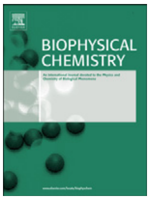
Biophysical Chemistry 144 (2009) 88–93

Contents lists available at ScienceDirect

Biophysical Chemistry

journal homepage: http://www.elsevier.com/locate/biophyschem



Non-Gaussian noise optimized spiking activity of Hodgkin–Huxley neurons on random complex networks

Yubing Gong [*], Yinghang Hao, Yanhang Xie, Xiaoguang Ma, Chuanlu Yang

School of Physics and Electronic Engineering, Ludong University, Yantai, Shandong 264025, PR China

ARTICLE INFO

Article history:
Received 17 June 2009
Received in revised form 2 July 2009
Accepted 2 July 2009
Available online 10 July 2009

Keywords:
Non-Gaussian noise
Neuron
Random complex networks
Spike coherence and synchronization
Stochastic dynamics

ABSTRACT

In this paper, we numerically study how the NGN's deviation q from Gaussian noise ($q=1$) affects the spike coherence and synchronization of 60 coupled Hodgkin–Huxley (HH) neurons driven by a periodic sinusoidal stimulus on random complex networks. It is found that the effect of the deviation depends on the network randomness p (the fraction of random shortcuts): for larger p ($p>0.15$), the spiking regularity keeps being improved with increasing q; while, for smaller p ($p<0.15$), the spiking regularity can reach the best performance at an optimal intermediate q value, indicating the occurrence of "deviation-optimized spike coherence". The synchronization becomes enhanced with decreasing q, and the enhancing extent for a random HH neuron network is stronger than for a regular one. These behaviors show that the spike coherence and synchronization of the present HH neurons on random networks can be more strongly enhanced by various other types of external noise than by Gaussian noise, whereby the neuron firings may behave more periodically in time and more synchronously in space. Our results provide the constructive roles of the NGN on the spiking activity of the present system of HH neuron networks.

1. Introduction

Since the pioneering study of firing dynamics of neurons by Hodgkin and Huxley (HH) [1], numerous works have been contributed to the effect of noise on the generation and propagation of the action potential in deterministic and stochastic HH neurons. Noise arises from both extrinsic (e.g., synapses) and intrinsic (e.g., channels) sources. Stochastic resonance (SR) and coherence resonance (CR) due to external noise in a deterministic HH neuron and related models of excitable dynamics has extensively been studied [2–8], and a great number of works have been contributed to the effect of channel noise on the firing dynamics in stochastic HH neurons [9–30]. Since information processing and signal transduction in neurons is fulfilled via coupled neurons and complex neuron networks, noisy dynamics of these systems have received considerable attention [29,30].

In all previous works, external or internal noise for the HH neuron is usually assumed to be of Gaussian behavior. However, experimental results for one kind of crayfish [3] and for rat skin [31] offer strong indications that there could be non-Gaussian noise sources in these sensory systems. This fact gives strong support to the study of the effect of non-Gaussian noise within biological systems. Over the last decade, a particular kind of non-Gaussian noise (NGN) have been widely studied in various nonlinear dynamical systems of physics, chemistry, and biology [32–44]. The non-Gaussianity of the NGN is characterized simply by a parameter q that measures the deviation from Gaussian noise ($q=1$) and determines the probability distribution of the noise. Thus, such a particular form allows one to easily control the deviation from the Gaussian behavior by changing a single parameter q. These facts allow us to apply the NGN to the HH neurons and study how it affects the neuron firings. Very recent study shows that the NGN can enhance spike coherence by inducing CR in an array of bi-directionally coupled HH neurons [45].

