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ORIGINAL PAPER

Effects of coupling strength and network topology on signal detection in small-world neuronal networks

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Abstract We study the effects of different coupling strengths and network topologies on signal detection in small-world neuronal networks. Research has previously revealed that the ability of detecting subthreshold signals could be significantly enhanced by appropriately fine-tuning the noise intensity. Here we show that the coupling strength and the structure of the underlying network can also lead toward enhanced signal detection. In particular, we show that there are two levels of the coupling strength at which the subthreshold signal can be detected at an appropriate noise intensity and network structure. We also show that the network structure has little impact on signal detection if the coupling is weak. On the other hand, for intermediate coupling strengths, we show that the shorter the average path length, the better the signal detection. Finally, if the coupling is strong, we show that there exists an intermediate average path length at which signal detection becomes optimal.

Keywords Neuronal network · Small-world network · Multiple stochastic resonance · Signal detection

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1 Introduction

Noise is ubiquitous in nonlinear systems. Contrary to the traditionally thought, noise plays a positive role sometimes. For example, under certain conditions, noise is reported to help nonlinear systems to detect weak signals [1]. This phenomenon is called as stochastic resonance, firstly introduced by Benzi et al in early 1980s to explain the periodic recurrence of ice ages [2,3]. Nowadays stochastic resonance is widely observed in various nonlinear systems [4–6].

Different from stochastic resonance whereby addition of certain amount of noise in nonlinear system makes weak signal could be amplified, coherence resonance is a phenomenon whereby addition of certain amount of noise in excitable system makes its oscillatory responses most coherent [7–9]. With further studies, Vider et al. found out that there existed more than one noise intensity at which the signal detection ability was enhanced, which is referred as stochastic multiresonance [10]. And this significant finding provides more than one optimal noise intensities for signal detection. In neuronal systems, there are various of noise sources such as the random switch of ion channel, the release of neurotransmitter [11–13]. Both experimental and theoretical studies have suggested that weak signal can be optimized by noise [14–16]. Thus stochastic resonance may be a underlining mechanism for the efficiency of information transmission in neuronal systems [17–19]. Inspired by Vider et al., we recently revealed that stochastic multi-resonance could occur in small-world neuronal networks constructed by FitzHugh–Nagumo neuronal models locally [20,21].

There are about 86 billion neurons in human brain and neurons interacts with each other via synapses [22,23], proper interactions between pairwise of neurons play a vital role in signal detection as well. Effects of various types of coupling item have been studied on neuronal networks' nonlinear dynamical behaviors through numerical stimulations recently. For example, it has been reported that coupling strength could induce different dynamical behaviors in excitatory and inhibitory chemically coupled neuronal networks [16]; proper time delays and proper coupling strengths could induce synchronization in chemically coupled neuronal networks [24]. Coupling strength could enhance stochastic resonance in electrically coupled networks as well [25]. With further studies, mutative coupling items instead of fixed coupling items are considered in neuronal networks, such as the adaptive coupling and the time-varying coupling strength. It has been proved that adaptive coupling not only enhances stochastic resonance but also enhances synchronization [26–28]. And fine-tuned time-varying coupling could make the spiking regularity maintain at a high level [29,30]. Moreover, spiking-time-dependent plasticity is a more biological synaptic modulation [31–33]. Effects of spiking-time-dependent plasticity on coherence resonance and synchronization have been studied recently [34,35]. Through above-mentioned works, although various types of coupling items could induce different neuronal network behaviors, coupling strength always plays a vital role in dynamical behavior of neuronal network.

It has been reported that the topology of brain network exhibits the small-world network characteristics [36,37]. The topology of neuronal network is developing and changing with the aging [38,39] as well as some brain disorders [40,41]. A good deal of numerical studies has been performed in a small-world structure network [42–48]. Effects of rewiring probability on signal detection in small-world neuronal networks have been studied by Yu et al., in which they pointed out that the rewiring probability could affect the signal detection ability when neurons are coupled in delay-free case [49]. The impacts of rewiring probability and time delay on synchronization have been studied in small-word networks as well [50,51]. Moreover, Perc has studied stochastic resonance in Newman–Watts small-world neuronal networks, in which he found that fine-tuning topology of neuronal networks and appropriate coupling strengths could enhance the ability of information detection [52]. Besides that, dynamical behaviors of neuronal system are also studied under other topologies of network [53–56].

As mentioned above, interactions between neurons and network topology are quite important to information transmission in neuronal network. In certain systems, noise could induce stochastic multi-resonance which will give us more than one optimal noise intensities for efficient signal detection. Inspired by the former studies, effects of the coupling strength and network topology on signal detection ability are studied in this paper. Based on our former study [21], we will investigate effects of coupling strength and network topology on signal detection ability in details. The paper is organized as follows: neuronal network model and algorithm of constructing network are presented in Sect. 2; Numerical results obtained are shown in Sect. 3; and Sect. 4 gives a summary of this paper.

