

## Excitation of coherent oscillations in a noisy medium

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We numerically study the influence of neuronal threshold modulation on the properties of cortical traveling waves. For that reason we simplify a Wilson-Cowan-type integrodifferential equation model of propagating neocortical activity to a spatially discrete version. Further we introduce a noisy threshold. Depending on the noise level we find different states of the network activity, ranging from asynchronous oscillations, traveling waves, to synchronous oscillations. Finally, we induce the transition between these different states by an external modulation.

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### I. INTRODUCTION

A common feature of locally coupled excitable media are traveling waves; accordingly they are observed in physical [1], chemical [2], and biological [3–5] systems. There are several mathematical models describing experimental observed dependence of traveling waves on the system parameters [6–8], like the threshold. A recent work verified the theoretical prediction that modulation of neuronal threshold with electrical fields can increase, decrease, and even block traveling waves in cortical slices [3,4].

A biological example for the occurrence of traveling waves is the deep sleep of mammals [5]. During most of non-REM (NREM) sleep, almost all cortical neurons undergo a slow oscillation in the membrane potential, switching between a silent hyperpolarized state, and active depolarized state of high frequency firing [5,9]. This repetitive change between a depolarized active state and a hyperpolarized silent state occurs, due to the interplay of intrinsic ion currents, in neocortical neurons and network interactions [5,10]. Further cortical slow waves can be generated and sustained by the cortex alone [5,11]. This allows us to study the mechanisms generating cortical slow waves and their excitation in an isolated model for cortical activity. Although slow waves, a striking feature of mammalian NREM sleep, are well studied, only little is known about how they are generated in the cortical network and how to enhance them by external signals.

As cortical slow waves contribute to the long-term consolidation of new memories [9,12], an enhancement of slow wave sleep should help to increase consolidation of previously learned tasks. In a recent study it was shown that transcranial application of slowly oscillating potentials (0.75 Hz), during emerging slow wave sleep, enhances declarative memory performance [9]. Studying open-loop control of cortical slow waves by threshold modulation, might lead to more efficient control signals, and finally improve efficiency of transcranial electric stimulations in clinical applications.

The paper is organized as follows: As numerical simulations of neural systems require spatial discrete networks, we will simplify a Wilson-Cowan-type integrodifferential equation model of propagating neocortical activity, introduced by Pinto and Pinto-Ermentrout, to a spatially discrete model. In

a second step we verify by a numerical simulation, that our simplified model reproduces the threshold dependence of the wave propagation speed in the Pinto-Ermentrout model. Additionally, we introduce a noisy threshold and study the influence of noise on the coherence of a single element and the activity in a one-dimensional (1D) ring. Further, we study wave propagation and coherent oscillation on a two-dimensional (2D) network. Finally, we modulate the threshold periodically and show how to induce synchronous oscillations in the 2D network.

### II. TRAVELING WAVES IN A SPATIAL DISCRETE MODEL

Experimentally acquired electroencephalography (EEG) data of slow wave oscillations show only the average activity of populations of neurons and give no information about biophysical details such as the spike form or the kinetics of the intrinsic ion currents. Following Freeman [13] and Wilson and Cowan [14] we assume that the functional units of the single brain regions consist of populations of neurons and not of single neurons. The neurons in these populations possess a high connectivity and have a quite similar response to similar inputs. This redundancy allows one to study networks of neuron populations. Here the single variables do not describe membrane potentials of single neurons but rather the average activity of a population of neurons. A very important model of the averaged cortical activity was developed by Wilson and Cowan [14]. In a recent work by Pinto and Ermentrout [3] this model was modified to represent traveling pulse propagation in the disinhibited neocortex. The Pinto-Ermentrout model is given by

$$\begin{aligned} \dot{u}(x,t) + u(x,t) &= \int dx' w(x-x') \theta[u(x',t) - \vartheta] - v(x,t), \\ \dot{v}(x,t) &= \epsilon u(x,t), \end{aligned} \quad (1)$$

where  $w(x-x') = e^{-|x-x'|/2}$  and  $\theta$  is the Heaviside function. As all real neural networks consist of single elements, i.e., the neurons, a continuum model is only valid for very large neural populations. Therefore a natural way to describe the dynamics is a discretization of Eq. (1),