It is well known that a single neuron in the vertebrate cortex connects to more than 10,000 postsynaptic neurons via synapses, forming complex networks [46]. Therefore, adding a number of long-range shortcuts among them is reasonable and feasible. The dynamics of coupled HH neurons on complex networks have gained much interest [30,47–54]. Two important dynamical phenomena, regarding the effects of random connectivity of networks, are the enhancement of temporal coherence and the spatial synchronization of action potentials [47,48]. Coherence and synchronization of coupled excitable neurons may elucidate how the coherent spontaneously synchronized oscillations observed in the brain cortex are established in many neuronal systems [49–51]. The study of dynamics of coupled HH neurons on small-world networks (SWN) has shown that random topologies give rise to fast response, if regular networks produce coherent oscillations on a slow time scale. Furthermore, random topology may speed the synchronization of neuron firings by taking advantage of a few long-range shortcuts [52]. Since the structural properties of complex networks, for example, the characteristic path length $L(p)$ and clustering coefficient $C(p)$ in SWN, vary together with p, the fraction of random shortcuts, the effect of p on the dynamics of complex networks has attracted increasing

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[*] Corresponding author. Tel.: +86 535 6697550.
E-mail address: ybgong63@hotmail.com (Y. Gong).

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doi:10.1016/j.bpc.2009.07.001

attention. An increase of p leads to an enhancement of coherence resonance (CR) and synchronization of neuron firings [53], and there is an optimal p for which the temporal coherence of the spikes of coupled neurons on complex networks achieves the best performance [30,54].

In this paper, we numerically study the effect of the NGN, especially the deviation q from Gaussian noise ($q=1$), on the spiking regularity and spatial synchronization of the HH neurons on random complex networks. Our results show that the effect of deviation q depends on the network randomness p. For smaller p (e.g., $p<0.15$), the spiking regularity becomes better with increasing q and reaches the best performance at an optimal q value, which indicates the occurrence of "deviation-optimized spike coherence"; while for larger p (e.g., $p>0.15$), the spiking regularity keeps being improved with increasing q. On the other hand, the synchronization of the HH neurons becomes enhanced with decreasing q, and the enhancing extent for the neurons on a random network is stronger than on a regular one.

2. Model and equations

According to the HH neuron model, the ion current across the biological membrane is carried mainly by the motion of sodium (Na^+) and potassium (K^+) ions through selective and voltage-gated ion channels embedded across the membrane. In addition, there is a leakage current present that is associated with other ions. The gating dynamics of each ion channel depends on four independent gates, each of which can switch between an open and a closed conformation. Consequently, in the presence of a sub-threshold periodic stimulus $I=6.0+\sin(0.3t)$, the noisy dynamics of the membrane potential of the HH neuron is given by

$$C\frac{dV}{dt} = -g_{\mathrm{Na}}^{\max}m^3h(V-V_{\mathrm{Na}}) - g_{\mathrm{K}}^{\max}n^4(V-V_{\mathrm{K}}) - G_{\mathrm{L}}(V-V_{\mathrm{L}}) + I(t) + \xi(t) \tag{1a}$$

$$\frac{dm}{dt} = \alpha_m(V)(1-m) - \beta_m(V)m, \tag{1b}$$

$$\frac{dh}{dt} = \alpha_h(V)(1-h) - \beta_h(V)h, \tag{1c}$$

$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n, \tag{1d}$$

with voltage-dependent transition rates:

$$\alpha_m(V) = \frac{0.1(V+40)}{1-exp[-(V+40)/10]}, \tag{2a}$$

$$\beta_m(V) = 4exp[-(V+65)/18], \tag{2b}$$

$$\alpha_h(V) = 0.07exp[-(V+65)/20], \tag{2c}$$

$$\beta_h(V) = \{1+exp[-(V+35)/10]\}^{-1}, \tag{2d}$$

$$\alpha_n(V) = \frac{0.01(V+55)}{1-exp[-(V+55)/10]}, \tag{2e}$$

$$\beta_n(V) = 0.125exp[-(V+65)/80]. \tag{2f}$$

Here, V denotes the deviation of the membrane potential of the neuron from its equilibrium state, and $C=1$ μFcm^{-2} is the membrane capacity. $g_{\mathrm{Na}}^{\max}=120$ mS cm^{-2}and $g_{\mathrm{K}}^{\max}=36$ mS cm^{-2} are the maximal sodium and potassium conductance, respectively. $V_{\mathrm{Na}}=50$ mV, $V_{\mathrm{K}}=-77$ mV, and $V_{\mathrm{L}}=-54.4$ mV are the reversal potentials for the sodium, potassium, and leakage currents. The leakage conductance here is assumed to be constant, $G_{\mathrm{L}}=0.3$ mS cm^{-2}. The gating variables m, h, and n describe the mean ratios of the open gates of the working channels [17], and the factors n^4 and m^3h are the mean portions of the open ion channels within the membrane patch. In the model, $\xi(t)$ in Eq. (1a) is assumed to be a non-Gaussian colored noise and have a particular form as [32–44]

