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Effects of channel noise on firing coherence of small-world Hodgkin-Huxley neuronal networks

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Abstract. We investigate the effects of channel noise on firing coherence of Watts-Strogatz small-world networks consisting of biophysically realistic HH neurons having a fraction of blocked voltage-gated sodium and potassium ion channels embedded in their neuronal membranes. The intensity of channel noise is determined by the number of non-blocked ion channels, which depends on the fraction of working ion channels and the membrane patch size with the assumption of homogeneous ion channel density. We find that firing coherence of the neuronal network can be either enhanced or reduced depending on the source of channel noise. As shown in this paper, sodium channel noise reduces firing coherence of neuronal networks; in contrast, potassium channel noise enhances it. Furthermore, compared with potassium channel noise, sodium channel noise plays a dominant role in affecting firing coherence of the neuronal network. Moreover, we declare that the observed phenomena are independent of the rewiring probability.

1 Introduction

In neuronal systems, information processing usually takes place in a noisy environment. Noise in neuronal system arises from many different sources, such as the quasi-random release of neurotransmitters by the synapses, random synaptic input from other neurons, and the random switching of ion channels. The first two sources are considered to be synaptic noise, while the last is acknowledged as channel noise. Synaptic noise is believed to be the dominant source of membrane potential fluctuations in neurons and can have a strong influence on their integrative properties [1]. The channel noise, because contributions of the inherently stochastic nature of voltage-gated ion channels to neuronal noise levels are widely assumed to be minimal, is frequently ignored when a large number of ion channels is involved. However, when the number of ion channels is moderate, channel noise may have significant impacts on the neuronal dynamics, as indicated both by experimental [2,3] and theoretical [4,5] studies.

The number of ion channels is determined by two factors, i.e. the channel density and the size of the membrane patch. Furthermore, the intensity of channel noise is mainly determined by the number of working ion channels participating in the generation of action potentials. Therefore, discussing the effects of the number of working ion channels on the neuronal dynamics can help us

to reveal the role of channel noise in neuronal systems. Experimentally, for a given membrane patch size, toxins such as tetrodotoxin (TTX) and tetraethylammonium (TEA) allow to reduce the number of working sodium or potassium ion channels, respectively [6]. It is also possible to examine the effects of changing the number of specific working ion channels on neuronal dynamics based on computational models. In this context, Schmid et al. [7,8] discussed the spiking activity of a single stochastic Hodgkin-Huxley (HH) model. They found that the spiking regularity of the single stochastic HH neuron can be increased or decreased by blocking some portion of either potassium or sodium ion channels. Then, Gong et al. [9] extended the works of Schmid et al. [7,8] by studying collective spiking regularity of an array of bidirectionally coupled stochastic HH neurons. Through numerical simulations, they found that sodium or potassium ion channel blocking can either enhance or reduce the collective spiking regularity. Additionally, Lago-Fernández et al. [10] investigated the role of different connectivity regimes on the dynamics of a network of HH neurons. They showed that in order to provide fast response, which is characteristic of random topologies, and coherence oscillations, which are more evident in regular topologies, a small-world (SW) topology is required. Thus, SW topology is a very important and meaningful network structure in neuronal systems. Considering this, Ozer et al. [11] extended the works of Schmid et al. [7,8] and Gong

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et al. [9] by using Newman-Watts SW network models as the underlying interaction topology between neurons, and showed that there exists an optimal faction of short-cut links between physically distant neurons, as well as an optimal intensity of intrinsic noise, which warrant an optimal collective spiking regularity.

As we know, SW networks have two distinct characteristics, one is that the normalized characteristic path length between nodes is small (i.e. comparable with that of a random network), and the other is that the normalized clustering coefficient is still large (i.e. comparable with that of a regular lattice). Watts-Strogatz [12] and Newman-Watts [13] models are two typical models of SW networks. These two types of SW network models can be generated from a ring lattice with connections between neighbors. For Watts-Strogatz models, the final topology is achieved by rewiring each link at random with a probability p, resulting in either a regular ($p = 0$), random ($p = 1$) or SW networks ($0 < p < 1$) [12]. While for Newman-Watts models, the random links are added between pairs of non-adjacent-vertices chosen at random [13]. Thus, we can see that Watts-Strogatz model has the same number of connections as the original network, while the new long-range random edges added in Newman-Watts model increase the total number of connections from that of the original network.

Our aim in this paper is to further extend the study about the impact of ion channels on neuronal dynamics by using Watts-Strogatz models as the network topology and studying firing coherence of the neuronal network instead of collective spiking regularity [9,11]. In fact, we investigate the effects of ion channel noises on firing coherence of a Watts-Strogatz SW neuronal network by controlling the fractions of working sodium or potassium ion channels, and the membrane patch size. We thus proceed with presenting the mathematical model and the network topology presently in use. Subsequently we describe the main results and summarize the paper.