2 Model and method

2.1 FitzHugh–Nagumo neuronal network model

In the FitzHugh–Nagumo system(FHN) [57,58], there are two regions of fast motion and therefore two jumps of the phase; for simplicity we consider here a simplified model with one jump, which, nevertheless, captures all important qualitative features of the phase dynamics [7]. Here, we also call the simplified model as FitzHugh–Nagumo model and use it as blocks to build the studied neuronal network. Then, equations of the studied neuronal network are presented as follows

$$\varepsilon \dot{x_i} = x_i - \frac{x_i^3}{3} - y_i + \frac{g}{k_i} \sum_{j=1}^{N} J_{ij}(x_j(t) - x_i(t)) \quad (1)$$

$$\dot{y_i} = x_i + a_i + A \sin\left(\frac{2\pi}{Te} t\right) + D\xi_i(t) \quad (2)$$

Here, x_i and y_i represent fast and slow variable of ith neuron, respectively. They are discriminated by parameter ε, which is set as $\varepsilon = 0.01$. $\frac{g}{k_i}\sum_{j=1}^{N} J_{ij}(x_j(t-\tau)-x_i(t))$ is the synaptic current received from other neurons in the network. J_{ij} denotes whether the ith neuron and the jth neuron are connected: if the ith neuron is connected to the jth neuron then $J_{ij} = J_{ji} = 1$, otherwise $J_{ij} = J_{ji} = 0$. Meanwhile, autapse (synapse that connects to itself) are not considered, thus J_{ii} always equals to zero for all neurons inside the network. g and k_i are the coupling strength and the connectivity degree of ith neuron. a is a systematic parameter. A single neuron exhibits either oscillatory behavior if $|a| < 1.0$ or excitable behavior if $|a| > 1.0$. In this work, a is set as 1.1 for each neurons to make each neurons inside the network stay at resting state in the absence of external stimulations.

$A\sin(\frac{2\pi}{T_e}t)$ is the subthreshold signal with period T_e and amplitude A. Here, T_e is set as 9 and A is set as 0.1 (the threshold is 0.136). Stochastic multiple resonance induced by noise has been studied in details in Ref. [20]. It has been shown that occurrence of stochastic multiple resonance depends on the period of subthreshold signal T_e. Here, we choose T_e to be 9 at which stochastic bi-resonance could be induced by noise. And other values of T_e which could let stochastic bi-resonance occur can also be applied in our current paper. And it does not influent the obtained results. In this paper, neurons are stimulated to generate spiking activities by Gaussian white noise $D\xi_i(t)$ [59], with $\langle\xi_i(t)\rangle = 0$ and $\langle\xi_i(t)\xi_j(t')\rangle = \delta_{ij}\delta(t-t')$. Here, the noise is uncorrelated both in space and time. Namely, $\delta_{ij} = 1$ if $i = j$, otherwise $\delta_{ij} = 0$; And $\delta(t-t') = 1$ if $t = t'$, otherwise, $\delta(t-t') = 0$. And D represents the noise intensity.

Neuronal networks considered in this paper contain $N = 200$ neurons.[1] The studied neuronal networks are constructed by employing the algorithm of Watts and Strogatz [37]. The scheme of constructing neuronal network is described as follows: Firstly a ring network with regular connectivities is constructed, where each neuron connects to its k nearest neighbors; Then rewiring each edge with a probability p randomly. k and p are chosen as 10 and 0.05 if not stated specifically.

2.2 Measurement

The mean field of the membrane potential $X(t) = \frac{1}{N}\sum_{i=1}^{N} x_i(t)$ is introduced to quantitatively characterize collective response of neuronal network. To quantitatively characterize the correlation of collective response of the neuronal network $X(t)$ with the subthreshold input signal $A\sin(\frac{2\pi}{T_e}t)$ as well as the ability to detect the input signal, we calculate the Fourier coefficient Q, defined as

$$Q_{\sin} = \frac{1}{T}\int_{t_m}^{t_f} 2X(t)\sin\left(\frac{2\pi}{T_e}t\right)\mathrm{d}t \quad (3)$$

$$Q_{\cos} = \frac{1}{T}\int_{t_m}^{t_f} 2X(t)\cos\left(\frac{2\pi}{T_e}t\right)\mathrm{d}t \quad (4)$$

$$Q = \sqrt{Q_{\sin}^2 + Q_{\cos}^2} \quad (5)$$

The integral interval is from t_m to t_f casting off the transient state from 0 to t_m. Here t_m and t_f are set as $t_m = 400$ and $t_f = 500$. Larger Q indicates stronger response of the entire neuronal network to the subthreshold signal. Namely, larger Q represents the stronger ability of detecting subthreshold signal.

Numerical integration of Eq. (1) is performed by using the explicit Euler method with the time step of 0.001 and the initial state is set as $x_i(0) = 0$, $y_i(0) = 0$. In the followings, the exhibited numerical results are obtained by averaging over 10 independent realizations to ensure the statistical accuracy with respect to the generation of Gaussian white noise and neuronal network.