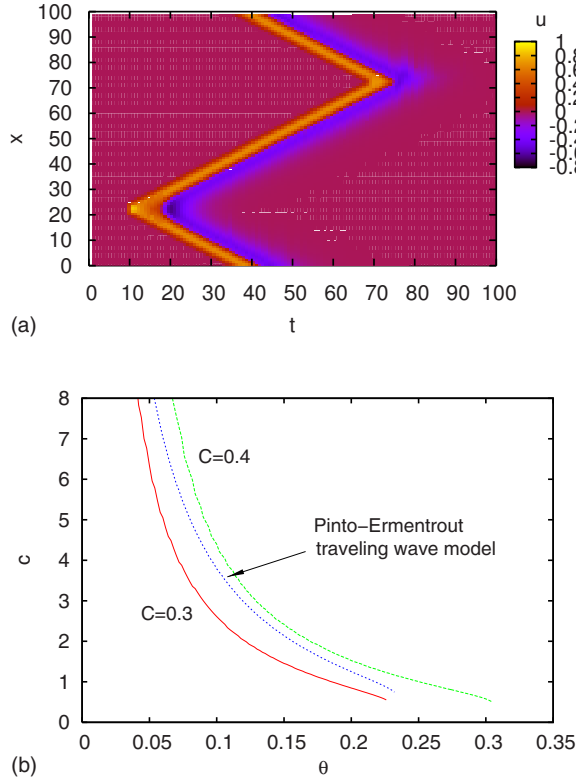


FIG. 1. (Color online) (a) Traveling wave in a 1D network with periodic boundaries. The wave propagates in both directions. Because of the periodic boundaries the wave fronts meet each other and eliminate themselves. (b) The threshold dependences of the velocity of wave propagation in a 1D network for the Pinto-Ermentrout model (blue/dotted) Eq. (1) for  $\epsilon=0.2$ , compared to the spatial discrete model, Eq. (2), with a nearest neighbor coupling, Eq. (3), for  $N=100$  elements with  $A=0.4$ ,  $\epsilon=0.2$ , and  $C=0.3$  (red/solid), respectively,  $C=0.4$  (green/dashed). The characteristic shape of  $c(\vartheta)$  stays qualitatively the same.

$$\begin{aligned} \dot{u}_i + u_i &= \sum_j W_{i,j} \theta [u_j - \vartheta] - v_i, \\ \dot{v}_i &= \epsilon u_i, \end{aligned} \quad (2)$$

where  $W_{i,j}$  is a normalized, towards periphery declining function. Now we go one step further and reduce the coupling function to a nearest neighbor coupling,

$$W_{i,j} := \begin{cases} A: & i=j \\ C: & |i-j|=1 \\ 0: & \text{else,} \end{cases} \quad (3)$$

where  $C$  represents the coupling strength. Figure 1 shows that our spatial discrete model qualitatively reproduces the dependence of the traveling wave's velocity of propagation  $c(\vartheta)$  on the threshold  $\vartheta$ .

### III. NOISY THRESHOLD

Each neuron is under the influence of multiple sources of noise, e.g., synaptic noise, channel noise, and Johnson noise

[15]. Mostly neuronal activity is described by stochastic differential equations with an internal noise in the form of a fluctuating input current. Here we will study the influence of a noisy threshold as done before in Refs. [16,17]. The threshold noise represents the probability that the population can fire even when the activity has not reached the threshold yet or stays quiescent even though the activity is above the threshold [18]. Contrary to what happens when the noise is added to the input current, fully white Gaussian noise cannot be applied. Moreover, the Gaussian distributed white noise term  $\xi_i(t)$  will be updated every  $\Delta t$  times, which leads to the random innovations  $D\xi_i(t_n)$ . Because of the discrete update the sequence  $\xi_i(t_n)$  is somehow colored [19]. But, for  $\Delta t = 0.1$ , which is two orders of magnitude lower than the time constant of our model, the coloring of the  $\xi_i(t_n)$  can be neglected. The threshold  $\vartheta$  then becomes  $\vartheta_0 + \xi_i(t_n)$ , where  $\xi_i(t_n)$  are the Gaussian white noise innovations with zero mean and intensity  $D$ .

#### A. Dependence of the collective behavior in a 1D network on the noise intensity

In order to measure the influence of noise on the collective dynamics of the network, we observe the dependence of the squared fluctuation  $\sigma^2$  of the mean field on the noise intensity  $D$ .

$$\sigma^2 := \langle (u(t) - \langle u(t) \rangle)^2 \rangle, \quad (4)$$

$$u(t) := \frac{1}{N} \sum_i u_i(t). \quad (5)$$

Figure 2 shows the squared fluctuation over  $D$  for different values of  $\vartheta$ . We see a pronounced maximum at  $D \approx \vartheta$ , indicating that the network shows coherent oscillations.

