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Spiking regularity in a noisy small-world neuronal network

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Abstract

The regularity of spiking oscillations is studied in the networks with different topological structures. The network is composed of coupled FitzHugh–Nagumo neurons driven by colored noise. The investigation illustrates that the spike train in both the regular and the Watts–Strogatz small-world neuronal networks can show the best regularity at a moderate noise intensity, indicating the existence of coherence resonance. Moreover, the temporal coherence of the spike train in the small-world network is superior to that in a regular network due to the increase of the randomness of the network topology. Besides the noise intensity, the spiking regularity can be optimized by tuning the randomness of the network topological structure or by tuning the correlation time of the colored noise. In particular, under the cooperation of the small-world topology and the correlation time, the spike train with good regularity could sustain a large magnitude of the local noise.

Keywords: Small-world network; Colored noise; Spike train; Coherence resonance

1. Introduction

Recently, increasing attention has been dedicated to the studies of complex networks that account for real systems [1–3]. A network can be described by nodes representing components in a system and by links representing their interactions. Among various complex networks, a prominent type is the small-world network introduced by Watts and Strogatz [4,5]. Such a network is characterized by a local neighborhood with a sparse set of long-range connections. The concept of small-world network has quickly attracted extensive attention due to the following reasons: On the one hand, this kind of connection exists commonly in our real life, such as in the cellular systems, in the metabolic systems, and in the gene regulatory systems [4]; On the other hand, the existence of a small fraction of long-range connections in a small-world network can change the essential features of the given system and determine the system's behaviors [6–11]. Particularly in relation to neuronal models, the small-world network is efficient for information exchange [10] and can enhance the efficacy of associated memory [11]. All existing studies illustrate that small-world topological structure can play a crucial role in a system's dynamics.

The human brain is probably the most complex and fascinating processor that we have known, and it works in a noisy environment. The neuron connectivity in the cortex and other brain regions is mainly local, with relatively sparse long-distance projections, suggesting a small-world topological structure [12]. Collective oscillations of groups of neurons are commonly observed in the brain and are of great significance in various physiological schemes [13,14]. Spiking regularity of neuron oscillations is connected with the origin of various body clocks and is nearly associated with every cognitive task, such as memory formation, information coding and perception [15–18]. On the other hand, it is a well-established fact that noise can have constructive effects on the dynamics of nonlinear systems including the brain. One of the most famous phenomena related to this counterintuitive fact is the coherent resonance (CR) [19,20], in which the regularization of the noise-induced oscillations is maximized at a certain noise level without an external drive. In neuroscience, experimental evidence of CR has been reported in the cat's somanosensory system [21], and theoretical support has been achieved in a variety of neuronal models [19,20,22–24]. Following advances

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in these studies of CR in various single neuron or regular neuronal networks, recent years we have witnessed a big increase in literature devoted to the analysis of CR in neuronal networks with small-world topological structure [8,25–27].

In the studies of CR mentioned above, whether in an individual unit or in networks with different topological structures, fluctuations are typically accounted for as white noise. However, for most systems, white noise is not a good approximation of the actual fluctuations which may be colored noise. Experimental results [28,29] have demonstrated that colored noise, rather than white noise, provides the best model for the background input. Theoretical work has also shown that correlation in the input noise can affect the statistics of firing patterns of a neuron [30] and response frequency of spiking neurons [31]. In the present article, the phenomenon of CR is investigated in a small-world neuronal network, in which colored noise instead of white noise is added to the system. It is found that CR of the system can be enhanced by increasing the randomness of the network structure at a proper coupling strength. Moreover, the noise correlation time has shown important effects on the CR of the studied system. In the small-world neuronal network, when the intensity and the correlation time of the colored noise are tuned to favorable values, the coherence of the spike train can be greatly improved. Comparing to the regular network, the resonant range in the small-world network could sustain a larger range of noise, indicating that the robustness of the spike train with good regularity against the noise can also be enhanced in the small-world network.