3 Result

3.1 Multiple stochastic resonance induced by coupling strength

An overlook of stochastic multi-resonance phenomena induced by noise and coupling strength is presented in Fig. 1. In this paper, Fourier coefficient Q is applied as a measure to quantify the ability of detecting subthreshold signal. Fourier coefficient Q calculated as a function of coupling strength g and noise intensity D is exhibited in Fig. 1. As we can see when coupling strength $g < 0.08$, Q only has one peak with increasing of noise intensity D, which indicates there exists

[1] Notation: A small-world network topology is applied in this paper. In order to satisfy the statistic characteristics of small-world network topology, the network size should be not too small. Usually, the network size should be larger than 100. Thus, we choose N be 200 in this paper. And for different network size N, we need to modulate value of k to keep the obtained results be preserved.

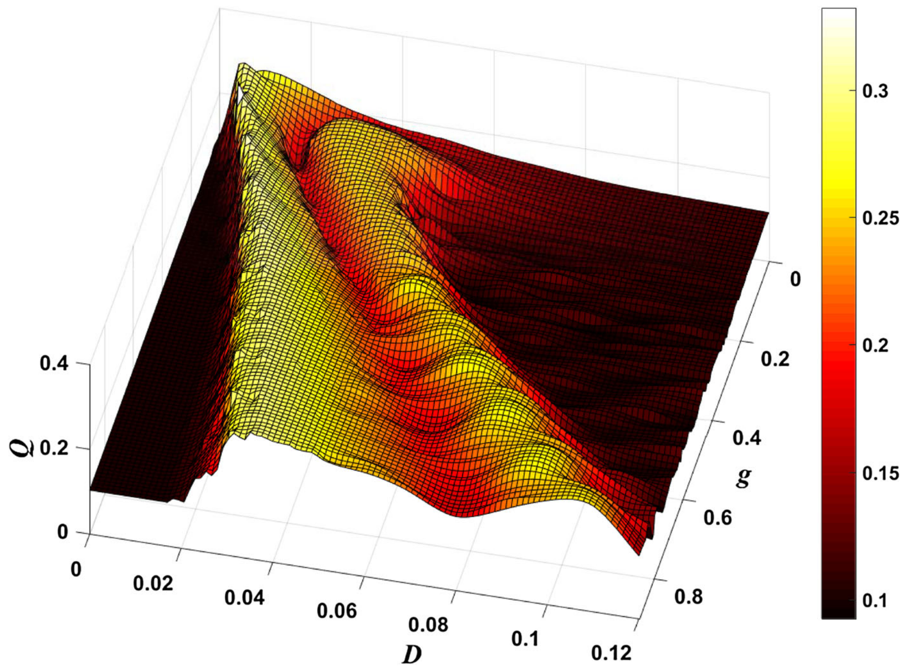

Fig. 1 Fourier coefficient Q as a function of noise intensity D and coupling strength g

an optimal noise intensity enhancing signal detection of neuronal network; while when coupling strength $g > 0.08$, Q has two peaks with increasing of noise intensity, indicating there are two optimal noise intensities enhancing signal detection, this phenomena is called stochastic bi-resonance and investigated systematically in Ref. [20]. While when the noise intensity D is fixed at an appropriate level there also exhibit multiple resonant behavior with increasing of coupling strength which indicating there exist not only one optimal coupling strength in signal detection. We can draw a conclusion that fine-tuned noise intensity and coupling strength can greatly enhance the signal detection ability of the studied neuronal network.

To get a better explanation about the effects of coupling strength on signal detection, we take an example by fixing the noise intensity D to be 0.04. And correspondingly, the dependence of Q with respect to coupling strength g is exhibited in Fig. 2. As demonstrated, there are two peaks of Q with increasing of coupling strength g. It indicates that coupling strength can induce multiple stochastic resonance when noise intensity is fixed at an appropriate level. It also enlighten us that when noise intensity is fixed at an appropriate level, there exist more than one coupling strength which can enhance the ability of detecting subthreshold signal of neuronal network.

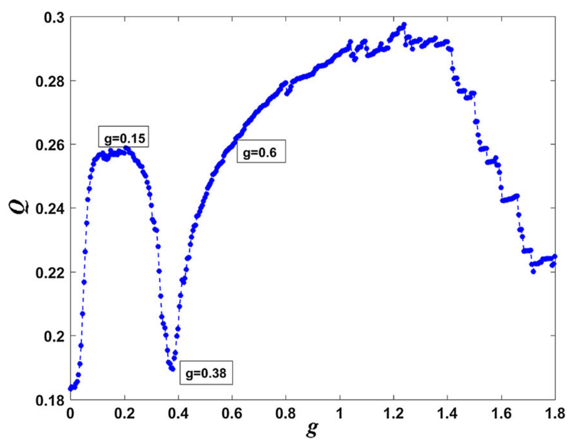

Fig. 2 Fourier coefficient of Q as function of coupling strength g, when noise intensity set as $D = 0.04$

