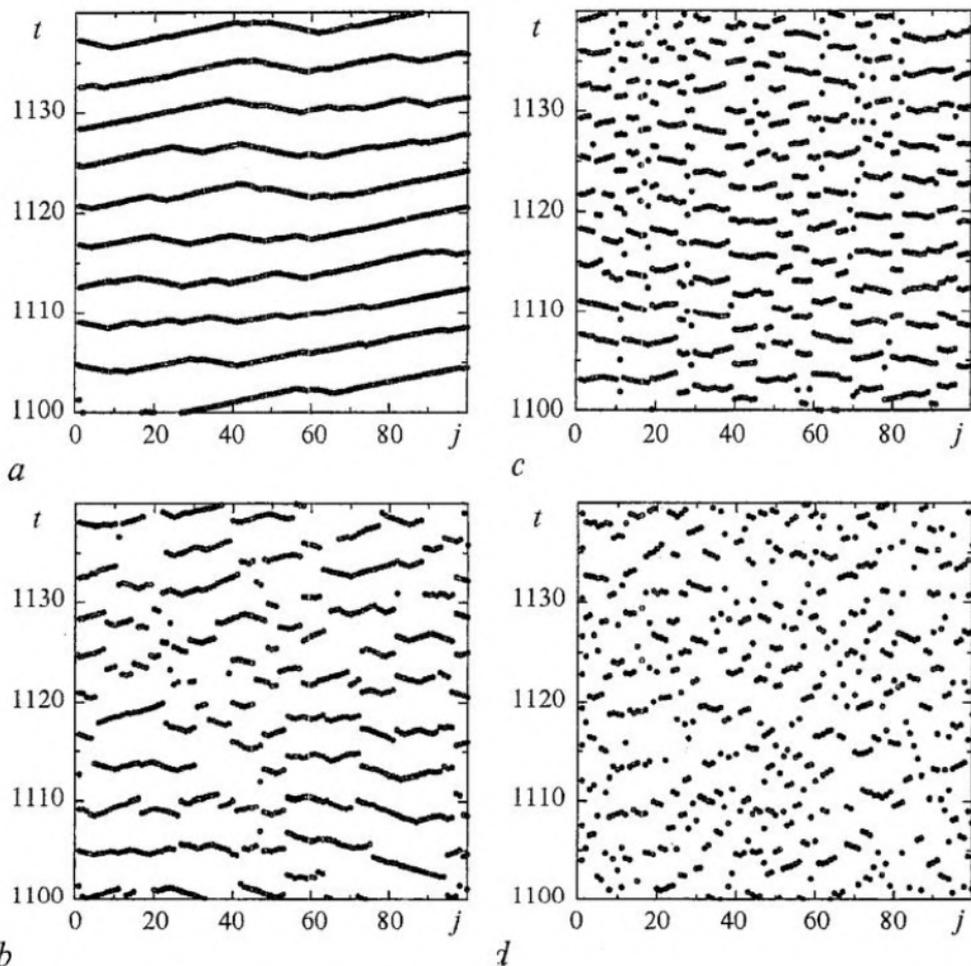


Fig. 2. Spatiotemporal structures for (a) $g=0.02$, $D=0.0002$; (b) $g=0.02$, $D=0.001$; (c) $g=0.01$, $D=0.0002$; (d) $g=0.005$, $D=0.0002$

Both temporal R_t and spatial R_s coherence measures characterize to what degree noise-induced spatiotemporal motions in a one-dimensional lattice can be regularized by tuning the coupling strength g and noise intensity D (Fig. 4). For fixed noise intensity, one can distinguish different behaviors of R_t as function of the coupling strength g . For weak interaction, R_t monotonically grows. Individual regularities of all elements is almost equal (except the first) and they slowly grow with increasing D . This is related to the effect of coherence resonance since the noise intensity is lower than the optimal value. The first element demonstrates a high degree of coherence, but it does not contribute much to the averaged R_t along the array. Thus, for weak coupling, cooperative dynamics does not manifest itself.

For strong interaction, R_t has a well-defined maximum for $D \approx 0.0004$ that is close to the optimal value for an individual system. In this case, noise-induced excitation waves from the first unit penetrate deeply along the array and causes spatial synchronization of firing events. Note, that individual regularities decrease near the boundaries. This fact shows that both noise-induced waves and the effect of mutual stochastic synchronization (discussed below) play an important role in the self-organizing process.

