

Effects of time delay and random rewiring on the stochastic resonance in excitable small-world neuronal networks

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The effects of time delay and rewiring probability on stochastic resonance and spatiotemporal order in small-world neuronal networks are studied in this paper. Numerical results show that, irrespective of the pacemaker introduced to one single neuron or all neurons of the network, the phenomenon of stochastic resonance occurs. The time delay in the coupling process can either enhance or destroy stochastic resonance on small-world neuronal networks. In particular, appropriately tuned delays can induce multiple stochastic resonances, which appear intermittently at integer multiples of the oscillation period of the pacemaker. More importantly, it is found that the small-world topology can significantly affect the stochastic resonance on excitable neuronal networks. For small time delays, increasing the rewiring probability can largely enhance the efficiency of pacemaker-driven stochastic resonance. We argue that the time delay and the rewiring probability both play a key role in determining the ability of the small-world neuronal network to improve the noise-induced outreach of the localized subthreshold pacemaker.

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I. INTRODUCTION

Noise can play a surprisingly constructive role in nonlinear dynamical systems [1]. The most relevant example of this fact is stochastic resonance (SR), where the response of a nonlinear system to a weak deterministic signal can be largely enhanced by a moderate intensity of additive noise [2]. Due to its potential applications in many different fields, the phenomenon of stochastic resonance has been extensively investigated in past decades [3]. For a neural system, due to its intrinsic excitability, random perturbations acting on an excitable steady state can typically evoke spiking responses [4]. Noise-induced stochastic resonance in spatially extended neuronal systems has been widely observed in many biological experiments and numerical simulations [5]. It has been shown both experimentally and theoretically that the ability of sensory neurons to process weak input signals can be significantly enhanced by adding noise to the system [6]. Furthermore, as an extension of SR, noise-induced signal propagation in coupled neuron systems has been thoroughly studied, and it is found that, with the aid of noise, the signal can be effectively transmitted between neurons [7]. It is therefore suggested that stochastic resonance is of great importance for understanding the weak signal detection and information propagation in neural networks.

SR in complex neuronal networks has attracted much attention in recent years [8]. Thereby, small-world network has been widely used due to its potential in capturing the characteristics of many real-world complex networks [9]. Indeed, small-world architectures have been found in several empirical studies of structural and functional brain networks in humans and other animals [10]. It is shown that, due to supporting both local and distributed information processing, models of neural systems with small-world topology display enhanced signal-propagation speed, computational

power, and synchronizability [11]. In particular, the effect of stochastic resonance in small-world networks depends largely on the fraction of rewired (random) links. Cao *et al.* numerically studied stochastic resonance in a coupled array of bistable oscillators with small-world connectivity, and found that both temporal SR and spatial synchronization of the oscillators can be considerably improved by increasing the order of randomness of the network due to long-range couplings [12].

While in the past the majority of scientific research dealing with the stochastic resonance on complex neuronal networks was devoted to the case that all constitutive neurons are subjected to the weak external signal, recently the focus has been shifting towards where only one neuron within the network is exposed to the periodic forcing, i.e., pacemaker-driven stochastic resonance [13]. Indeed, pacemaker plays an important role in real-life systems and is vital for many biological systems [14]. Perc first studies the stochastic resonance on excitable small-world neuronal networks via a pacemaker, and finds that only for intermediate coupling strengths is the small-world topology able to enhance the stochastic resonance [15]. Moreover, the effect of stochastic resonance on Newman-Watts networks of Hodgkin-Huxley neurons can be amplified via fine-tuning of the small-world network structure, and also depends significantly on the coupling strength among neurons and the driving frequency of the pacemaker [16].

In biological neural systems, information transmission delays are inevitable in intra- and interneuronal communications, mainly because of the finite speed of action potential propagating across neuron axons, and also due to time lapses occurring by both dendritic and synaptic processes. Delays arising from the propagation of action potential in neuronal systems can amount to several tens of milliseconds [17]. Thus it is important to understand how such temporal delays affect collective dynamics of coupled neuronal ensembles. Recently, specific effects of time delay on qualitative and quantitative

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properties of neuronal dynamics have been reported, such as introducing or destroying stable oscillations [18], enhancing or suppressing synchronization between neurons [19], generating spatiotemporal patterns [20], as well as inducing multiple stochastic resonances [21]. Notably, it has been shown that appropriately tuned delays can induce multiple stochastic resonances in scale-free neuronal networks independently of the placing of the subthreshold periodic pacemaker [21]. Most recently, Gan *et al.* investigated the stochastic resonance in paced time-delayed scale-free FitzHugh-Nagumo (FHN) neuronal networks, and found that delay-induced stochastic multiresonances appear at every integer multiple of the pacemaker's oscillation period [22]. However, the effect of information transmission delay on the stochastic resonance in small-world neuronal networks has never been investigated so far.