In order to get a deeper understanding of coupling strength-induced multiple stochastic resonance, three typical spatiotemporal patterns and the corresponding distribution of inter-spike intervals are presented, as shown in Fig. 3. According to the results shown in Fig. 2, when the coupling strength of network takes some small values which are around $g = 0.15$, Q reaches the first locally maximum; when the coupling strength of network takes some moderate values which are near $g = 0.38$, Q decreases to a locally minimum;

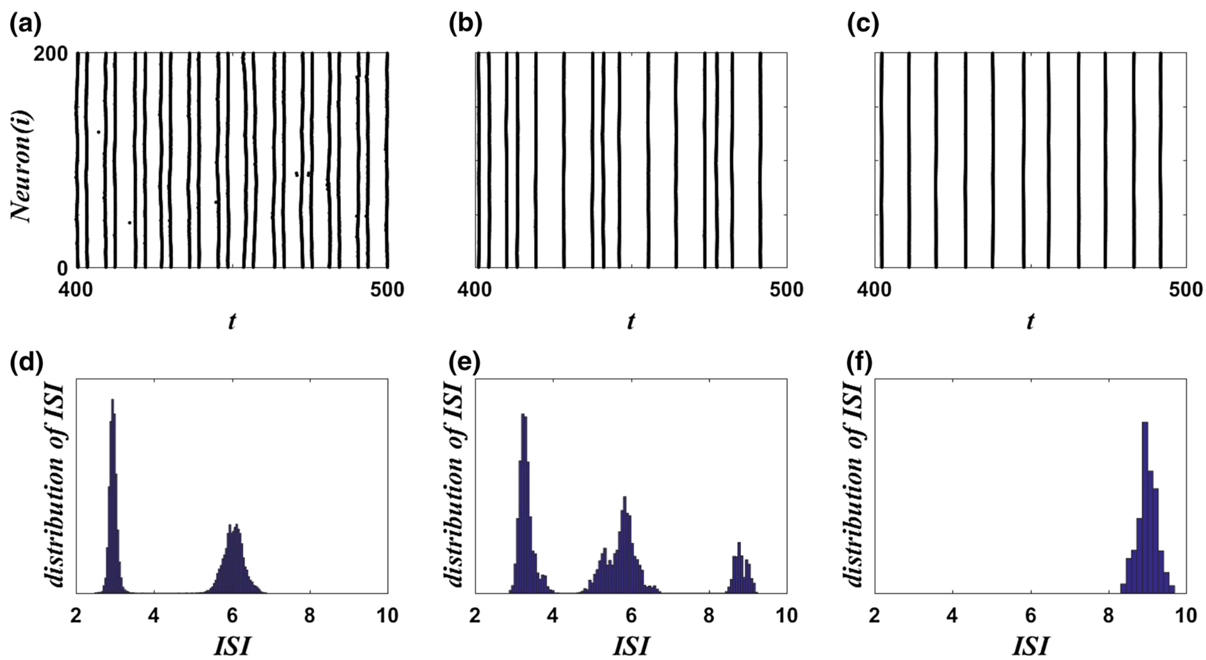

Fig. 3 Time-space plots and the distribution of ISI (Inter-spike-interval). Time-space plots with **a** $g = 0.15$ **b** $g = 0.38$ **c** $g = 0.6$ and the distribution of ISI with **d** $g = 0.15$ **e** $g = 0.38$ **f** $g = 0.6$. Other parameter are set as $D = 0.04$

and when the coupling strength of network takes some large values which are larger than 0.6 and smaller than 1.2, Q reaches to large values for the second time.

Take $g = 0.15$ for an example to show the characteristics of the corresponding spatiotemporal pattern and distribution of inter-spike intervals for these small values of g. The firing pattern is quite regular and neurons spike twice within one period ($T_e = 9$) as exhibited in Fig. 3a and the corresponding ISI distribution exhibited in Fig. 3d are concentrating round two points which are approximately 3 and 6, the sum of them is 9 equaling to the subthreshold signal period T_e. Thus, the output of the neuronal system has relatively high correlation with input signal, which results in a local maximal value of Q; as the coupling strength g increased to 0.6, the firing pattern exhibited in Fig. 3c is quite regular and the ISIs concentrate around 9, thus system has high correlation with input signal as well; when $g = 0.38$, as illustrated in Fig. 3b, e, the firing pattern is not regular. Thus, the output of neuronal network cannot follow the rhythm of input signal and then Q takes small values.

With the above obtained results presented in Figs. 1, 2 and 3, we can see that stochastic multi-resonance could be induced by coupling strength and noise intensity. Namely, fine-tuned noise intensity and coupling strength can enhance the ability of detecting subthreshold signal of the neuronal system. It is known that network topology plays a vital role both in functional achievements and brain disorders. Here, we present that the ability of detecting subthreshold signal of the studied neuronal system could be enhanced by approximately tuning coupling strength and noise intensity. Thus, we further interested in discussing how network properties influent the effects of coupling strength and noise intensity on the ability of signal detection. We will focus on discussing this in details in the following section.