2. Model description

The model used here consists of N Fitz-Hugh–Nagumo (FHN) neurons in which a small-world network topology is implemented as follows. Firstly, a regular lattice is considered, in which each neuron connects to its k nearest neighbors. Next, each local link is visited once and is removed and reconnected with the rewiring probability p to a randomly chosen neuron. It should be noted that a lot of network realizations exist for a given p. Herein, $N=100$, $k=4$, and p takes different values between 0 and 1. In those networks the rewiring parameter p controls the topology of the networks: when $p=0$ only local connections are present, and conversely when $p=1$ any two neurons in the network can be connected with the same probability. The adopted FHN model is simplified from the Hodgkin–Huxley (HH) model and is a relative simple but representative model for spiking neurons. The FHN neuron has been utilized extensively to investigate various dynamical processes including coherence resonance [32–35].

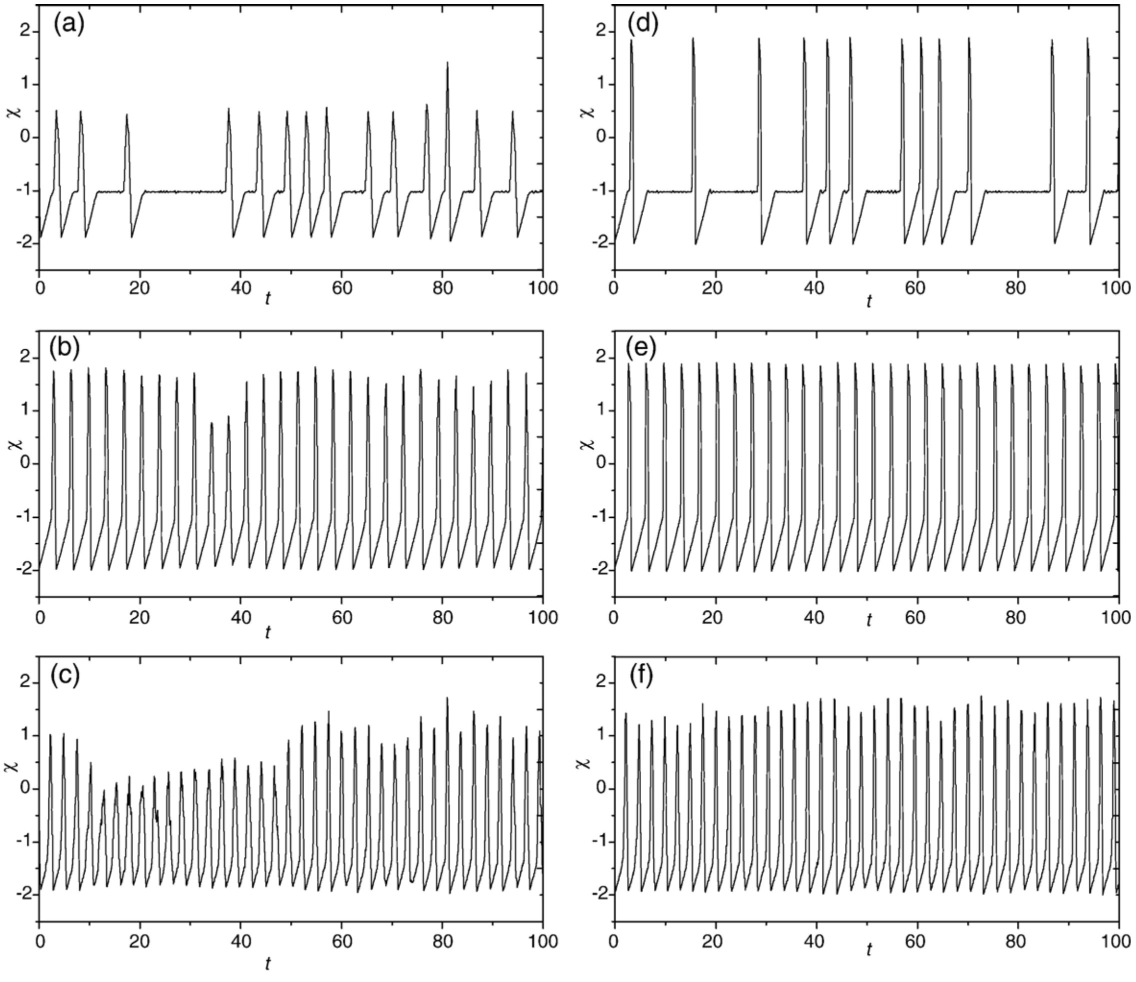

Fig. 1. The time series of the FHN system [Eqs. (1) and (2)] at different noise amplitudes in (a)–(c) the regular network ($p=0$) and (d)–(f) the small-world network ($p=0.2$). From top to bottom $D=0.0001$, $D=0.0003$, and $D=0.002$. $\varepsilon=0.01$, $a=1.02$, $g=0.05$, $\tau=0.05$.