In this paper, we extend the subject by studying delay-induced multiple stochastic resonances on excitable small-world neuronal networks. The studied network is locally modeled by Rulkov map-based neurons, and the topological structure exhibits the small-world property. A subthreshold periodic signal is introduced to one single neuron of the network, thus acting as a pacemaker trying to impose its rhythm on the whole ensemble. Moreover, the information transmission delay is introduced into the coupling process. We aim to investigate the dependence of stochastic resonance and spatiotemporal order in small-world neuronal networks on the synaptic time delay and the rewiring probability. Accordingly, the remainder of this paper is organized as follows. In Sec. II, we introduce the mathematical model

of the time-delayed small-world neuronal network. Main results are presented in Sec. III, where the effects of time delay and rewiring probability on the stochastic resonance in small-world neuronal networks are systematically investigated. Finally, a brief conclusion of this paper is given in Sec. IV.

II. MATHEMATICAL MODEL

The map-based neuron model proposed by Rulkov *et al.* [23], despite its intrinsic simplicity and low dimensionality, can capture the main dynamical features of more complex time-continuous neuronal models, but at essentially lower computational costs, thus allowing detailed analysis of the dynamics of large ensembles [24]. In the present study, we use the two-dimensional map to simulate the dynamics of individual neuron in the small-world network. Then, the temporal evolution of each unit can be described by the following set of discrete equations:

$$x_i(n+1) = \frac{\alpha}{1+x_i^2(n)} + y_i(n) + \sigma \xi_i(n) + D \sum_{j=1}^N \varepsilon_{i,j} [x_j(n-\tau) - x_i(n)], \quad (1)$$

$$y_i(n+1) = y_i(n) - \beta x_i(n) - \gamma, \quad (2)$$

where $x_i(n)$ is the fast dynamical variable of the map, representing the membrane potential of the i th neuron, and $y_i(n)$ is the slow dynamical variable of the map, denoting the slow gating process. n is the discrete time index. The

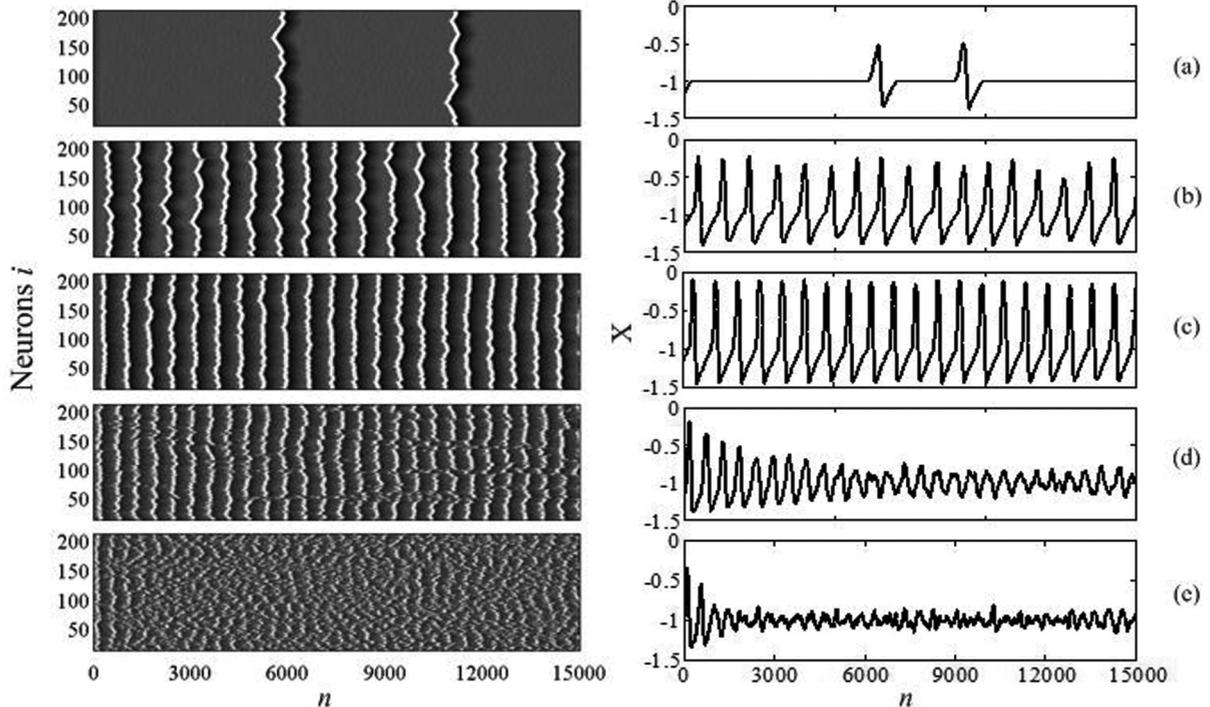


FIG. 1. Spatiotemporal patterns (left panel) and mean-field activity (right panel) of the small-world neuronal network obtained for different noise intensity σ . (a) $\sigma = 0.006$, (b) $\sigma = 0.01$, (c) $\sigma = 0.025$, (d) $\sigma = 0.06$, and (e) $\sigma = 0.085$. The color coding is linear, white depicting 0.1 and black depicting -1.7 values of $x_i(n)$.