3.2 Effects of neuronal network topology on signal detection ability

Since WS small-world network is considered in this paper, the network topology is mainly controlled by the parameter k and the rewiring probability p. In the followings, effects of connectivity k and rewiring probability p on signal detection are investigated. Here noise intensity is fixed as $D = 0.04$. In order to avoid the effects of randomness on signal detection as explained in "Appendix", we only consider a proper range of coupling strength, i.e., $g < 1.0$.

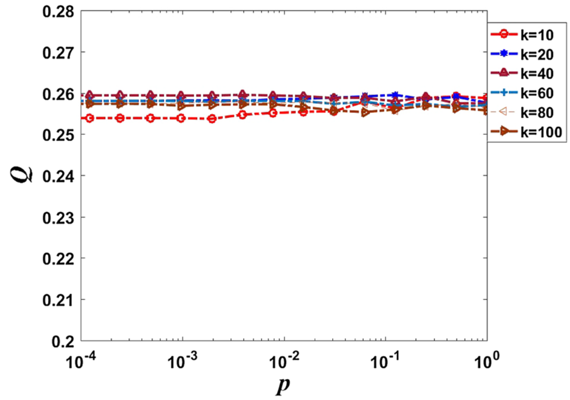

Fig. 4 Fourier coefficient Q as function of rewiring probability p with different k, when noise intensity set as $D = 0.04$ and coupling strength set as $g = 0.15$

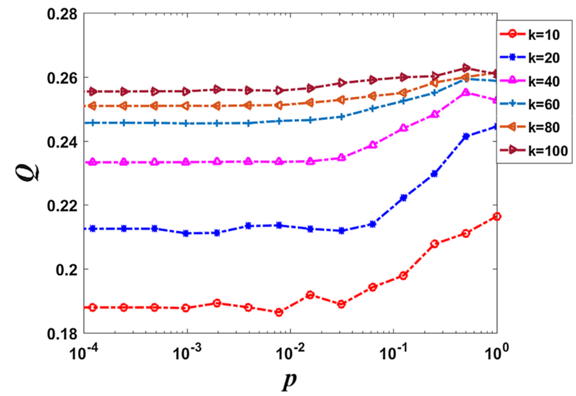

Fig. 5 Fourier coefficient Q as function of rewiring probability p with different k with noise intensity $D = 0.04$ and coupling strength $g = 0.38$

As presented in Fig. 3, when the values of coupling strength are around $g = 0.15$, the neurons in network have a nearly periodic-2 spiking pattern as exhibited in Fig. 3a and the neuronal network has a relatively strong signal detection ability; when the values of coupling strength are larger than $g = 0.5$ and less than $g = 1.0$, the neuronal network has a nearly periodic-1 spiking and neuronal network can also efficiently catch the input signal; for the values of coupling strength are near $g = 0.38$, the neuronal network has a relatively weak ability of signal detection as exhibited in Fig. 3b. These typical values of coupling strength are quite important for the signal detection in neuronal network, and influences of network topology on signal detection are studied under above-mentioned values of coupling strength. Coupling strength is classified as small (when the values of coupling strength are around $g = 0.15$), middle (when the values of coupling strength are near $g = 0.38$) and large (when the values of coupling strength are larger than $g = 0.5$ and less than $g = 1.0$) values of coupling strength, respectively. For simplicity, we take these typical values of coupling strength from above-mentioned classification.

When the system is weakly coupled, e.g., $g = 0.15$, we calculate the dependence of Q on the rewiring probability p for various values of k, as shown in Fig. 4. From this figure, we can see that Q almost does not change with increasing of p; and Q also does fluctuate greatly with changing of parameter k. It indicates that network topology of the considered WS small network has little influences on the detecting ability of the neuronal system when neurons inside are weakly coupled with each other.

When system is coupled with a middle coupling strength, e.g., $g = 0.38$, dependence of Q with respect to p for various values of k is presented in Fig. 5. When k is fixed, Fourier coefficient Q is always higher for larger values of rewiring probability p. When the rewiring probability p is fixed, Fourier coefficient Q increases monotonically with increasing of connectivity k. Thus, the ability of signal detection can be enhanced with increasing of k and the rewiring probability p in this case. The characteristic path length [37] is employed to explain this obtained result. The characteristic path length $L(p)$ is defined as follow: the shortest path that connect two neurons in the network, then averaging all the path lengths in the network. The characteristic path length in our work reflects the averaging shortest path with which two neurons are connected. Characteristic path length $L(p)$ as a function of rewiring probability p with different k is presented in Fig. 6. We can observe that shorter path length will indicate a higher value of Q as shown in Fig. 5. Thus, we can draw an conclusion that with the change of rewiring probability p and k, the signal detection ability can be enhanced at a shorter characteristic path length of network.