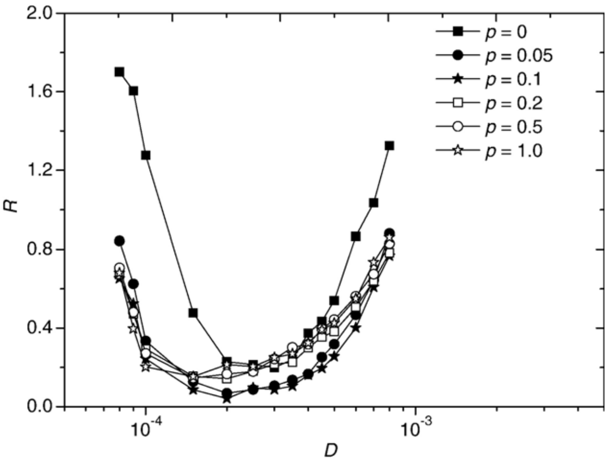

Fig. 2. The coherence factor R versus the input noise intensities D at different rewiring probabilities p, $\varepsilon=0.01$, $a=1.02$, $g=0.05$, and $\tau=0.02$.

The dynamics of each FHN neuron in the network is described by the following equations:

$$\varepsilon\frac{dx_i}{dt} = x_i - \frac{x_i^3}{3} - y_i + \sum_j g_{ij}\left(x_j - x_i\right) + C_i(t) \tag{1}$$

$$\frac{dy_i}{dt} = x_i + a_i \tag{2}$$

where $x_i(t)$ is a fast variable representing the membrane voltage of ith neuron, and $y_i(t)$ is a slow variable. The parameter a_i is a control parameter of the ith element. For a single FHN model, if $|a_i|>1$, the system has a stable fixed point, while $|a_i|<1$ a limit cycle appears. The system with fixed point dynamics ($|a_i|$ slightly larger than unity) is excitable because it will return to the fixed point after a large excursion when it is perturbed away from the fixed point. Herein, the control parameter a_i is supposed the same for all neurons, that is, a_i ($i=1,\ldots, N$) is identical to $a_0=1.02$. The time constant $\varepsilon=0.01$ determines the speed of the firing process. The parameter g_{ij} is the coupling parameter between two neurons i and j, and its value is determined by the coupling pattern of the system. If these two oscillators are coupled to each other, $g_{ij}=g$, and otherwise, $g_{ij}=0$. Each neuron is subjected to an incoherent noise $C_i(t)$, which is uncorrelated from unit to unit. $C_i(t)$ is zero-mean Gaussian colored noise with correlation given by $\langle C(t_1)C(t_2)\rangle = (D/\tau)\ \exp\left(-\frac{|t_1-t_2|}{\tau}\right)$, This colored noise, produced by the Ornstein–Uhlenbeck (OU) stochastic process, can be depicted as:

$$\tau\frac{dC_i}{dt} = -C_i + \xi_i(t) \tag{3}$$

Here $\xi_i(t)$ is Gaussian white noise with $<\xi_i(t)>=0$, and $<\xi_i(t)\xi_i(t')>=2D\delta\ (t-t')$. D is the strength of $\xi_i(t)$. Therefore, the colored noise is characterized by two parameters, noise intensity D and correlation time τ.

3. Results and discussion

The stochastic differential Eqs. (1) (2), and (3) are numerically integrated using the Euler scheme with a fixed time step of 0.002. It has been reported that noise-excited oscillations in a neuron appear to be rather irregular for both small and large noise amplitudes, while relatively regular oscillations appear for a moderate noise intensity [20]. Here we focus on the collective behavior of the network and measure the average activity $x(t) = (1/N)\sum_{i=1}^{N} x_i(t)$. The response of the neuronal network to the colored noise of different intensities is shown in Fig. 1 (a)–(c) and (d)–(f) in a regular network ($p=0$) and in a small-world network ($p=0.2$), respectively. It can be seen that for the two networks, relatively regular oscillations can be observed for the moderate noise intensity, indicating that CR phenomenon might occur both in the regular and in the small-world networks. Moreover, oscillations in the small-world network seem more "regular" compared to those in the regular network at the same noise amplitude.