Considering a single element, we find that for small and for large noise the spikes appear irregular while the system oscillates coherently for moderate noise  $\vartheta \approx D$ . This effect was first described in [20] for a single excitable system and is called coherence resonance. We will discuss this interesting case for a single element later.

#### B. Dependence of the collective behavior of a 2D network on the noise

In [4] it was shown that applying electrical fields on a neural tissue, leads to effects which can be described by a threshold modulation. For that reason we study the dependence of the collective behavior in a two-dimensional network with periodic boundaries on the noise intensity  $D$  and the threshold  $\vartheta$ . We display the different states in a phase diagram as shown in Fig. 3. We find three different states which can be walked through by tuning either the noise intensity or the threshold of the single element. In the *traveling waves possible* state, an external induced traveling wave can propagate through the network. Up to a certain intensity the noise supports the traveling wave; that means the wave propagates even for large values of  $\vartheta$  (solid line in Fig. 3).

In the traveling waves state the noise occasionally excites a single element, which starts a traveling wave that can

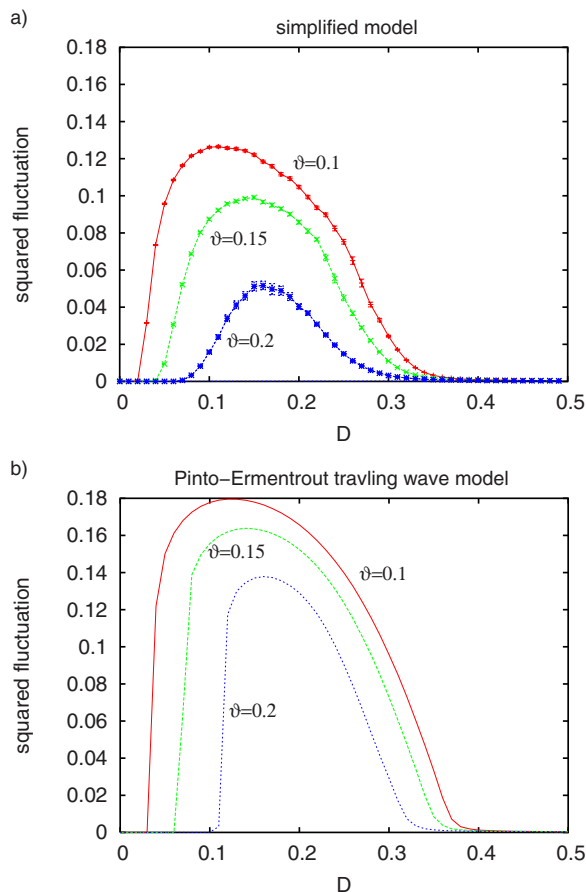


FIG. 2. (Color online) The squared fluctuations of the mean field of a 1D ring consisting of 100 units. (a) The simplified model with  $\epsilon=0.2$ ,  $A=0.4$ ,  $C=0.3$ . (b) The Pinto-Ermentrout traveling wave model with  $\epsilon=0.2$ . Both for  $\vartheta=0.1$  (red/solid),  $\vartheta=0.15$  (green/dashed), and  $\vartheta=0.2$  (blue/dotted). The mean-field fluctuations of both show a strong maximum at  $\vartheta \approx D$ , indicating a coherence resonance of the collective network dynamics.

propagate stably (dashed line in Fig. 3). In the *oscillatory* state the whole network oscillates synchronously. On the transition from the traveling waves state to the oscillatory state the frequency of the traveling wave occurrence rises until the traveling waves occur with resonance frequency where the whole network starts to oscillate synchronously.

### C. Influence of noise on the wave propagation

As seen in Fig. 3, with noise a wave can propagate even for values of the threshold where no traveling waves are observed in the deterministic case. A similar effect was observed experimentally in [21] in subexcitable chemical reactions. Here we are mainly interested if the influence of noise only increases the maximal threshold where waves can still propagate or if it also increases the wave propagation speed  $c(\vartheta)$ . At a first glance, this seems to be reasonable, as in our model the wave propagation speed  $c(\vartheta)$  depends sensitively on the threshold. The numerical simulation in Fig. 4 shows that the noise not only increases the maximal threshold where waves can still propagate, it also increases the wave

propagation speed. Physically the noise acts as a threshold reducer and as such enhances traveling waves.