slow temporal evolution of $y_i(n)$ is due to the small values of parameters $\beta = \gamma = 0.001$, while α is the main parameter determining the dynamics of individual neurons. For $\alpha > 2$, the fast variable $x_i(n)$ can exhibit spiking-bursting activity, whereas if $\alpha < 2$, each unit is governed by a single excitable steady state ($x^* = -1, y^* = -1 - \alpha/2$) that can be derived analytically by setting $x(n) = x(n+1)$ and $y(n) = y(n+1)$ in an individual map. Here, we set $\alpha = 1.95$; each neuron thus occupies the excitable steady state ($x^*, y^*) = (-1, -1.995)$, which are also the initial conditions we will use in all subsequent calculations. σ^2 is the variance of Gaussian noise satisfying $\langle \xi_i(n) \rangle = 0$ and $\langle \xi_i(n) \xi_j(m) \rangle = \delta_{ij} \delta_{nm}$. Hence the parameter σ determines the noise intensity. D is the coupling strength between coupled neurons. The matrix $\varepsilon = (\varepsilon_{i,j})$ is a connectivity matrix for the small-world network: $\varepsilon_{i,j} = 1$ if neuron i is connected to neuron j , $\varepsilon_{i,j} = 0$ otherwise, and $\varepsilon_{i,i} = 0$. τ is the time delay among neurons, which is one of the main parameters to be varied below.

As mentioned in the Introduction, we will study delay-induced multiple stochastic resonances in small-world neuronal networks. To obtain a small-world network, we follow the random rewiring procedure proposed by Watts and Strogatz [9]. Starting from a ringlike network with regular connectivity comprising $N = 200$ neurons, where each unit is connected to its $k = 6$ nearest neighbors, we rewire each edge at random with probability p . By increasing the probability p , the architecture of the network is tuned between two extremes: regular ($p = 0$) and random ($p = 1$) networks. For $0 < p < 1$, the resulting networks show small-world property. The small-world network has a small value of characteristic path length L , comparable with that of a random network, while gets a large value of clustering coefficient C , comparable with that of a regular network. According to [9], the characteristic path length is defined as the average number of edges in the shortest path between any two nodes, while the clustering coefficient is the average fraction of all $k_i(k_i - 1)/2$ allowable edges that actually exist among node i and all its k_i neighbors. The rewiring probability p is another main parameter to be investigated in this paper.

Finally, we introduce the subthreshold periodic driving $I^{\text{ext}}(n)$, which takes the form of a pulse train defined as

$$I^{\text{ext}}(n) = \begin{cases} h & \text{if } (n \bmod t) \geq (t - w), \\ 0 & \text{otherwise,} \end{cases} \quad (3)$$

where the parameter t is the oscillation period of the pulse train, w is the width of each pulse, and h is the amplitude of the pulses. Here, $I^{\text{ext}}(n)$ acts as a pacemaker, which is added additively to the fast variable of a single neuron within the small-world network. In fact, this kind of driving signal has been widely used to study pacemaker-driven stochastic resonance in scale-free and small-world neuronal networks [15,21]. In our numerical simulations we choose the parameter values to be $h = 0.0015$, $w = 50$, and $t = 700$, which guarantee that without the introduction of noise ($\sigma = 0$) the pacemaker $I^{\text{ext}}(n)$ is subthreshold, meaning that it cannot by itself induce large-amplitude spikes from any of the excitable neurons. It's worth noting that the frequency of the subthreshold periodic signal used here is identical to the global-resonance frequency [25]

of individual map-based neurons constituting the small-world network.

In order to quantitatively characterize the correlation of temporal output of the small-world neuronal network with the driving frequency of the pacemaker ω , we calculate the Fourier coefficient Q , which is defined as

$$Q_{\sin} = \frac{1}{Tt} \sum_{n=1}^{Tt} 2X(n) \sin(\omega n), \quad (4)$$

$$Q_{\cos} = \frac{1}{Tt} \sum_{n=1}^{Tt} 2X(n) \cos(\omega n), \quad (5)$$

$$Q = \sqrt{Q_{\sin}^2 + Q_{\cos}^2}, \quad (6)$$

where Tt is the operation period of the pacemaker, $\omega = 2\pi/t$ is the frequency of the pulse train, and $X(n) = (1/N) \sum_{i=1}^N x_i(n)$ is mean-field activity of the network. In the following, for each set of parameter values, the variable $x_i(n)$ is recorded for $T = 300$ periods of the pacemaker, and the final results are obtained by averaging over 20 independent runs to warrant appropriate statistical accuracy with