Space-time plots of the neuronal network which are coupled at a middle level are exhibited in Fig. 7 for different k under the rewiring probability being fixed as $p = 0.05$. With increasing of k, the spatiotemporal patterns of the neuronal network become more and more regular and the inter-spike intervals are more and

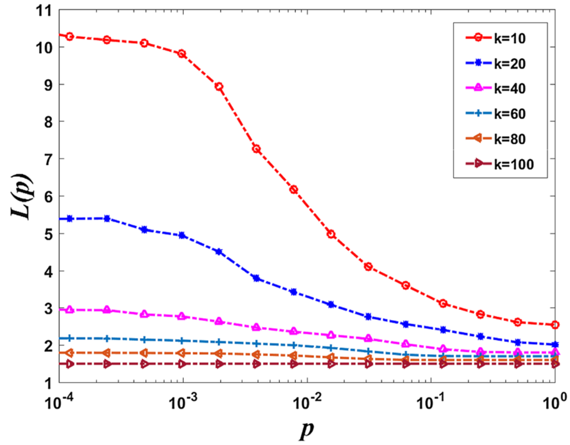

Fig. 6 The characteristic path length $L(p)$ as a function of rewire probability p with various k

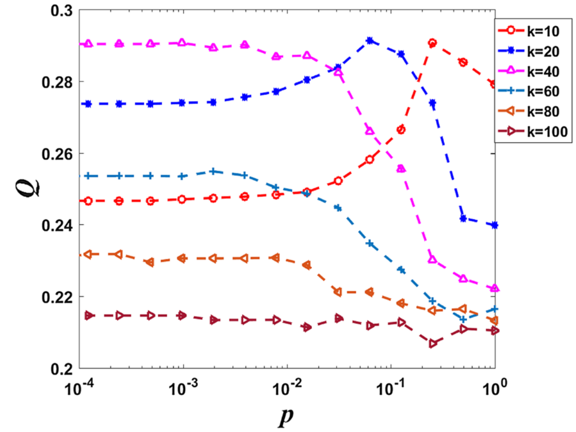

Fig. 8 The Fourier coefficient Q as function of rewiring probability p with different k, with noise intensity $D = 0.04$ and coupling strength $g = 0.6$

more closer to the period of subthreshold signal T_e. With the results shown in Fig. 6, the characteristic path length of neuronal network is shorter with increasing of k when the rewiring probability p is fixed. When the coupling strength is not too small, here, $g = 0.38$, the more shorter the network characteristic path length is, the more easily coherent the pairwise of neurons in network are. And meanwhile, the period of the firing activities become more and more coherent with the input signal, which results in the enhancement of the ability of detecting subthreshold signal.

When the system is coupled with some strong coupling strengths, e.g., $g = 0.6$, variations of Q as a function of rewiring probability p for different values of k are exhibited in Fig. 8. A resonance-like behavior is observed for $k = 10$ and $k = 20$, and Q changes not too much for $k = 100$, while for other values of k, Q almost not changes at first and then decreases with increasing of p. Moreover, dependence of Q with respect to k for various p is also exhibited in the left panel of Fig. 9. It is shown that, when p is not too large ($p < 0.15$), there exist some intermediate k at which Q takes maximal values, which indicates the neuronal system could detect the subthreshold signal efficiently. These results imply that network topology could also have great influences on the ability of detecting signals when neurons are coupled strongly.

Inspired by the observations in the neuronal system with coupling strength takes middle values, as presented by Figs. 5 and 6, we guess that the observed effects of network topology on signal detection in the current case also have close relationship with the characteristic path length L of the network. In Fig. 8, Q takes local maximum at $p \approx 0.25$ for $k = 10$ and at $p \approx 0.0625$ for $k = 20$, respectively. By calculation, we get that the characteristic path length L equals 2.825 when $p = 0.25$, $k = 10$ and 2.562 when $p = 0.0625$, $k = 20$. Up to now, we do not catch any relationship between Q and L. Thus, we further analyze the results shown in Fig. 9. In the left panel of Fig. 9, a purple band is added to show the region where Q takes large values $Q > 0.28$, and the characteristic path length L is in the same region is also

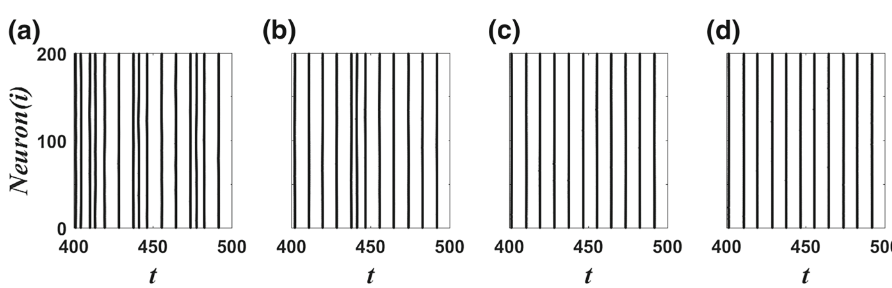

Fig. 7 Space-time plots with different k, under $D = 0.04$, $g = 0.38$ and $p = 0.05$. **a** $k = 10$; **b** $k = 20$; **c** $k = 40$; **d** $k = 80$