The coupling strength $g \approx 0.012$ corresponds to some critical behavior where the

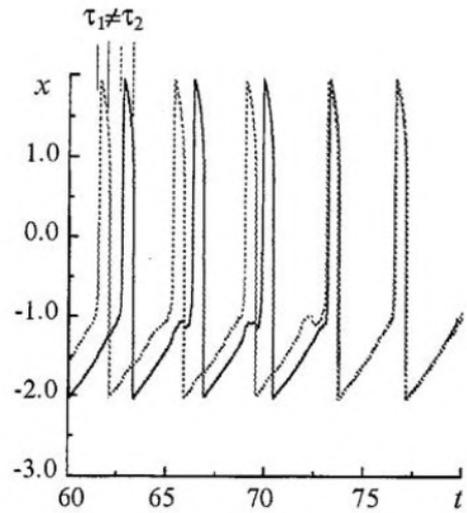


Fig. 3. Causality of firing events

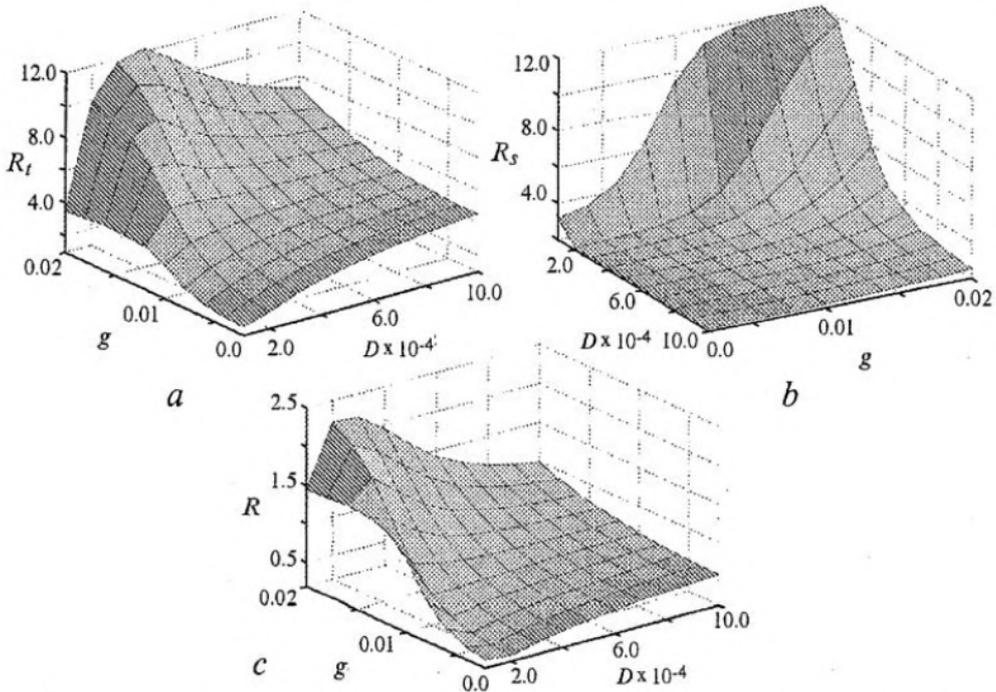


Fig. 4. Integral characteristics for (a) the temporal regularity R_t , (b) the spatial regularity R_s , and (c) the summarized regularity $R = R_t / 7.8 + R_s$

above mechanisms contribute in an equal way. Within a wide range of noise intensities, R_t maintains a constant value. The one-dimensional array becomes insensitive to variation of the noise intensity D . This is related to the combination of individual coherence resonance effects and the regularization in the form of excitable waves.