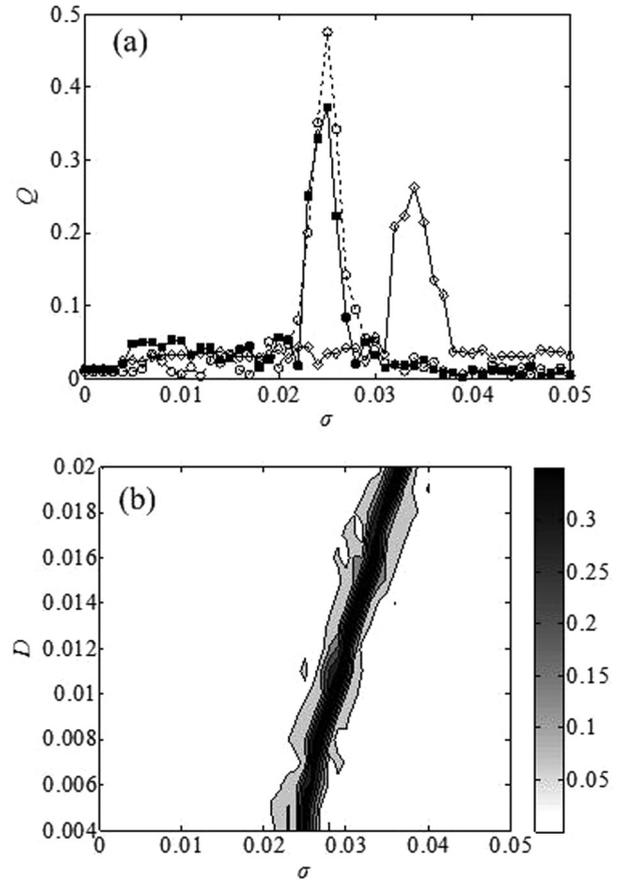


FIG. 2. (a) Dependence of Q on the noisy intensity σ for different placing of the pacemaker, which is respectively introduced to one randomly selected neuron within the network (circles), all neurons of the network (squares), and an individual neuron (diamonds), $\tau = 0$, and $D = 0.005$. (b) Dependence of Q on the noise intensity σ and the coupling strength D when the pacemaker is introduced to one single neuron within the small-world network, $\tau = 0$.

respect to the small-world network generation and numerical stimulation.

III. RESULTS

To investigate the effect of synaptic time delay on the stochastic resonance in small-world neuronal networks, we first set the rewiring probability $p = 0.1$. In this case, the clustering coefficient of the network is $C = 0.48$ and the characteristic path length is $L = 4.17$. For $p = 1$, they would take on the values $C = 0.022$ and $L = 3.75$, while for $p = 0$, they would be $C = 0.6$ and $L = 17.08$. Hence we get a small-world network with $p = 0.1$.

First, we set $\tau = 0$, i.e., there is no time delay between neurons, and introduce the pacemaker to one randomly selected neuron within the small-world network. Figure 1 shows the spatiotemporal patterns observed on the network for different values of noise intensity σ . It can be seen that the temporal dynamics of each excitable neuron follows the rhythm of the subthreshold pacemaker optimally only by an intermediate noise intensity $\sigma = 0.025$ [Fig. 1(c)]. The dependence of Q on the input noise intensity σ is shown in Fig. 2(a). It can be observed that the value of Q exhibits a bell-shaped dependence on σ , indicating that there exists an optimal noise intensity by which Q is maximal, i.e., the temporal coherence between

the temporal output series of each excitable neurons and the driving frequency of the pacemaker ω achieves an optimum. Thus it confirms the existence of stochastic resonance in the studied small-world neuronal network without delay, whereby the pacemaker can successfully impose its rhythm on the whole ensemble, as demonstrated in Ref. [15].

However, when the pacemaker is imposed on all neurons of the small-world network, the maximal Q value decreases [Fig. 2(a)], implying that the phenomenon of stochastic resonance become less efficient, just like in scale-free neuronal networks [21]. This mainly results from the competition between excitations from external forcing and synaptic inputs between coupled neurons. Moreover, SR can also occur in an individual neuron with the same external excitation, but for higher noise level compared with the same neuron coupled to the network, because of the lack of excitatory synaptic currents from other neurons.

Figure 2(b) plots the dependence of Q on the noise intensity σ and the coupling strength D between neurons. It can be seen that the stochastic resonance phenomenon arises irrespective of the value of D , but the optimal value of σ shifts towards higher values with the increase of coupling strength. Similar results are also obtained when other individual neuron or all neurons are subject to the weak periodic forcing. Thus we can conclude that pacemaker-driven stochastic resonance on the small-world neuronal network occurs independently of the placing of the pacemaker. Moreover, one single paced neuron

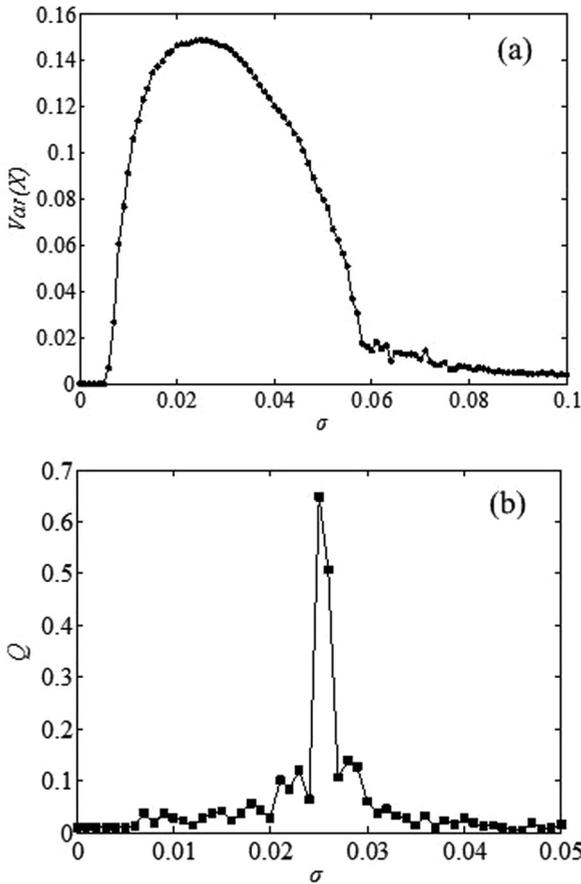


FIG. 3. (a) Dependence of $Var(X)$ on the noisy intensity σ , $X(n) = (1/N) \sum_{i=1}^N x_i(n)$. (b) Dependence of Q on the noisy intensity σ , $X(n) = (1/N) \sum_{i=1}^N x_i^2(n)$.