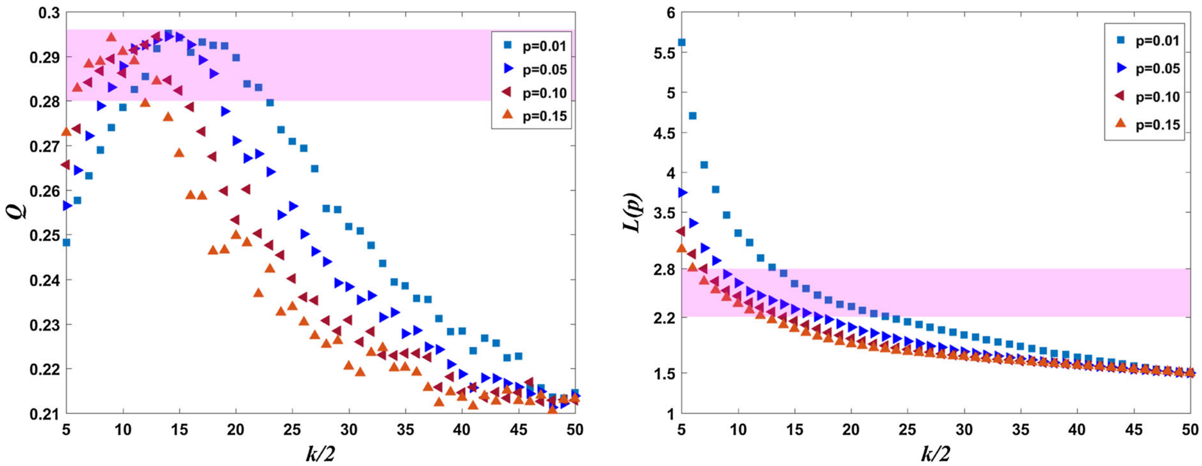

Fig. 9 The Fourier coefficient Q and characteristic path length L as function of $k/2$ with different rewiring probability p, with noise intensity $D = 0.04$ and coupling strength $g = 0.6$

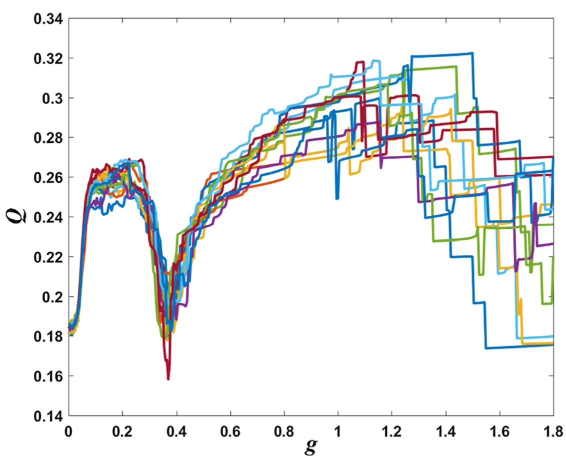

Fig. 10 Fourier coefficient Q as a function of coupling strength g using different random seeds for generating noise, under noise intensity $D = 0.04$

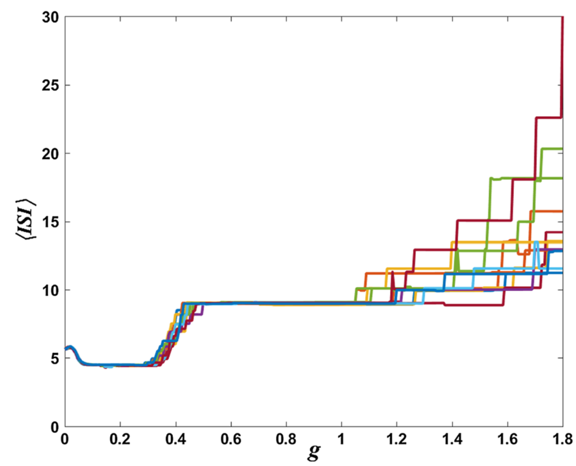

Fig. 11 The $\langle ISI \rangle$ as a function of coupling strength g using different random seeds for generating noise, under noise intensity $D = 0.04$

colored with a purple band in the right panel of Fig. 9 correspondingly. Then, we find that L falls into the interval $[2.2, 2.8]$ when $Q > 0.28$. It means that, when p is fixed, the ability of detecting subthreshold signal of the neuronal systems could be enhanced when the characteristic path length $L \in [2.2, 2.8]$. Therefore, conclusion may be drawn that when system is coupled at a large value, there exists an optimal interval of the characteristic path length, in which the subthreshold signal could be detected efficiently.