The spatial regularity R_s behaves in a simpler way. It grows with increasing coupling and with decreasing noise intensity, approaching a maximal value $R_s=1$ (Fig. 4, *b*). Let us introduce a spatio-temporal regularity as the sum of the spatial component R_s and the temporal component R_t (normalized to its maximal value in the individual system):

$$R = R_t/R_{t,\max} + R_s. \quad (4)$$

This index allows us to characterize both the possibility of excitation waves and the temporal degree of coherence. It is interesting to note two peculiarities. First of all, the maximal value is shifted to a smaller value of the noise intensity $D \approx 0.00025$. Moreover, there is region of minimal value of R that corresponds to the absence of coherence in the noise-induced firing events along an array. This region is located at the same range of D as a global maximum but shifted to weak couplings.

In this section we investigated the propagation of noise-induced waves and the appearance of spatio-temporal structures in homogeneous media ($g_j = \text{const.}$, $a_j = \text{const.}$ for $j=2, \dots, 100$). How will the observed structures transform if the excitable media is disordered, i.e. the excitation thresholds and coupling strengths are randomly distributed along an array?

4. Cluster synchronization

The collective dynamics of an ensemble of coupled excitable units of significant interest for many biomedical applications [21]. A population of identical units with the same coupling properties serves as the simplest model. In nature, however, full identity in the properties and operating conditions of the units can only be an idealization. In our work, in contrast to most previous studies, we investigate ordering effects in ensembles of elements that are

- (i) nonhomogeneous, i.e. the activation parameters a_j are random numbers distributed uniformly on $[1.0; 1.1]$;
- (ii) coupled with the strengths g_j which have a random uniform distribution on some range $\Delta = g_{\max} - g_{\min}$ ($g_{\min} = 0.005$, but g_{\max} and, hence, the mean level $(g_{\max} + g_{\min})/2$) are varied).

Thus, our model provides disorder between interacting units in different ways. The question of interest is how such elements adjust their motions in accordance with one another to reach some kind of coherence?

In our experiments with varying distribution intervals for the coupling strength and with a certain level of noise, three basic types of space-time behavior in a one-dimensional array (1) of 100 units was observed. For a vanishing and very narrow Δ , the behavior is totally incoherent that is reflected in the irregular pattern of black (firing state) and white points (Fig. 5, *a*). The firing events in individual units occur at frequencies that are randomly spread in the range $[0.05; 0.27]$ (Fig. 5, *b*). In this case, no stable frequency- or phase-locked groups can be detected. A qualitatively different behavioral pattern is encountered for a broader range of coupling (Figs 5, *c* and *d*). Here, synchronized groups, i.e., clusters of stochastic elements, appear. Within each cluster the frequency difference between any two oscillators vanishes or is small in comparison with the difference between neighboring clusters. To describe spatiotemporal patterns (Figs 5, *a* and *c*) in terms of the causality principle let us calculate the probability of interruption of firing on the j -th element. In the clusterless case, the distribution of probability along