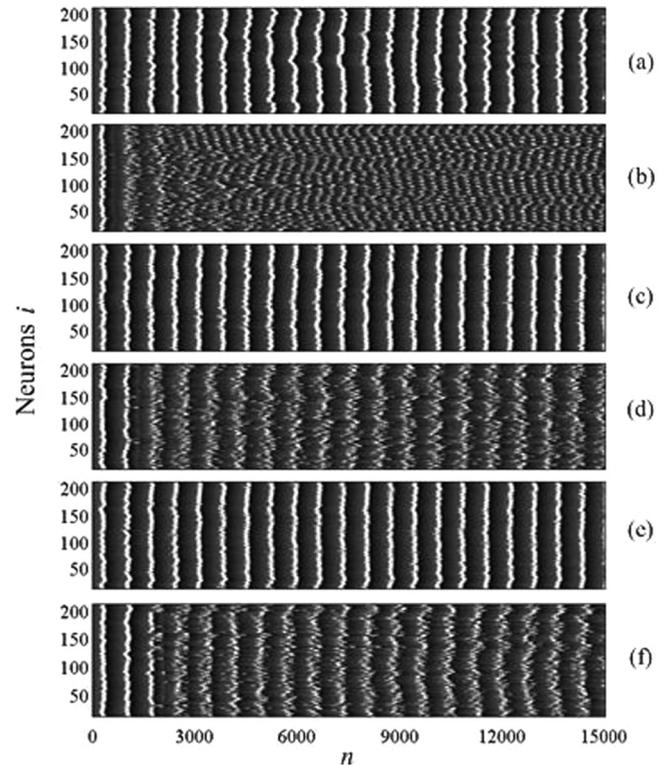


FIG. 4. Spatiotemporal patterns of the small-world neuronal network obtained for different time delay τ . From top to bottom, τ is equal to (a) 0, (b) 300, (c) 700, (d) 1000, (e) 1400, and (f) 1800. The noise intensity is $\sigma = 0.025$. The color profile in each plot is the same as in Fig. 2.

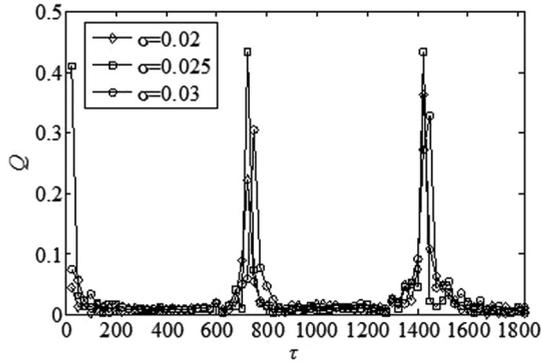


FIG. 5. Dependence of Q on the delay τ for different noise intensity σ , $D = 0.005$.

is actually more effective in generating ordered excitatory fronts in accordance with the weakly imposed rhythm than the global forcing of the whole network. Indeed, global input is not common in real neuronal systems, and local input is far more likely. In particular, for neural systems with a large amount of neurons, it is unnecessary and impossible to add external signals to all the involved individuals. Only weak and local input is reasonable, guaranteeing low energy consumption and efficiency in large neuronal networks [21]. Hence, in what follows, we focus on the case of only one single neuron within the small-world network chosen as the input for the weak periodic forcing.

In this paper, the mean field of the network is used to describe the average activity of all neurons. From Fig. 1, we can see that the synchronous and regular state of neural networks is characterized by large-amplitude periodic oscillations of the mean field, whereas small-amplitude irregular fluctuations mark the absence of spatiotemporal order of neuronal activity. So the variance of mean-field oscillations $Var(X)$ is a quantitative measure of collective temporal coherence of the system. Figure 3(a) shows the dependence of $Var(X)$ on the noise intensity σ . It can be observed that the largest value of $Var(X)$, characterizing the most regular and synchronous activity of the network, is obtained by $\sigma = 0.025$, which is equal to the resonance noise intensity. Moreover, we can also define the network response as $X(n) = (1/N) \sum_{i=1}^N x_i^2(n)$. It

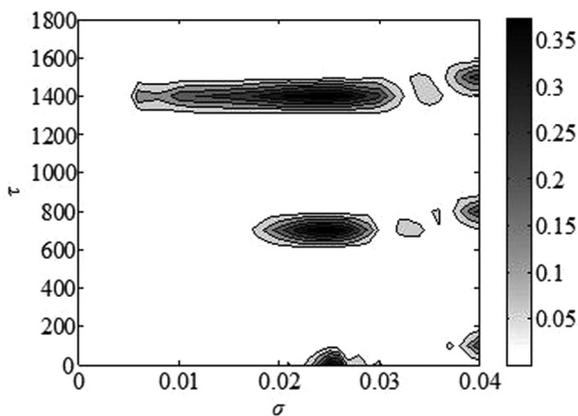


FIG. 6. Contour plot of Q in dependence on the time delay τ and the noise intensity σ .

does not change the behavior of the neural system, except the resonance peak values [Fig. 3(b)]. Besides, the signal-to-noise ratio is also frequently used as a measure for stochastic resonance. According to [26], the Fourier coefficients are exactly proportional to the square of the spectral power amplification; then the signal-to-noise ratio S can exhibit the same resonant behavior as Q .