$$\frac{d\xi(t)}{dt} = -\frac{1}{\tau}\frac{d}{d\xi}V_q(\xi) + \frac{\sqrt{2D}}{\tau}\Gamma(t) \tag{3a}$$

and

$$V_q(\xi) = \frac{D}{\tau(q-1)}ln\left[1+\frac{\tau}{D}(q-1)\frac{\xi^2}{2}\right], \tag{3b}$$

where $\Gamma(t)$ is Gaussian white noise with zero mean and auto-correlation function $\langle\Gamma(t)\Gamma(t')\rangle=\delta(t-t')$, D and τ are parameters related to the noise intensity and the correlation time; q stands for the deviation from the Gaussian behavior.

Theoretical analysis shows that the stationary probability distribution has the form [36]:

$$P_q^{st}(\xi) = \frac{1}{Z_q}\left[1+\frac{\tau}{D}(q-1)\frac{\xi^2}{2}\right]^{\frac{1}{1-q}}, \tag{4}$$

where Z_q is the normalization factor. This distribution can be normalized only for $q<3$. The first moment is always equal to zero $\langle\xi\rangle=0$, and the second moment $\langle\xi^2\rangle=2D/[\tau(5-3q)]$ is finite only for $q<5/3$. Furthermore, for $q<1$, the distribution has a cut-off and it is only defined for $|\xi|<\xi_c\equiv\sqrt{2D/[\tau(1-q)]}$. The effective noise intensity $D_q=[2(2-q)/(5-3q)]^2\,D$ and the effective correlation time $\tau_q=2(2-q)\tau/(5-3q)$ of $\xi(t)$ diverge near $q=5/3$. Thus, the value of q to be used in our simulations will be restrained $q<5/3$.

The random neural network herein is constructed as follows [30,54]: We start with a regular ring which comprises $N=60$ identical HH neurons. Each neuron has two nearest neighbors. Links are then randomly added between non-nearest vortices. In the limit case, when all neurons are coupled to each other, the network contains $N(N-1)/2$ edges. Using M to denote the number of added random shortcuts, then the fraction of random shortcuts (randomness) reads $p=M/[N(N-1)/2]$, which is chosen as the control parameter herein. One should note that for a given p a lot of network realizations exist.

The dynamics of the membrane potential of the coupled deterministic HH neurons on the random complex networks can be described by

$$C\frac{dV_i}{dt} = -g_{\mathrm{Na}}^{\max}m_i^3h_i(V_i-V_{\mathrm{Na}}) - g_{\mathrm{K}}^{\max}n_i^4(V_i-V_{\mathrm{K}}) - G_{\mathrm{L}}(V_i-V_{\mathrm{L}}) + I(t) + \xi_i(t) + \sum_j \varepsilon_{ij}\left(V_j-V_i\right), \tag{5a}$$

and

$$\frac{dx_i}{dt} = \alpha_{x_i}(V_i)(1-x_i) - \beta_{x_i}(V_i)x_i, \tag{5b}$$

where $x=m$, h, n and $1\le i\le N$, with N being the number of neurons, and ε_{ij} is the coupling strength between the two neurons i and j, which is determined by the coupling pattern of the system. If neuron i and j are connected, they have coupling strength $\varepsilon_{ij}=0.1$; otherwise the coupling strength is $\varepsilon_{ij}=0$.