### D. Noise-induced coherence

The phase diagram shows that coherent oscillations in the network can arise by tuning the noise intensity  $D$ . This behavior was studied in several works for global coupling [22,23]. Here we show numerically that it also occurs with local coupling. We advert that this order is achieved by increasing the intensity of the independent local noise and not by an external periodic forcing as in the case of stochastic resonance. Further, it does not depend on an additional constant drive or the oscillatory nature of the elements.

While the stochastically driven single elements of our network show coherence resonance, the deterministic system does not show self-sustained oscillations but noise of an optimal intensity generates a quasiregular signal. Such noise-driven excitable systems are often considered as coherence resonance oscillators [23]. To explain the influence of noise on the network we first study the influence of noise on the single element. For this purpose we use two different measures. As a measure for the temporal order in the single element we use the characteristic correlation time [20]

$$\tau_c := \int_0^T C^2(t) dt,$$

where  $C(t)$  is the normalized autocorrelation function. We integrate up to  $T=1000$  instead of  $T=\infty$  to prevent divergence in case of a periodic signal. A simple sine wave would have the correlation time  $\tau_c=500$ . As a measure for the spatial coherence in the network we use the squared fluctuation of the mean field. The simulation shows that the synchronization occurs at the same noise intensity as coherence resonance in the single element (Fig. 5). As in a previous work shown for Hodgkin-Huxley neurons, the coherence resonance (CR) is enhanced in two different ways depending on the coupling [24]. For weak coupling only the single element shows CR and no spatiotemporal order is observed. For strong enough coupling, as shown in Fig. 5, the maximum of the local and global coherence measure both jump to a maximum at almost the same noise intensity, indicating spatiotemporal coherence in the network. The reason for that observation is that by the coupling the noise-induced limit cycles stabilize and thus synchronize.

The application of homogenous noise on our network would lead to an identical behavior of all elements. Therefore a single uncoupled element (with an adjusted self-coupling) shows the same behavior as the mean field. As shown in Fig. 5(a), the correlation time of a single element is much less than the correlation time of a network with heterogeneous noise. The mutual stabilization of the noise-induced limit cycles cannot take place if all elements behave exactly the same. For that reason we expect a similar increase as the synchronization with rising noise heterogeneity as shown in [25]. This should also apply to the demonstrated increase of synchronization with rising parameter heterogeneity.

a)

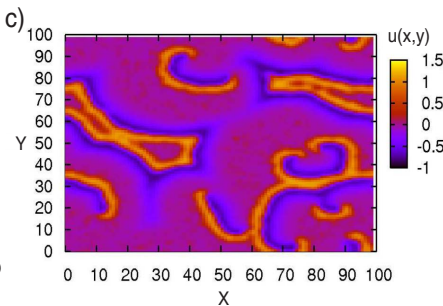
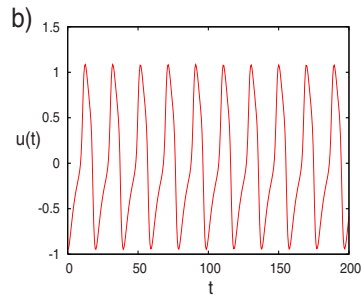
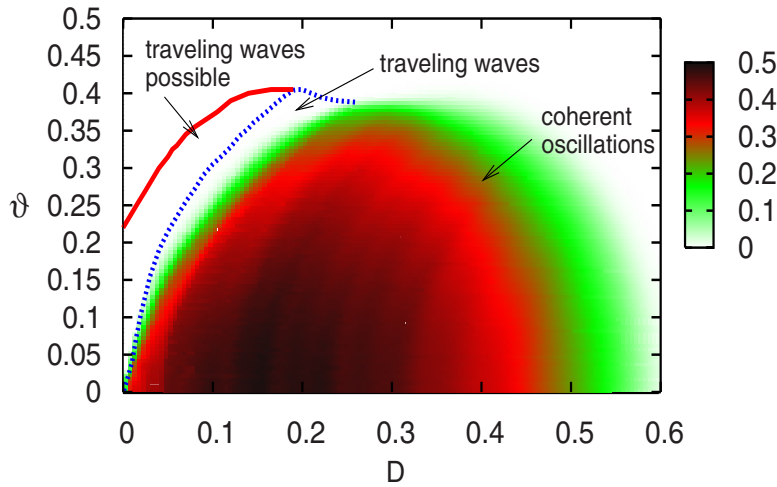