In the following, we examine the effect of time delay on the stochastic resonance in the small-world neuronal network. Figure 4 shows the space-time plots of the network obtained for different values of τ . Here, we fix the coupling strength as $D = 0.005$ and the noise intensity $\sigma = 0.025$. Clearly, the information transmission delay can drastically influence the system's behavior, and spatiotemporal patterns

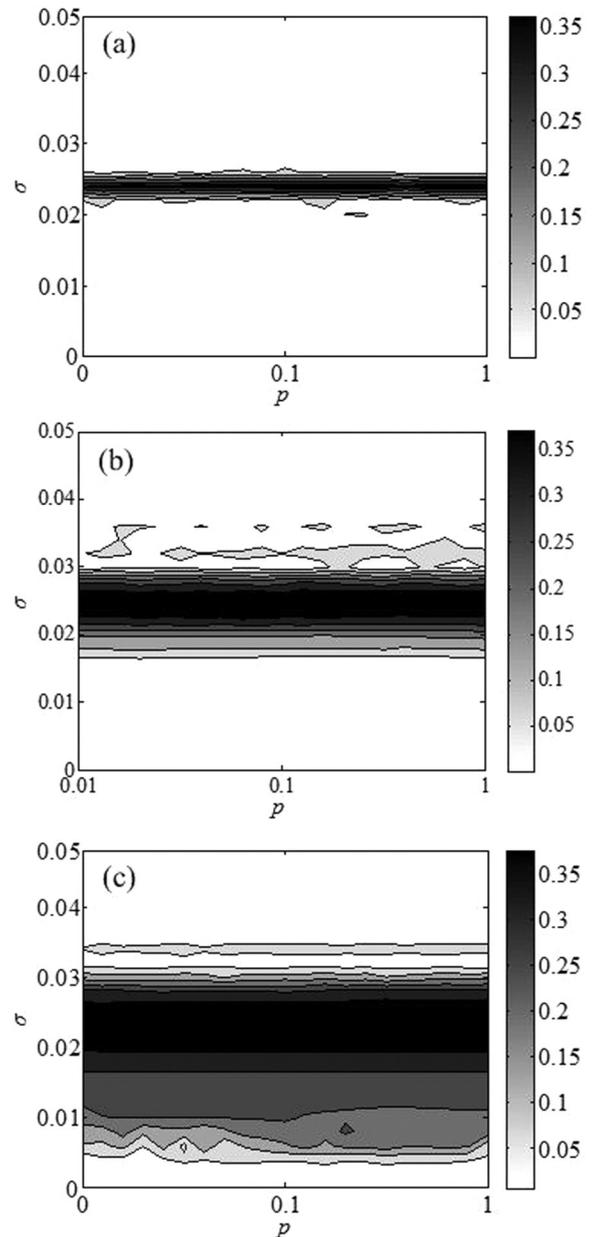


FIG. 7. Contour plots of Q in dependence on the noise intensity σ and the rewiring probability p for different time delay τ , $D = 0.005$. (a) $\tau = 0$, (b) $\tau = 700$, and (c) $\tau = 1400$.

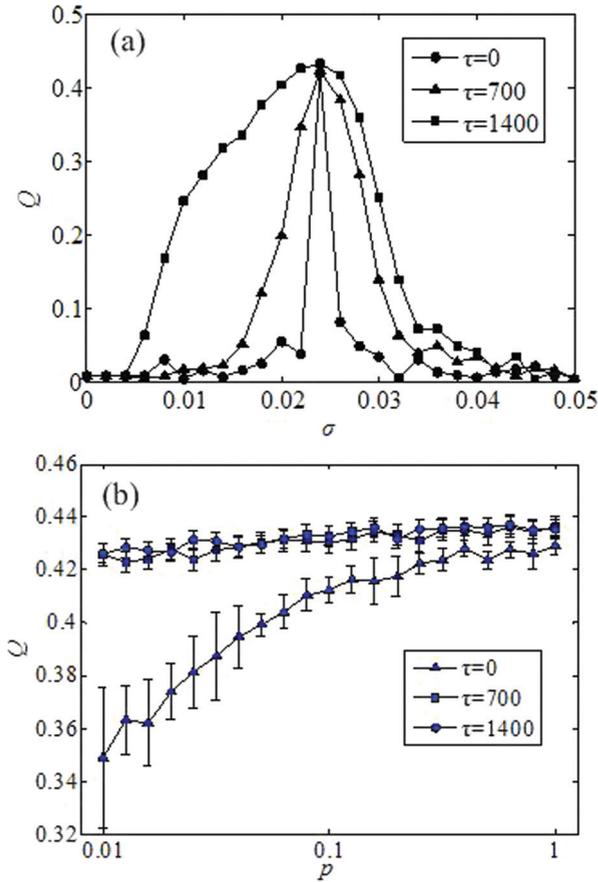


FIG. 8. (Color online) (a) Dependence of Q on the noise intensity σ for different time delay τ . (b) Dependence of Q on the rewiring probability p for different time delay τ .