Numerical integration of Eqs. (5a) and (5b) is carried out by the explicit forward Euler algorithm with a time step 0.001 ms. Periodic boundary conditions (i.e., the first neuron connects to the 60th neuron) are used and the parameter values for all the neurons are identical except for the noise terms $\xi_i(t)$. The collective behavior of the neurons is

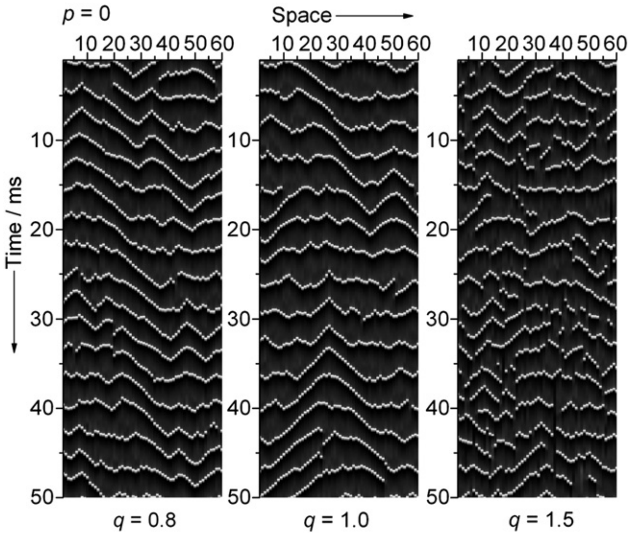

Fig. 1. Spatio-temporal patterns of the membrane potentials V_i of the HH neurons on regular ring ($p=0$). The spiking regularity and synchronization for a smaller q value is better than those for a larger one. The voltage scale is from -80 to 40 mV.

defined as the average membrane potential $V_{\mathrm{ave}}(t)=\frac{1}{N}\sum_{i=1}^{N}V_i(t)$. We use the coefficient of variation $(CV)\lambda_C$ and λ_S to quantitatively characterize the collective spike coherence in the coupled neurons and the spike coherence in any averaged individual neuron of the coupled neurons, respectively. λ_C is defined as

$$\lambda_C=[\lambda]\text{ with }\lambda=\frac{\langle T\rangle}{\sqrt{\langle T^2\rangle-\langle T\rangle^2}},\tag{7}$$

where [•] denotes the average over 50 different network realizations for each p. $\langle T\rangle=\frac{1}{N'}\sum_{i=1}^{N'}(t_{i+1}-t_i)$ and $\langle T^2\rangle=\frac{1}{N'}\sum_{i=1}^{N'}(t_{i+1}-t_i)^2$ are the mean and mean-squared inter-spike interval, respectively, and t_i is the time of the ith spike in the time series of $V_{\mathrm{ave}}(t)$, and N' is the number of collective spikes. A collective spike occurs when the state variable $V_{\mathrm{ave}}(t)$ crosses a certain threshold value from below, and it turns out that the threshold value can vary in a wide range without altering the resulting spiking dynamics. Unlike the firing of a single neuron, the collective (averaged) spike train does not show “all-or-nothing” behavior and change its spiking form with the varying system's conditions. Therefore, the appropriate change in threshold value will vary the quantitative behavior, but will not vary the qualitative behavior of the spikes. For the collective spikes under study, it is most appropriate to choose $V_{\mathrm{ave}}(t)=0$ as the threshold value. λ_S is defined as:

$$\lambda_S=\frac{1}{N}\sum_{i=1}^{N}\lambda_i,\text{ with }\lambda_i=\frac{\langle T'\rangle}{\sqrt{\langle T'^2\rangle-\langle T'\rangle^2}}\tag{8}$$

where N is the neuron number, $\langle T'\rangle=\frac{1}{N''}\sum_{i=1}^{N''}(t_{i+1}-t_i)$ and $\langle T'^2\rangle=\frac{1}{N''}\sum_{i=1}^{N''}(t_{i+1}-t_i)^2$ are the mean and mean-squared inter-spike interval, respectively, and t_i is the time of the ith spike in the time series of $V_i(t)$, and N'' is the number of the spikes in an individual neuron. λ_i and λ_S characterize the spike coherence of an individual neuron and of an averaged individual neuron. The detection threshold for the occurrence of a spike is $V_i(t)=0$. Larger values of λ_C or λ_S means better spiking regularity.