To characterize the temporal coherence of the oscillation quantitatively, the coherence factor R of the variable x is described by the following formula [20]:

$$R = \frac{\sqrt{\mathrm{Var}\ (T_k)}}{\langle T_k\rangle} \tag{4}$$

where $T_k=t_{k+1}-t_k$, and t_k is the time of the kth pulse in the time series of x. A smaller R corresponds to a better spiking regularity. Biologically, this quantity is of importance because it is related to the timing precision of the information processing in neural systems [36]. Note that a pulse occurs when the state variable x exceeds a certain threshold value x_0 (here taken arbitrarily as $x_0=0.5$) and it turns out that the threshold value can vary in a wide range without altering the results.

Fig. 2 plots the coherence factor R against the input noise intensity D at different rewiring probabilities p. Here each R is attained by averaging over 30 network realizations for each p. It can be observed that R in all the curves first decreases and then increases with the increase of the noise intensity, indicating that there exists an optimal noise level at which the collective oscillations are the most ordered whatever p is. The lowest point is called maximal coherence factor R_{m} and the noise intensity at

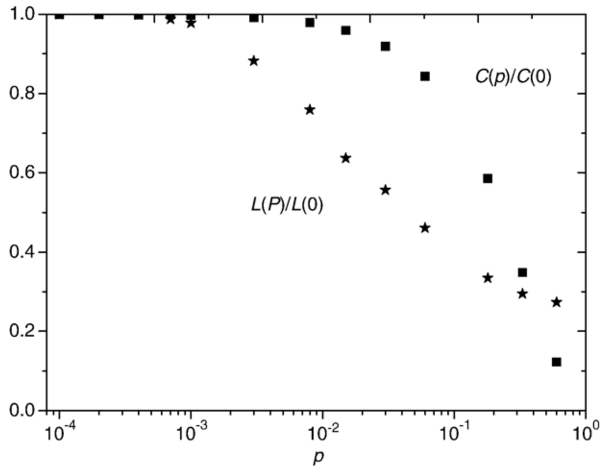

Fig. 3. Characteristic path length L and clustering coefficient C as a function of the rewiring probability p in small-world networks with $N=100$ and $k=4$. They are normalized by each value at $p=0$.

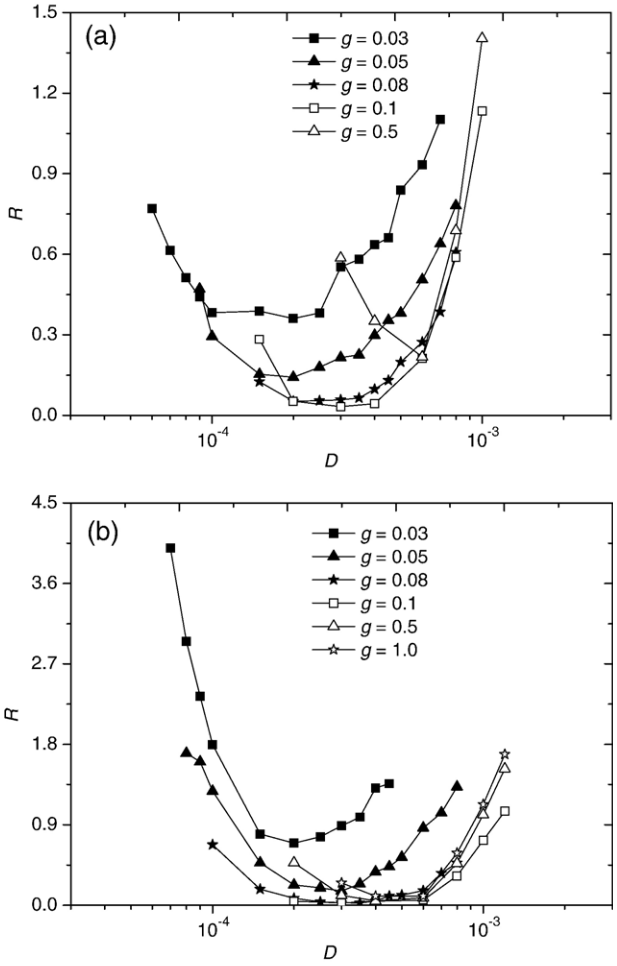

Fig. 4. The coherence factor R versus the input noise intensities D at different coupling strength g in (a) the small-world network, $p=0.20$; (b) the regular network, $p=0$. $\varepsilon=0.01$, $a=1.02$, and $\tau=0.02$.