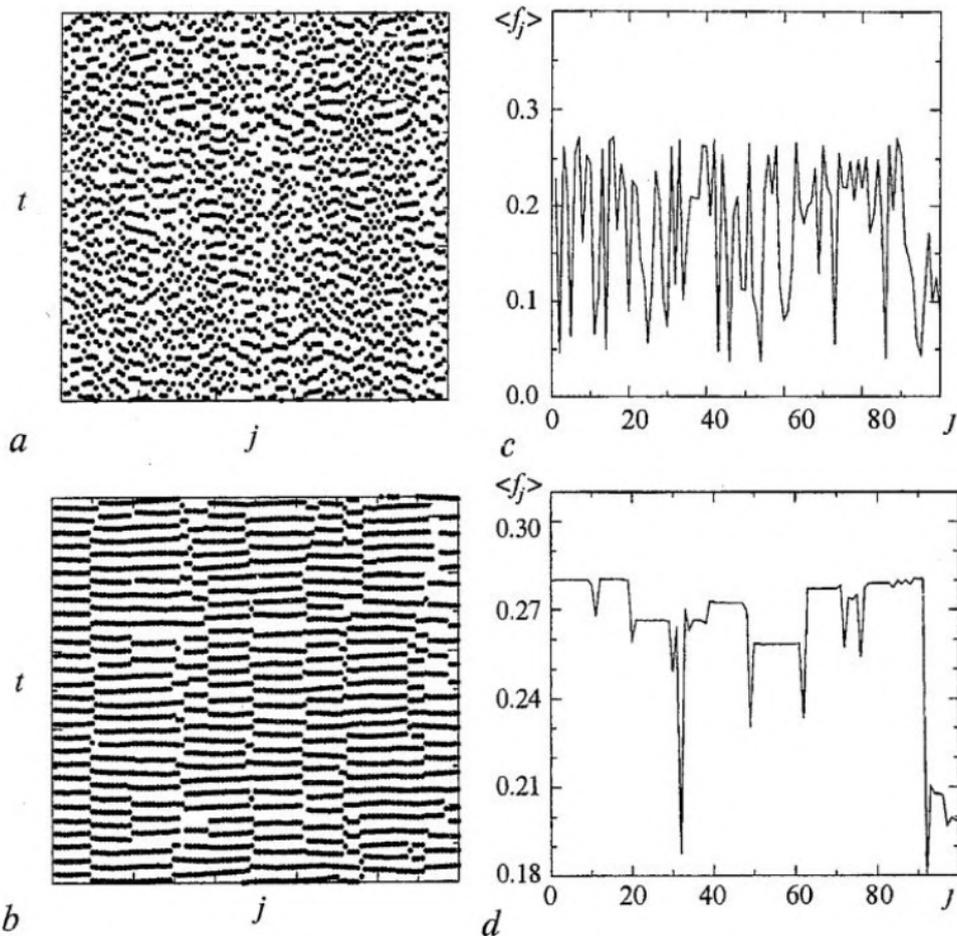


Fig. 5. Spatiotemporal evolution and mean firing frequencies $\langle f_j \rangle$ of an array of 100 excitable units at $D=0.025$ for different widths of the coupling range for $\Delta=0.002$ (a, b) and for $\Delta=0.1$ (c, d). A sequence of clusters are clearly seen in the latter case

an array is random (Fig. 6, a). For a cluster structure, the function P contains a number of local maxima whose locations coincide with the boundary of the respective clusters (Fig. 6, b). Hence, interruption of mutually-conditioned discharges takes place in excitable

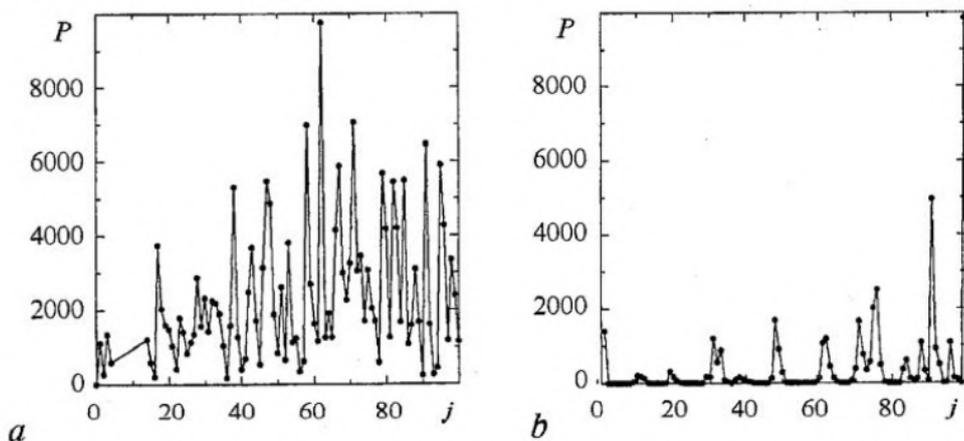


Fig. 6. Probability of firing interruption (a) without clustering and (b) with a cluster structure