of regularity and disorder appear intermittently as the delay τ increases. In particular, for $\tau = 0$, $\tau = 700$, and $\tau = 1400$ the excitatory fronts of neuronal dynamics are periodically ordered and follow the rhythm of the pacemaker, while for $\tau = 300$, $\tau = 1000$, and $\tau = 1800$, the regularity of excitatory fronts is completely collapsed, and neuronal firings lose consistency with the forcing frequency ω . These observations

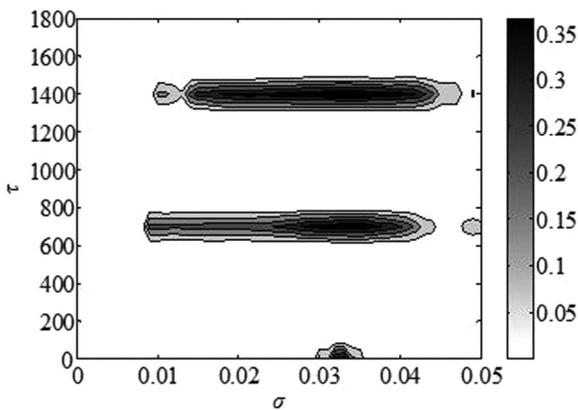


FIG. 9. Contour plot of Q in dependence on the time delay τ and the noise intensity σ .

demonstrate that the time delay can either enhance or destroy the ordered periodic fronts of neuronal excitations on small-world networks. In particular, the delay-induced transitions to stochastic resonance of neuronal activity appear intermittently as the delay time increases.

Figure 5 plots the dependence of Q on τ for different noise intensity σ . It can be seen that, as the delay increases, three maxima of Q appear at $\tau = 0$, $\tau = 700$, and $\tau = 1400$ for $\sigma = 0.025$, corresponding to the spatiotemporally ordered patterns shown by Figs. 4(a), 4(c), and 4(e), respectively. For other σ , we can also observe several maxima of Q within the considered range of time delay, but with small amplitudes. The dependence of Q on the time delay τ and the noise intensity σ is shown in Fig. 6. Evidently, there exists some narrow-banded regions with high values of Q , indicating multiple stochastic resonances occurring in the time-delayed

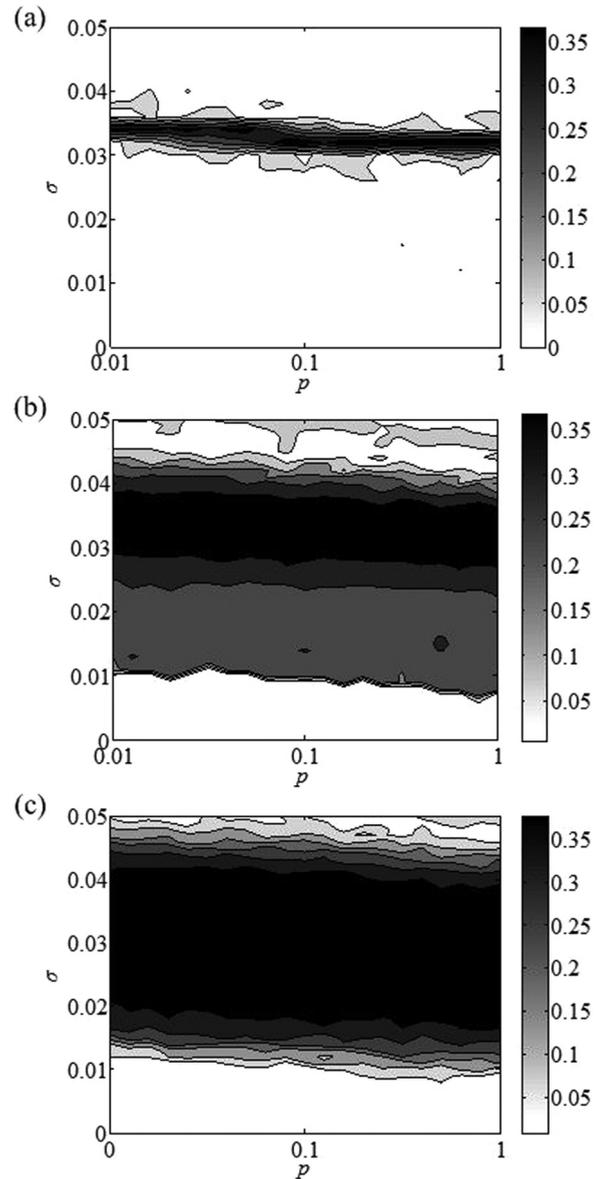


FIG. 10. Contour plots of Q in dependence on the noise intensity σ and the rewiring probability p for different time delay τ , $D = 0.015$. (a) $\tau = 0$, (b) $\tau = 700$, and (c) $\tau = 1400$.

small-world neuronal network. Moreover, all these resonance regions are roughly located at the integer multiples of the forcing period of the pacemaker. Indeed, the delay-induced multiple stochastic resonances of neuronal activity are due to the locking between the delay time and the global-resonant oscillation period of individual neurons if the latter is close to the oscillation period of the pacemaker [21].