R_m is called resonant noise intensity D_r. It can be seen that the largest and the smallest R_m occur for the rewiring probability $p=0$ and $p=0.1$, respectively, implying that the increment of the disorder of the network topological structure plays a positive role in enhancing CR, yet there is an optimal rewiring probability around $p=0.1$. Meanwhile, the resonant noise intensity D_r shifts to the left gradually as p increases. Usually a small-world network is characterized by two important parameters: a small average path length $L(p)$ and a large clustering coefficient $C(p)$. $L(p)$ is defined as the mean of the number of edges in the shortest path between each neuron and all the other ones in the network, and $C(p)$ is defined as the probability that two neurons that are connected to a third neuron, are themselves connected. It can be found from Fig. 3 that when p is in the vicinity of 0.1, the small-world properties of the networks are especially apparent, therefore, the advantage of small-world topology to enhance CR of the system is remarkable in this case. In fact, in some previous work about small-world networks, it was also found that certain pronounced dynamical behavior can appear for an optimal randomness of the network topological structure. For example, an optimal level of topological randomness can lead the system to exhibit maximum order and the spatiotemporal chaos is tamed in an array of coupled pendulum networks [37]. In the coupled Hodgkin–Huxley neurons, there are optimal random shortcuts at which the collective spike coherence and individual neuron show the best temporal coherence [38].

With the increase of the coupling strength g, R_m drops first and then rises, and the resonant noise intensity D_r shifts rightwards, as shown in Fig. 4(a) and (b). Then, there exists an optimal coupling strength in both the regular and the small-world networks. Moreover, CR of the neuronal network can be improved by increasing the randomness of the network just for smaller g. If the couplings are very strong, all neurons behave almost as a single one, and increasing p may only reinforce the trend and weaken the effect of the noise. Thus, increasing the disorder of the network suppresses instead of enhancing CR in the case of very strong couplings, which can be seen more clearly from Fig. 5, and this result is similar to that reported in Ref. [39]. Moreover, the resonant noise intensity D_r becomes larger with the increase of p in Fig. 5, which is contrary to the case in Fig. 2.

Besides the noise intensity, the network topological structure and the coupling strength, noise correlation time is another important factor affecting the regularity of spiking oscillations. In the small-world network as shown in Fig. 6(a), it can be seen that R_m takes the smallest value at $\tau=0.3$, namely, there exists a correlation time for the best spiking regularity. Meanwhile, the resonant noise intensity D_r is almost independent of the correlation time τ and the resonant range becomes wider as τ increases from 0.01 to 0.1. If τ becomes larger, D_r can no longer resist the influence of the correlation time and the resonant range enlarges further. Fig. 6(b) displays R in the regular neuronal network at various noise correlation time, and there is also a noise correlation time $\tau=0.1$ corresponding to the smallest R_m. It can be seen that within the studied range of τ, D_r shifts to the right with the increase of τ; however, the difference in their resonant ranges at different τ is difficult to discern intuitively just from Fig. 6(b).

In order to further explore the differences of the dynamical behaviors between the regular and small-world networks, Fig. 7 (a)–(c) compare the two networks from the aspect of the

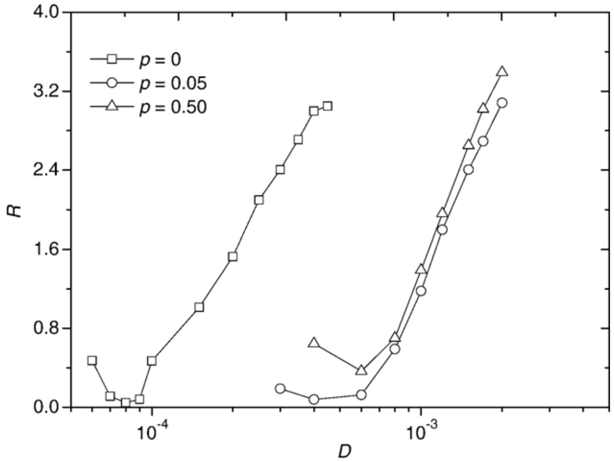

Fig. 5. The coherence factor R versus the input noise intensities D at different rewiring probabilities p, $\varepsilon=0.01$, $a=1.02$, $\tau=0.02$, and $g=0.5$.