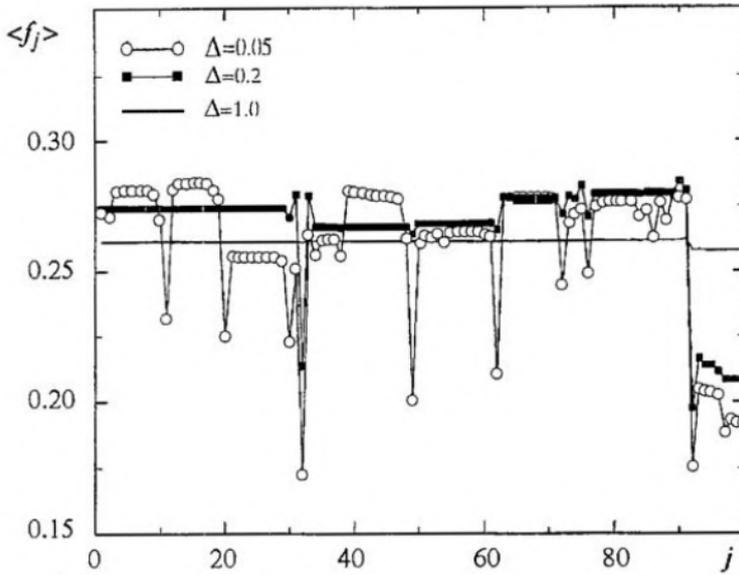


Fig. 7. Reduction of the number of frequency-locked clusters with an increasing width of the coupling range ($D=0.025$)

units at the boundary of a cluster. With a broader coupling interval, the number of clusters decrease (Fig. 7) until finally the global synchronous state (one-cluster state), where all units fire simultaneously, is achieved. Since the incoherent behavior and the totally synchronized behavior are well understood [22, 23], we focus our study on clustering of noise-induced oscillations.

Let us consider now an individual cluster as a spatial meta-unit of an array and describe its main properties. Because of the assumed distribution of system parameters, the elements in a cluster have different randomly scattered frequencies for vanishing coupling, i.e. there is no correlation between the firing events of different cells. With interaction, a frequency locking effect which is responsible for cluster formation takes place (Fig. 8, a). In this case, the elements composing the cluster display regular synchronous firings. However, the variance of the pulse duration $\sigma_{\tau_j}^2 = \langle \tau_j^2 \rangle - \langle \tau_j \rangle^2$ changes within a cluster. It is minimum in the center of cluster and the difference in σ_j between neighboring elements increases near the ends of the cluster (Fig. 8, b). Thus, with frequency entrainment, oscillators demonstrate different degrees of mutual synchronization.

Frequency-locking entrainment is closely related to the phase conditions. For stochastic systems one has to use the notion of «effective synchronization» [24]. In the presence of Gaussian noise (or another random process with unlimited distribution function) the phase-locked state inevitably has to be broken at some moment. Thus, the system is supposed to be effectively synchronized if the phase locking is observed during a finite but long enough time (determined a priori). A measure of stochastic synchronization is the cross-diffusion coefficient $D_{\text{eff}}^j = 1/2 d/dt [\langle \phi_j^2(t) \rangle - \langle \phi_j(t) \rangle^2]$ [25]. This quantity describes the spreading in time of an initial distribution of the phase difference $\phi_j(t)$ * [26] between neighboring elements. In our study, the cross-diffusion coefficient attains a vanishing value within each cluster (Fig. 8, c) and assumes different nonzero values for inter-cluster units. This agrees with the stronger condition of phase synchronization which provides high degree of collective entrainment within clusters of

* We use the instantaneous phase introduced as $\Phi_j(t) = 2\pi(t - t_k)/(t_{k+1} + t_k) + 2\pi k$, where t_k is the time of the k th firing as defined by the threshold crossing of $x_j(t)$ at $x=1.0$.