The spatial synchronization of the firings of the neurons is characterized by the standard deviation σ defined as:

$$\sigma=[\langle\sigma(t)\rangle]\text{ with }\sigma(t)=\sqrt{\frac{\frac{1}{N}\sum_{i=1}^{N}V_i(t)^2-\left(\frac{1}{N}\sum_{i=1}^{N}V_i(t)\right)^2}{N-1}},\tag{9}$$

where ⟨•⟩ denotes the average over time and [•] the average over 50 different network realizations for each p. The value of $\sigma(t)$ measures the spatial synchronization of neurons' spikes at a fixed time t. Large values of $\sigma(t)$ represents large deviation between the neurons, and small values of $\sigma(t)$ shows good synchronization.

3. Result and discussion

Throughout this work, we choose $\tau=1.0$, $D=5\times10^{-5}$. For a regular network of neurons ($p=0$), increasing q leads to bad spiking regularity. In Fig. 1, the spatio-temporal patterns for different q values are presented. It is clearly shown that the spiking regularity becomes better with decreasing q. Specifically, the spiking regularity for $q=0.8$ is better

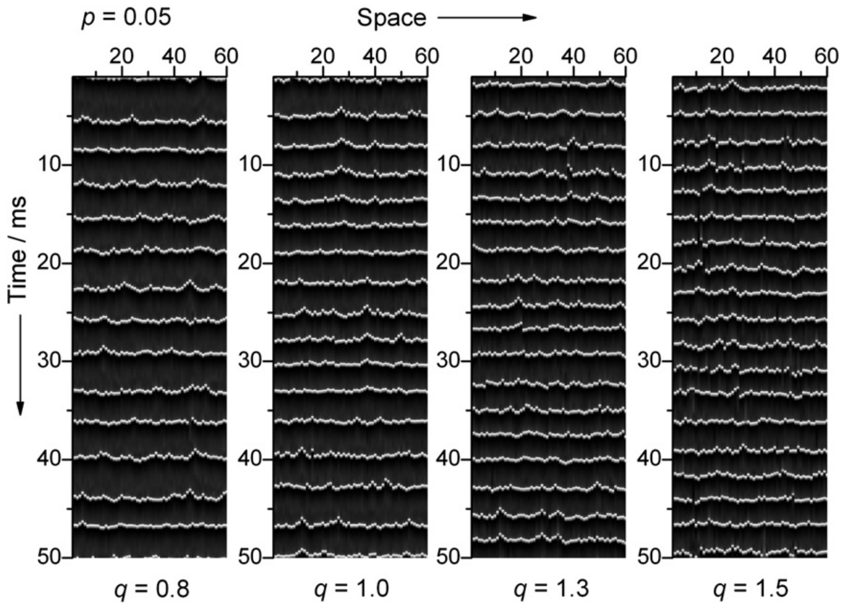

Fig. 2. Spatio-temporal patterns of V_i for different q values when $p=0.05$. The spiking regularity for intermediate q (e.g., $q=1.3$) is better than the others. The voltage scale is the same as in Fig. 1.