To gain more insight into the dependence of delay-induced stochastic resonance in small-world neuronal networks on the rewiring probability, we plot the dependence of Q on both σ and p for different values of τ . Results presented in Fig. 7 show several interesting features. First, it is evident that stochastic resonance occurs for each particular value of p when the time delay is identical to integer multiples of the oscillation period of the pacemaker. Moreover, the spans of noise intensities that warrant relatively high values of Q largely extend as τ increases [Fig. 8(a)], but change little with the increase of the rewiring probability p . Finally, the small-world topology has a significant effect on the stochastic resonance in small-world neuronal networks. In Fig. 8(b), we plot the variation of Q with respect to p for different values of τ while keeping the noise intensity $\sigma = 0.025$. Evidently, when $\tau = 0$ the value of Q increases rapidly with p . It is thus indicated that, for small time delays, increasing the rewiring probability can largely enhance the efficiency of the pacemaker-driven stochastic resonance in small-world neuronal networks. While, for larger time delays, such as $\tau = 700$ and 1400 , Q retains large values, which change much less profoundly as p is varied, implying no clear effect of small-world topology on the stochastic resonance in neuronal networks.

At last, we explore the influence of coupling strength between neurons on the delay-induced stochastic resonance transitions in small-world neuronal networks. For $D = 0.015$, we conduct the same investigation and find that delay-induced multiple stochastic resonances are clearly observed at the integer multiples of the forcing period, as shown in Fig. 9. The dependence of Q on both σ and p for different values of τ is presented in Fig. 10. Similarly, the spans of optimal noise intensities σ largely extend as τ turns larger, and the value of Q increases with the rewiring probability p more rapidly when

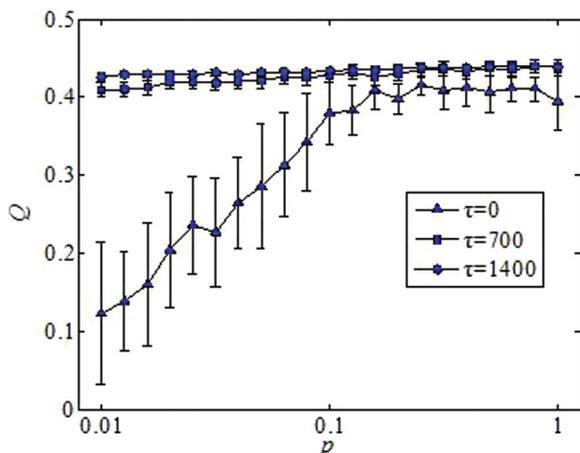


FIG. 11. (Color online) Dependence of Q on the rewiring probability p for different time delay τ , $\sigma = 0.03$.

$\tau = 0$; see Fig. 11. More interestingly, for $D = 0.015$, larger σ is required for the maximal Q as p tends to 1 (Fig. 10). Similar results are also obtained by studying the pacemaker-driven stochastic resonance in small-world neuronal networks without time delay [15]. We can thus conclude that both p and τ have a nontrivial impact on the stochastic resonance in small-world neuronal networks.

IV. CONCLUSIONS

In this paper, we investigate stochastic resonance in small-world neuronal networks in dependence on the noise intensity, the time delay, and the rewiring probability. The obtained numerical results show that the phenomenon of stochastic resonance can occur irrespective of the pacemaker introduced to one single neuron or all neurons of the network, i.e., an intermediate intensity of additive noise is able to optimize the temporal response of the neural system to the subthreshold periodic signal. It is demonstrated that the time delay between neurons can either promote or destroy stochastic resonance in small-world neuronal networks. Delay-induced multiple stochastic resonances appear intermittently at the integer multiples of the oscillation period of the pacemaker. Furthermore, a larger time delay can always extend the span of optimal noise intensity warranting ordered excitatory fronts of neuronal dynamics in accordance with the rhythm of the pacemaker. More importantly, it is found that the small-world topology has a significant impact on the stochastic resonance in neuronal networks. In case of small time delays, increasing the rewiring probability can largely enhance the efficiency of the pacemaker-driven stochastic resonance, while for larger time delays, the variation of the rewiring probability has little resonance effect. In sum, both time delay and rewiring probability play an important role in the stochastic resonance on small-world neuronal networks, determining the ability to enhance the noise-induced outreach of the localized subthreshold pacemaker.

For now, effects of external modulations on the steady state of neuronal dynamics are focus issues in neuroscience. Induced spike trains in the presence of external stimuli are considered to be related with information processing in neural systems. In real systems, these external modulations could be caused by various neurotransmitters and/or by synaptic inputs. In this paper, it has been shown that appropriately tuned time delay in synaptic process can enhance weak signal detection by inducing multiple stochastic resonances on neuronal networks. Moreover, the pacemaker plays an important role in several different organs, tissue, and certain types of cells [14]. We thus expect the presented results could facilitate our understanding of biological processes that rely on an effective pacemaker for their proper functioning. We also hope our findings have important implications for the weak signal detection and information propagation in neural systems.

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