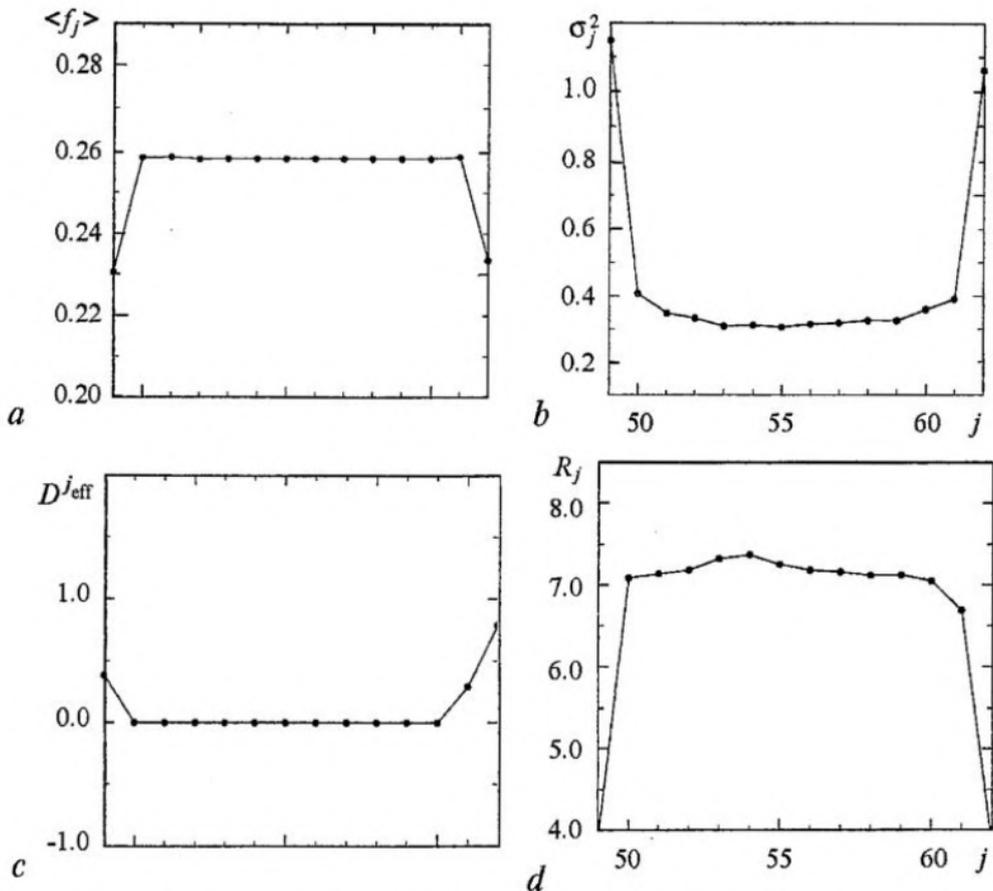


Fig. 8. Mean firing frequency $\langle f_j \rangle$ (a), deviation of pulse duration σ_j^2 (b), effective cross-diffusion coefficient D_{eff}^j (c) and noise-induced regularity R_j (d) within a single cluster. The widths of the coupling interval and noise intensity are fixed at 0.1 and 0.025, respectively

stochastic oscillators. Hence, the notion of effective synchronization can be generalized to the spatially extended group of elements. Similar effects have been observed for coupled Van der Pol oscillators with fluctuations [19]. What are the coherence properties of such frequency-locked clusters? It is clearly seen that the regularity exhibits a maximum value inside the synchronized state (Fig. 8, d), while the outer-cluster elements demonstrate a lower level of coherence. Comparative analyses of the regularity and pulse deviation functions allow us to assume that high coherence behavior within a cluster is related to synchronization phenomenon.

In general, the collective response of a cluster is characterized by two aspects. The first is a synchronization effect that leads to the frequency and phase entrainment. The second is the regularity of each functional unit due to coherence resonance effects. Remarkably, the regularity averaged over the spatial coordinate can be maximized within each cluster by tuning the noise (Fig. 9). At weak external noise, a cluster considered as a whole functional unit demonstrates weak coherence in spite of the fact that firings in the elements of the cluster tend to occur simultaneously. This is related to the relatively large fluctuations of the pulse duration of each composed elements. With increasing D , the coherence of the temporal and spatial structure of the firing process is enhanced and reaches a maximum. At large noise, the frequency and phase fluctuations grow rapidly and this leads to the destruction of the coherence properties for the composed units and, hence, of the spatial coherence structure. Because of the phenomenon of array-enhanced coherence resonance [23], the regularity of the whole cluster is much higher than that of the uncoupled elements (compare the curves 1, 2 and the dashed curve in Fig. 9).