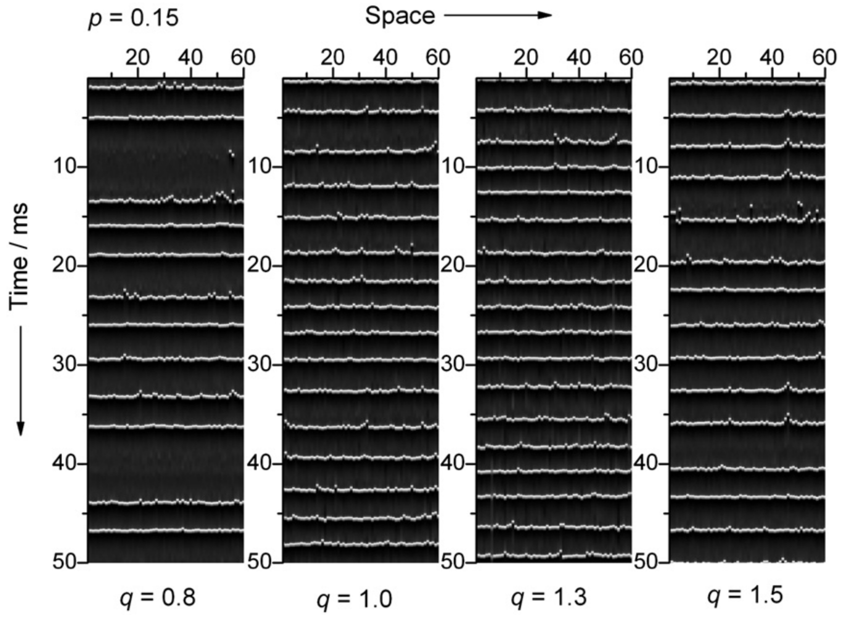

Fig. 3. Same as the caption to Fig. 2 except $p = 0.15$. The voltage scale is the same as in Fig. 1.

than that for $q = 1.0$, which represents the enhancement of the spiking regularity by the NGN. For random HH neuron networks, the effect of q depends on the value of p, the number of randomly added links. The spatio-temporal patterns for $p = 0.05, 0.15, 0.25$ are displayed in Figs. 2, 3, and 4, respectively. One can see from Fig. 4 that for $p = 0.25$, the spiking regularity keeps being improved with increasing q, and reaches the best performance at $q = 1.5$, the largest value in the proper range of q values chosen in this work. While, it can be seen from Figs. 2 and 3 that for $p = 0.05$ and 0.15, the spiking regularity first becomes better with increasing q, arriving at the best performance at an intermediate q ($q = 1.3$), but then becomes poorer as q is further increased ($q = 1.5$). These behaviors show that for the HH neuron networks with larger p, the spiking regularity becomes enhanced with increasing q, but for the networks with smaller p, the spiking regularity can be optimized by appropriate intermediate q values.

The values of λ_C and λ_S, characterizing the collective spike coherence for all the neurons and the spike coherence for an individual neuron on networks, respectively, are plotted as functions of p for different values of q in Figs. 5 and 6, respectively. It is seen from Fig. 5 that there is always a maximal λ_C value appearing at around $p = 0.15$, presenting the optimal collective spike coherence with respect to p. Interestingly, for a given p (≥ 0.15), λ_C increases with increasing q, representing improved collective spiking regularity. However, the spike coherence for an individual neuron changes with varying q in a different way. It is seen from Fig. 6 that for a given q (with exception of $q = 1.5$) the maximal λ_S value appears at around $p = 0.05$; for a given p (<0.15), the maximal λ_S value appears at an intermediate value of q, representing q-optimized spiking regularity. This coincides with the space-time plot shown in Figs. 2 and 3, where the spatio-temporal patterns for $q = 1.3$ are the most regular. This

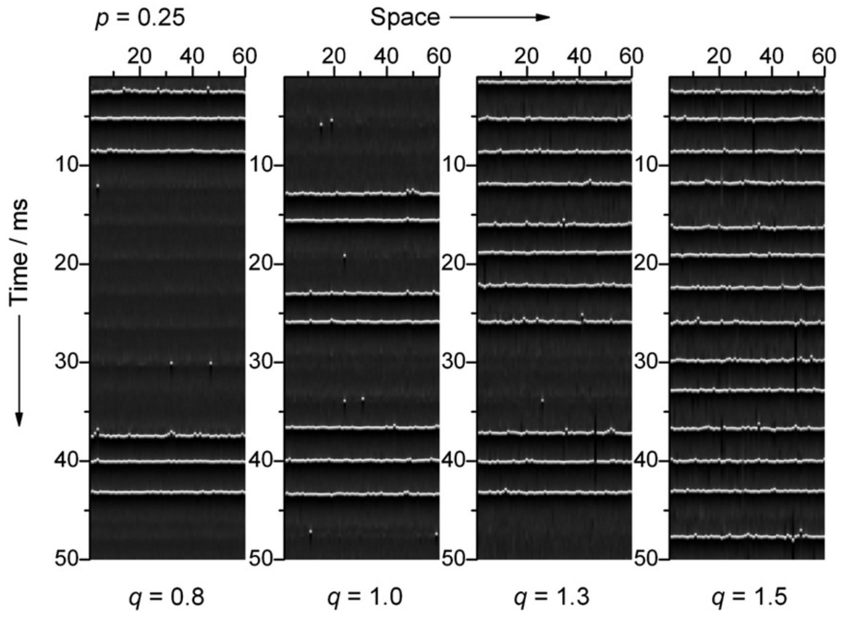

Fig. 4. Spatio-temporal patterns of V_i for different q values when $p = 0.25$. The spiking regularity for larger q is better than those for smaller ones, becoming the best at $q = 1.5$. This means that the spiking regularity for the neuron networks with $p = 0.25$ keeps being enhanced with increasing q value. The voltage scale is the same as in Fig. 1.