FIG. 3. (Color online) (a) The phase portrait for an 100\*100 network with  $\epsilon=0.2$ ,  $A=0.4$ ,  $C=0.3$ , and periodic boundary conditions. The color indicates the size of the squared fluctuation: below the red (solid) line traveling waves are possible (traveling waves possible state), and below the blue (dashed) line traveling waves are induced by noise automatically (traveling waves state). (b) The oscillation of the mean field for  $\vartheta=0.2$  and  $D=0.2$ . (c) Noise induces traveling waves for  $\vartheta=0.38$  and  $D=0.18$ .

IV. THRESHOLD MODULATION

We modulate the threshold with a square wave and observe the influence of the modulation  $\vartheta(t)$  for the different network states. With the modulation term the Heaviside function in Eq. (2) becomes

$$\theta[u_j(t) + \xi_i(t) + \vartheta(t) - \vartheta_0].$$

We find that the length of the positive and negative parts of the modulation are of minor importance while the resonance

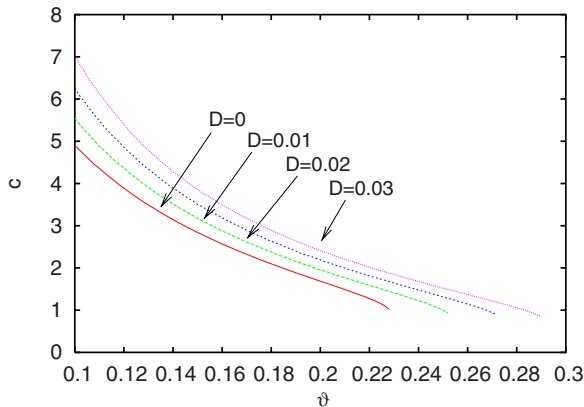


FIG. 4. (Color online)  $c(\vartheta)$  for a 50\*50 network with  $A=0.4$ ,  $C=0.3$ ,  $\epsilon=0.2$ , and periodic boundary conditions. The wave propagation speed and the maximal threshold where wave propagation is possible increase with the noise intensity  $D$ .

frequency always shows the most effect. Besides the square wave modulation we modulate with only the positive part—and only the negative part of the square wave (Fig. 6).

For small  $D$  (traveling wave and traveling wave possible state) the modulation barely increases the squared fluctuation more than a simple constant threshold modulation. Also the negative modulation has no influence on the oscillation; the positive and the symmetrical modulation show nearly the same effect.

For large noise, however, the squared fluctuation can be increased strongly by square wave modulation, while simple constant modulation has nearly no effect. The negative modulation is less important than the positive modulation, while the square wave has the largest effect.

V. CONCLUSION AND OUTLOOK

We showed that the Pinto-Ermentrout traveling wave model can be simplified to a spatially discrete network with nearest neighbor coupling, without losing the main feature—the characteristic shape of  $c(\vartheta)$ . Introducing a noisy threshold we found that the network shows pronounced coherence resonance. Extending the model to a two-dimensional network we showed in a phase diagram the dependence of different network states on the noise intensity and the threshold height. The transition from silent network to self-induced traveling wave to coherent oscillation state can be achieved by either tuning the threshold or the noise intensity. Further-