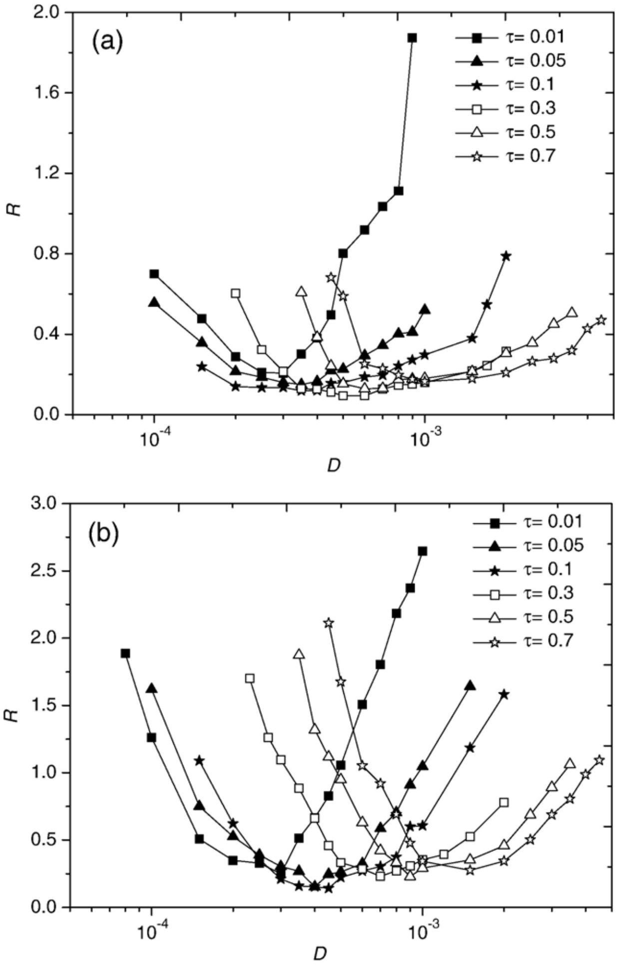

Fig. 6. The coherence factor R versus the input noise intensities D at different noise correlation time τ in (a) the small-world network, $p=0.2$; (b) the regular network, $p=0$. $\varepsilon=0.01$, $a=1.02$, and $g=0.05$.

maximal coherence factor R_m, the resonant noise intensity D_r and the resonant range, respectively. Fig. 7(a) shows that R_m in the small-world neuronal network is smaller than that in the regular neuronal network at the same noise correlation time, which mainly results from the increase of the network randomness. From Fig. 7(b), it can be observed that in the small-world network, when $\tau<0.1$, the precise value of the resonant noise intensity D_r has feeble dependence on the correlation time τ. As τ is large, D_r increases monotonically. In the regular network, D_r always takes a large value with the increase of the noise correlation time τ. It is easy to observe that D_r in the small-world network is smaller than that in the regular network at the same τ, which illustrates the advantage of the small-world topological structure over the regular topological structure. Therefore, weaker noise can induce oscillations with a better coherence in a small-world network than that in a regular network.

Based on the maximal coherence factor R_m, here the resonant range is quantified and defined as $W=D_2-D_1$. D_2 and D_1 are the noise intensity corresponding to $(1+5\%)R_m$, and D_2 is larger than D_1. The larger W is, the less tuning the noise intensity is required in order to increase the regularity of the spike train. Fig. 7(c) displays the resonant range W versus the noise correlation time τ, it shows that W increases with the increase of τ in both networks and large τ plays the positive role of enlarging the resonant range. Moreover, W in the dashed line is larger than that in the solid line at the same τ, which means that the spike train with good regularity could sustain a larger range of local noise in a small-world network than in a regular network. Ref. [40] has demonstrated that when the noise is colored, the pulse detection becomes more robust, because the number of false positive events decreases with increasing