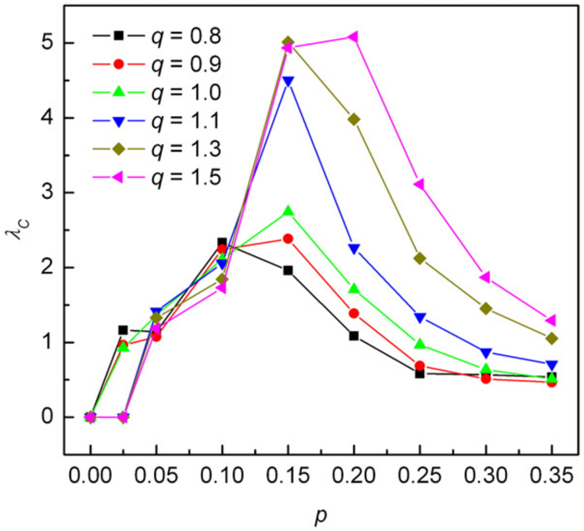

Fig. 5. Dependence of λ_C on p for different q values. For $p>0.15$, λ_C increases with increasing q, representing the enhancement of collective spiking regularity (color online).

means that there is an optimal intermediate value of q at which the spiking regularity can reach the best performance. However, it is also seen from Figs. 5 and 6 that for a given larger p (>0.15), the values of λ_C and λ_S increase with increasing q, indicating the enhancement of the spiking regularity. This quantitatively describes the spatio-temporal patterns shown in Fig. 4.

In Fig. 7, the change of the standard deviation σ is plotted as a function of p. It can be seen that the value of σ decreases with increasing p, representing the enhancement of the synchronization. For a given p, the σ value decreases with decreasing q, which means that for a given network randomness, decreasing q may improve the synchronization of the firings of the neurons. Specifically, the synchronization for $q<1.0$ is better than that for $q=1.0$, which shows that the firings of the neurons may become more synchronous in space under various other types of noise than under Gaussian noise.

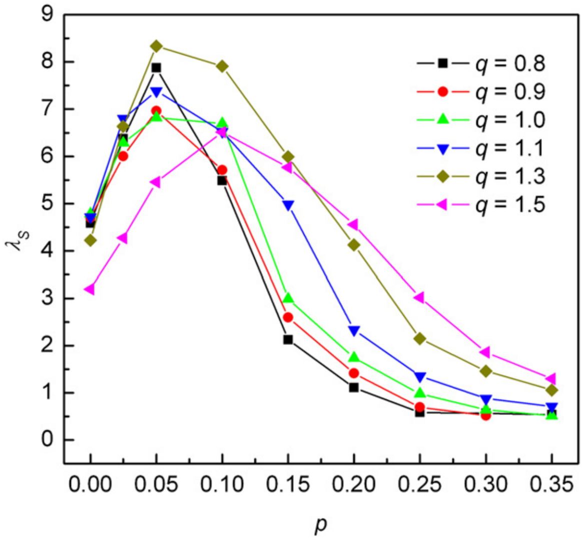

Fig. 6. Dependence of λ_S on p for different q values. When $p>0.15$, λ_S increases with increasing q, but when $p<0.15$, it first increases and then decreases with increasing q. This means that the effect of q on the spiking regularity of the averaged individual neuron depends on the network randomness. For larger p, the spiking regularity becomes better with increasing q, but, interestingly, for smaller p, it will reach the best performance at an optimal q value (color online).