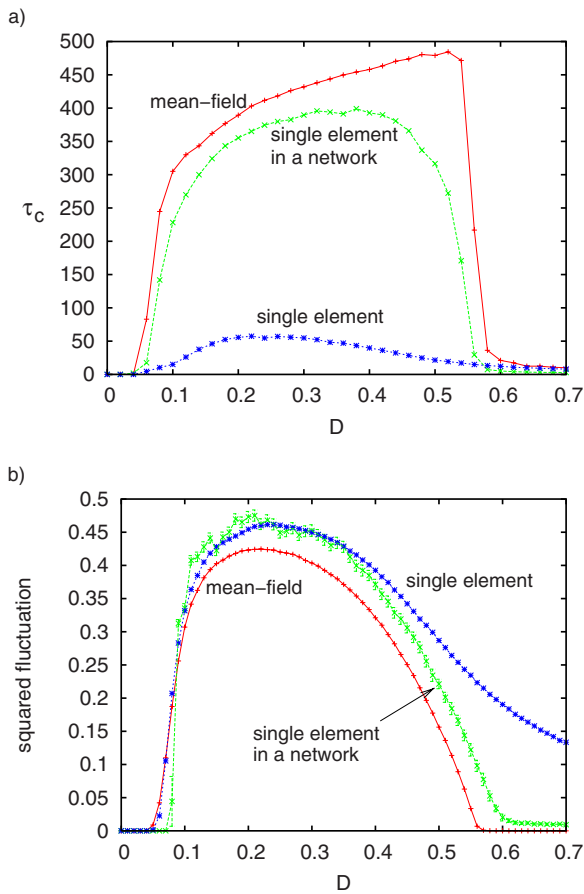


FIG. 5. (Color online) (a) The correlation time  $\tau_c$  for the mean field (red/solid), a single element (green/dashed) in the  $50 \times 50$  network  $A=0.4$ ,  $C=0.3$ , and for a single element (blue/dotted)  $A=1.6$ ,  $C=0$  with  $\vartheta=0.2$  and  $\epsilon=0.2$ . Note that  $\tau_c$  is only a measure for temporal coherence, not for the amplitude of the mean-field oscillations. (b) The associated squared fluctuation as a measure for spatial coherence in the network and a measure of activity for a single element.

more, the wave propagation speed and the maximal threshold where wave propagation is possible increase with the noise intensity. For small noise intensities a threshold modulation with a periodic signal has nearly the same effect as threshold modulation with a constant signal. For larger noise intensities, however, a constant threshold modulation has no effect, while symmetric, positive, and negative modulation increase the oscillation of the network.

In future we will investigate the influence of the coupling range, asymmetric coupling, and network architecture on the different network states. In future works the noise-induced phase transition—shown in our model—will be investigated in chemical and biological systems.

For instance, the threshold and noise level dependence of the network states and the wave propagation speed can be

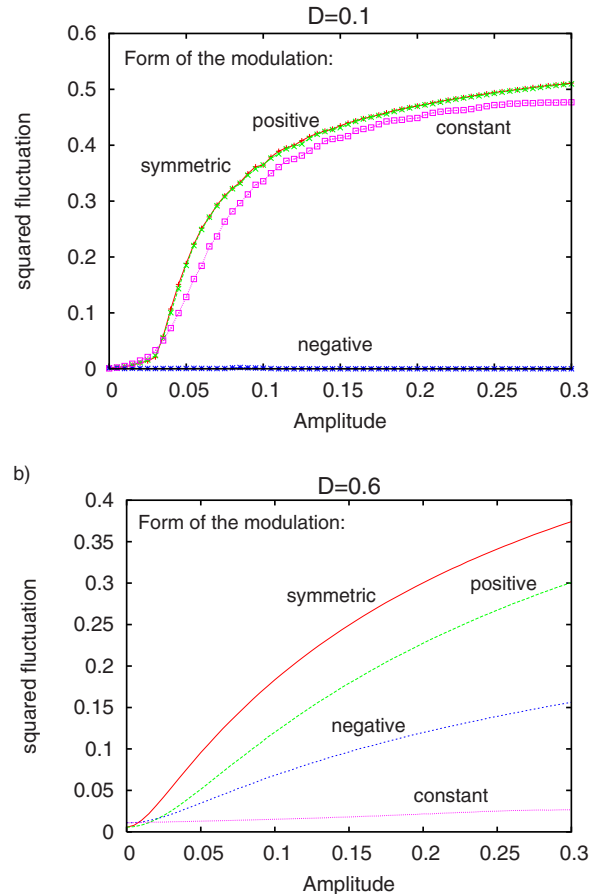


FIG. 6. (Color online) The squared fluctuation over the amplitude of the modulation for a  $50 \times 50$  network with  $\vartheta=0.3$ ,  $\epsilon=0.2$ ,  $A=0.4$ ,  $C=0.3$  and periodic boundary conditions for (a)  $D=0.1$  and (b)  $D=0.6$ . Both compare modulation with a square wave (red/solid), modulation with only the positive part of the square wave (green/dashed), modulation with only the negative part of the square wave (blue/dotted), and constant threshold modulation (purple).

examined with an experimental setup similar to that in [4]. With a high density electrode array [26], threshold height and noise intensity can be tuned individually. Another method to tune the noise intensity is to vary the temperature of the tissue [15,27], however, this is only possible in a certain range as the tissue will be damaged otherwise.

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