4 Summary

Effects of coupling strength and network topology on signal detection in a small-world neuronal network are numerically studied. Through numerical stimulations, multiple stochastic resonance can be found with increasing of coupling strength. It indicates that subthreshold signal can be amplified under more than one coupling strengths as noise intensity is fixed at an appropriate level. Moreover, effects of network topology on signal detection are also studied when the neuronal networks are coupled with weak, medium and

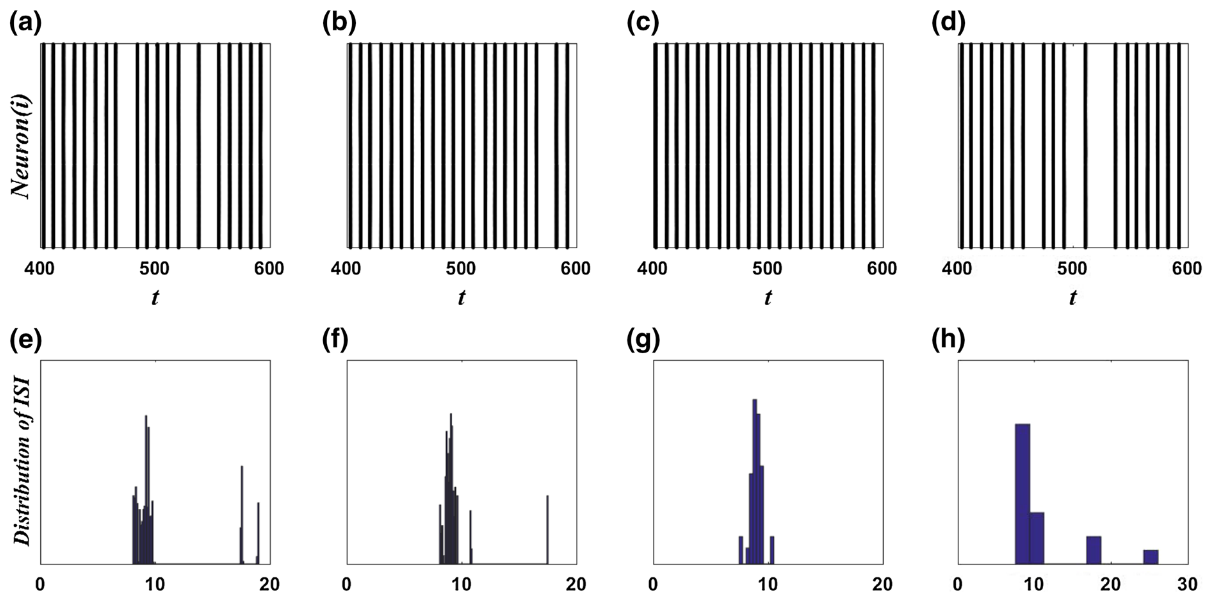

Fig. 12 Time-space plots and the distribution of ISI (Inter-spike-interval) with four independent random seeds. When the coupling strength $g = 1.2$ and $D = 0.04$

large coupling strengths. When neurons are weakly coupled, network topology has no significant influences on signal detection of neuronal network. When neurons are coupled with some intermediate coupling strengths, the ability of detecting subthreshold signal could be enhanced by tuning k and the rewiring probability p if the corresponding characteristic path length L is short. Finally, when neurons are coupled strongly, an optimal interval of the characteristic path length of the network is revealed, within this interval the neuronal network detects the subthreshold signal efficiently. Due to the importance of interaction between neurons and the topology of neuronal network mentioned in the introduction, we hope that the obtained results could shed lights on the efficiency of signal detection in biology neuronal network.

5 Appendix

In Sect. 3.1, we exhibit the firing pattern of three values of coupling strength, we try to explain the reason why we do not choose $g \approx 1.2$ which corresponds to the second peak of Q in this section. In Fig. 2, to ensure the statistical accuracy, we run 10 times of independent realizations using different random seeds of generating noise and averaging the values of Fourier coefficient Q. In Fig. 10, we exhibit the ten curves of Q as a function of g using different random seeds, from which we can see that the tendency is obviously the same as the curve in Fig. 2. But with increasing of coupling strength g (for approximately $g > 1.0$), the curve is quite sensitive to the random seeds. Moreover, the mean value of *ISIs* is calculated as a function of coupling strength g as exhibited in Fig. 11. As shown in this figure, $\langle ISI \rangle$ fluctuates largely when $g > 1.0$. Then, we can image that firing patterns could be quite different for different random seeds. Take $g = 1.2$ for an example, as exhibited in Fig. 12, the firing patterns and the distribution of *ISIs* are presented for four randomly chosen seeds. In Fig. 12a, b, there exists some irregular spiking in firing pattern and a large part of *ISIs* concentrate around 9 and a small part concentrate around 18. In Fig. 12c, the firing patterns are quite regular and *ISIs* concentrate around 9. While for fourth random seed, the firing pattern is irregular again and *ISIs* are distributed in a much wide range and concentrate round 9, 18 and 27. Then, we can see that there are different patterns with different random seeds in this case. Thus, to weaken the influence of randomness, we set coupling strength g be smaller than 1.0 when effects of network topology on the ability of detecting subthreshold signal of the neuronal networks are investigated.

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Compliance with ethical standards

Conflict of interest We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

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