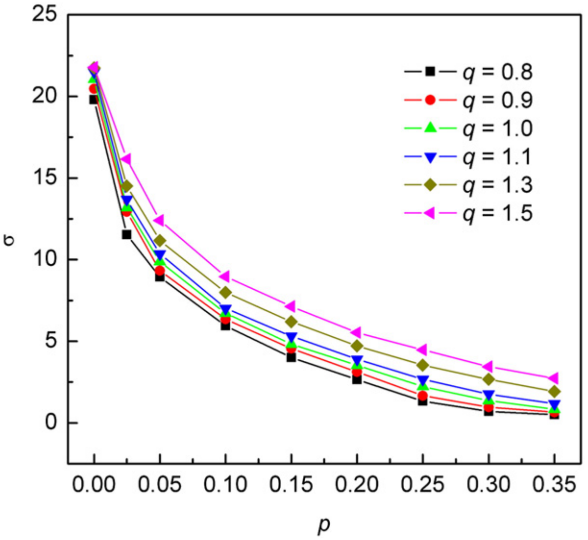

Fig. 7. Dependence of σ on p for different q values. For any a given p value, σ decreases with decreasing q, indicating the enhancement of the synchronization by smaller q. Meanwhile, the decrease of σ with decreasing q for $p=0$ is much smaller than that for $p\neq 0$, representing that the effect of q on the synchronization for the regular neuron network is much smaller than for the random neuron networks (color online).

Taking into account both the effect of q on the spiking regularity and the effect on the synchronization, one can draw a conclusion that the spike coherence and synchronization can be optimized by the NGN with appropriate deviation q.

The above evolutions of λ_S and σ with changing q for different p values reflect the dependence of neuron firings on the deviation of the NGN and the number of coupled neurons. As seen in the theoretical analysis of $\xi(t)$, the deviation q determines the probability distribution $P_q^{st}(\xi)$ and the effective noise intensity via $D_{\text{eff}}=[2(2-q)/(5-3q)]^2 D$. As q is increased, the width of $P_q^{st}(\xi)$ grows and high values of $\xi(t)$ become more frequent, thus the value of D_{eff} increases. On the other hand, the value of p determines the number of coupled neurons and increasing p means the increase of the number of neurons. More neurons would require bigger noise strength to fire collectively. Therefore, when q and p are appropriate or optimal, the neuron firings will become more or most regular. However, when q is small but p is large, low values of $\xi(t)$ become frequent and they are insufficient for more coupled neurons to produce regular firings; while when q is large and p is small, $\xi(t)$ becomes so strong that it may dominate the firings of the fewer coupled neurons and make them chaotic, and hence the firings become deteriorated, even destroyed.

The enhancement of the synchronization may also be related to the q-dependent noise intensity. In general, the synchronization varies with changing noise intensity, and will become improved when noise intensity becomes smaller. Since the effective noise intensity decreases with decreasing q, thus the coupled neurons may exhibit more synchronous firings under smaller q ($q<1$) values.

4. Conclusions

We have numerically studied the effect of the deviation q of the NGN from Gaussian noise ($q=1$) on the spiking activity of the HH neurons on random complex networks. It is found that for the networks with larger randomness p ($p>0.15$), the temporal spiking regularity keeps being enhanced with increasing q. While, for the networks with smaller p ($p<0.15$), there is an optimal q at which the firings of the neurons exhibit the best spiking regularity, indicating the behavior of "deviation-optimized spike coherence". It is also found that the synchronization of the firings of the neurons becomes enhanced with decreasing q value. It is seen from these two effects that the spike coherence and synchronization can be optimized by the NGN with appropriate deviation q.

Since the deviation of the NGN determines the probability distribution and hence may denote the type of the noise, the phenomenon of deviation-optimized spike coherence and synchronization show that various other types of external noise ($q \neq 1$), rather than Gaussian noise ($q = 1$), can more strongly enhance the spiking regularity and synchronization of the HH neurons on the random complex networks, by which the neurons may behave more periodically in time and more synchronously in space. Our results provide the constructive roles of the NGN on the spiking activity of the HH neurons on random networks under study.

Acknowledgement

The authors acknowledge the support from the Science Foundation of Ludong University (L20072805).

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