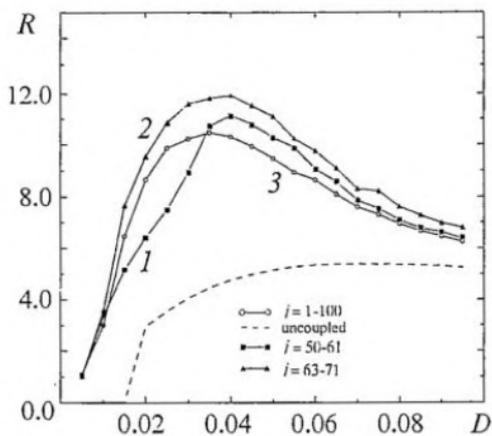


Fig. 9. Illustration of synchronization-enhanced coherence resonance for the system (1) demonstrating cluster structure for $\Delta=0.1$. The regularity averaged over spatial the coordinate R is plotted versus noise intensity for individual clusters (curve 1 and 2) and for the whole array with a cluster structure (curve 3). Dashed curve corresponds to the uncoupled array

Let us return to the full system. Now an array composed by excitable elements can be considered in macro level as a sequence of clusters whose size and structure is determined by a random distribution of firing properties and the degree of interaction. Fig. 10 illustrates the ordering effect caused by the stochastic synchronization and the resulting high coherence within each cluster at the optimal level of noise. The coherence of the net output is averaged over a set of clusters. Because of the frequency difference between clusters, the regularity of the array output is lower than the maximum value of each cluster (curve 3 in Fig.9).

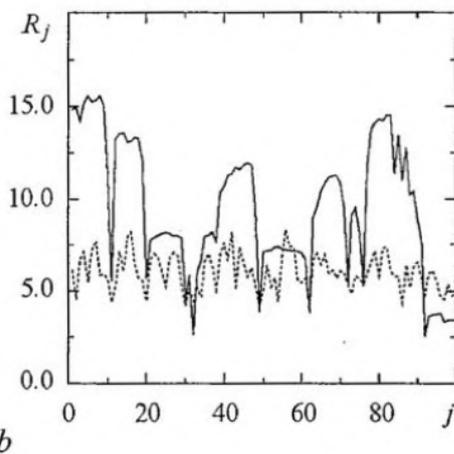
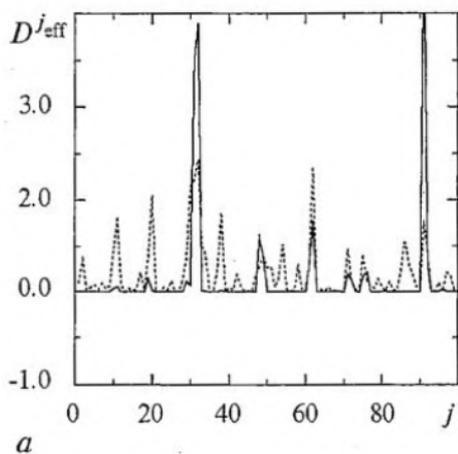


Fig. 10. Synchronous (a) and coherence (b) properties along the array with cluster structure for varying noise level. The width of the coupling interval is fixed at 0.1

5. Conclusions

Our investigations of the coherence properties in an ensemble of diffusively coupled excitable systems showed that self-organization can manifest itself in two ways:

(i) A one-dimensional lattice of excitable units with at least one inhomogeneous element (in our case, a unit with lower excitation threshold) demonstrates excitation waves. The degree of coherence of such a structure can be enhanced by tuning the noise intensity and/or the coupling strength;

(ii) A random distribution of the system parameters responsible for the excitatory properties and the strength of interaction leads to cluster formation defined as stochastic phase locking and as a mean frequency entrainment between a group of cells. Composed by a number of elements with different properties, each cluster can be considered as a «spatial» excitable unit exhibiting coherence resonance. Gain of regularity within each cluster is associated with the effect of stochastic synchronization.

We believe that these effects can be of importance for biological applications where the background noise may play a constructive role in ordering phenomena in a large networks of excitable elements through the synchronization mechanisms.

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ОБРАЗОВАНИЕ ИНДУЦИРОВАННЫХ ШУМОМ ПРОСТРАНСТВЕННЫХ СТРУКТУР В ВОЗБУДИМЫХ СРЕДАХ

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Исследуется образование когерентных структур в популяции возбудимых систем, находящихся под воздействием шума. Показано, что однородные одномерные решетки с хотя бы одним «вырожденным» элементом демонстрируют индуцированные шумом волны зажигания, степень упорядоченности которых имеет максимум при некоторой оптимальной интенсивности шума. При случайном разбросе параметров одномерного массива, ответственных за возбуждение и силу взаимодействия элементов, наблюдается эффект кластерной синхронизации индуцированных шумом колебаний.



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