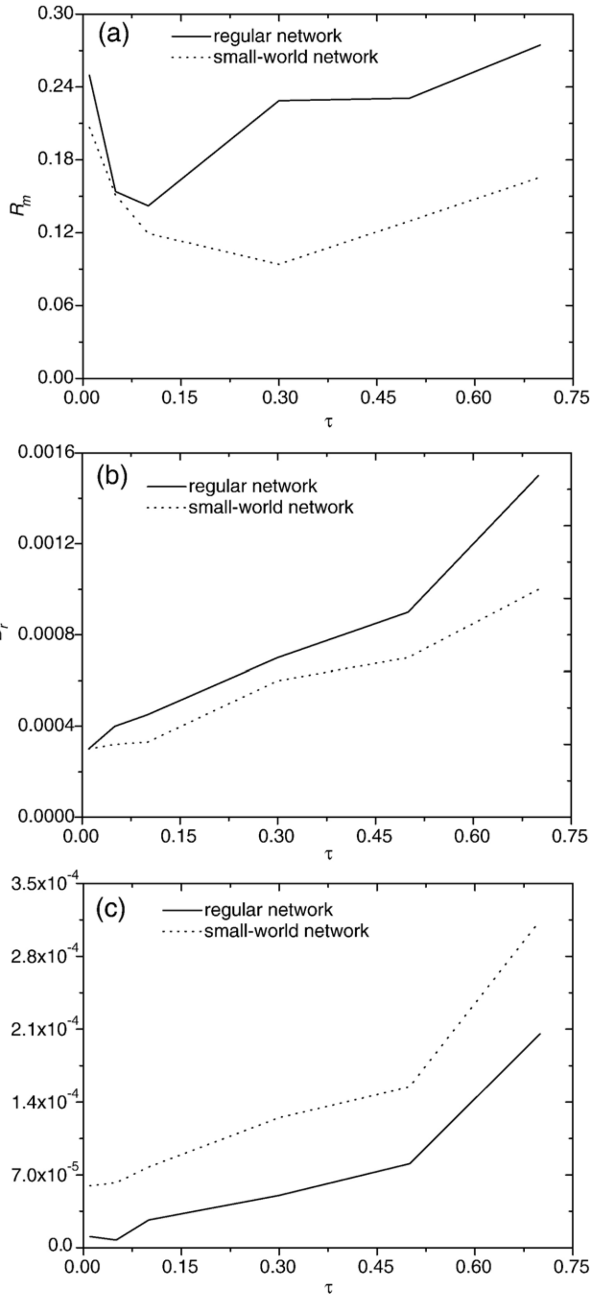

Fig. 7. (a)–(c) The maximal coherence factor R_m, the resonant noise intensity D_r and the resonant range W versus the noise correlation time τ in the regular network (solid line, $p=0$) and in the small-world network (dashed line, $p=0.2$), respectively. $\varepsilon=0.01$, $a=1.02$, and $g=0.05$.

temporal correlation while the number of correctly detected events is almost unaffected. Ref. [41] has reported that a single resonant unit can reach a great reduction in the need for noise tuning and the appearance of the phenomenon is mainly due to the departure of the additive noise from Gaussian behavior. Herein, under the cooperation of the small-world topology and the colored noise, the robustness of the regular spike train against the noise can be enhanced considerably.

4. Conclusions

In this paper, the regularity of the spike oscillations in networks composed of coupled Fitz-Hugh–Nagumo neurons is investigated. The neuronal network possesses regular network or small-world network structure characteristics and is driven by additive colored Gaussian noise. It is found that the spiking regularity of the network has the best performance at a certain noise intensity regardless the topological structure of the network, indicating the occurrence of coherence resonance. Comparing to the regular network, more ordered spiking can be induced by weaker noise in the small-world network at intermediate coupling strength, and there is an optimal level of topological randomness corresponding to the best coherence of the spike train. Another attention is paid to the effects of the correlation time of the colored noise on the spike train of the system. There is an optimal noise correlation time corresponding to the best spiking regularity both in the small-world and in the regular neuronal networks. In addition, the resonant range becomes wider with the increase of the noise correlation time, and the resonant range in the small-world network could sustain a larger range of noise. Therefore, neuron oscillations in a network with small-world topology driven by colored noise with favorable intensity and correlation time perform excellently on the convergence of regularity and robustness. It is expected that findings reported in this paper can shed light on deeper understanding of the neuron oscillations in complex neuronal systems.

Acknowledgments

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