2 Neuronal network model

HH neurons have been frequently employed as local neuronal models in discussing the dynamics of neuronal systems [7–11,14–22]. In this paper, we also apply HH neurons, but a stochastic version of them, to build up a neuronal network. The stochastic HH neuronal model is an extension of the original HH model [23] by taking into account the fluctuations of the numbers of open sodium and potassium ion channels around the corresponding mean value [24,25]. The dynamics of the studied neuronal network is described by the following set of ordinary differential equations:

$$C\frac{dV_i}{dt} = -G_{\mathrm{Na}}(m_i, h_i)(V_i - V_{\mathrm{Na}}) - G_{\mathrm{K}}(n_i)(V_i - V_{\mathrm{K}})$$
$$- G_{\mathrm{L}}(V_i - V_{\mathrm{L}}) + D\sum_j \varepsilon_{ij}(V_j - V_i), \quad (1)$$

$$\frac{dm_i}{dt} = \alpha_{m_i}(V_i)(1 - m_i) - \beta_{m_i}(V_i)m_i + \xi_{m_i}(t), \quad (2)$$

$$\frac{dh_i}{dt} = \alpha_{h_i}(V_i)(1 - h_i) - \beta_{h_i}(V_i)h_i + \xi_{h_i}(t), \quad (3)$$

$$\frac{dn_i}{dt} = \alpha_{n_i}(V_i)(1 - n_i) - \beta_{n_i}(V_i)n_i + \xi_{n_i}(t), \quad (4)$$

where $1 \le i \le N$, with N being the system size. $C = 1\ \mu\mathrm{F\,cm}^{-2}$ is the capacity of the cell membrane, and $V_{\mathrm{Na}} = 50.0$ mV, $V_{\mathrm{K}} = -77$ mV and $V_{\mathrm{L}} = -54.4$ mV are the reversal potentials for the sodium, potassium and leakage currents, respectively. While the leakage conductance is assumed to be constant, $G_{\mathrm{L}} = 0.3$ mS cm^{-2}, the potassium and sodium conductance read as follows

$$G_{\mathrm{Na}}(m_i, h_i) = g_{\mathrm{Na}}^{max} x_{\mathrm{Na}} m_i^3 h_i, \quad G_{\mathrm{K}}(n_i) = g_{\mathrm{K}}^{max} x_{\mathrm{K}} n_i^4, \quad (5)$$

where $g_{\mathrm{K}}^{max} = 36$ mS cm^{-2} and $g_{\mathrm{Na}}^{max} = 120$ mS cm^{-2} denote the maximal conductance (when all the channels are open). The factor x_{K} and x_{Na} ($0 \le x_{\mathrm{K}}, x_{\mathrm{Na}} \le 1$) are the fractions of working, i.e. non-blocked ion channels, to the overall number of potassium and sodium ion channels [24], respectively. x_{Na} and x_{K} are assumed to be equal for all the neurons, i.e. each neuron has the same number of non-blocked sodium or of non-blocked potassium ion channels. D is the coupling strength of electrically coupled term $\sum_j \varepsilon_{ij}(V_j - V_i)$, and assumed to be constant. D is taken as 1.0 throughout this paper. The coupling matrix element $\varepsilon_{ij} = 1$ if neurons i and j are connected, and zero otherwise. Here the coupling matrix is assumed to be symmetric, i.e., $\varepsilon_{ij} = \varepsilon_{ji}$ ($i, j = 1, \dots, N$).

Equations (2)–(4) show the variations of the gating variables m_i, h_i and n_i, which represent the fractions of sodium channel activation, sodium channel inactivation and potassium channel activation, respectively. And $\alpha_{y_i}(V_i)$ and $\beta_{y_i}(V_i)$ ($y_i = m_i, h_i, n_i$) are the voltage-dependent transition rates, which are given explicitly by the expressions [23]:

$$\alpha_{m_i}(V_i) = \frac{0.1(V_i + 40)}{1 - \exp\left[-\dfrac{(V_i + 40)}{10}\right]}, \quad (6a)$$

$$\beta_{m_i}(V_i) = 4.0\exp\left[-\frac{(V_i + 65)}{18}\right], \quad (6b)$$

$$\alpha_{h_i}(V_i) = 0.07\exp\left[-\frac{(V_i + 65)}{20}\right], \quad (6c)$$

$$\beta_{h_i}(V_i) = \left\{1 + \exp\left[-\frac{(V_i + 35)}{10}\right]\right\}^{-1}, \quad (6d)$$

$$\alpha_{n_i}(V_i) = \frac{0.01(V_i + 55)}{1 - \exp\left[-\dfrac{(V_i + 55)}{10}\right]}, \quad (6e)$$

$$\beta_{n_i}(V_i) = 0.125\exp\left[-\frac{(V_i + 65)}{80}\right]. \quad (6f)$$

Moreover, $\xi_{m_i}(t), \xi_{h_i}(t), \xi_{n_i}(t)$ are the channel noises. Here, we assume that they are independent and have statistical properties of Gaussian white noise. The first-order
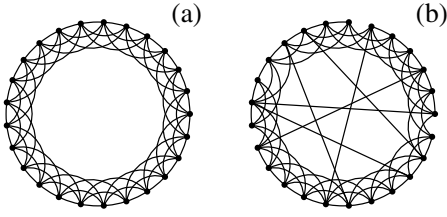
Fig. 1. Examples of considered network topologies. For clarity regarding k and p only 25 vertices are displayed in each panel. (a) Regular ring characterized by $p = 0$ with periodic boundary conditions. Each vertex is connected to its $k = 6$ nearest neighbors. (b) Realization of small-world topology via random rewiring of a certain fraction p of links (in this case 6 out of all 150 were rewired, hence $p = 0.04$).

Fig. 2. (Color online) Characteristic path length L and the clustering coefficient C as a function of the rewiring probability p in Watts-Strogatz networks with $N = 100$ and $k = 8$. Displayed values are normalized with the characteristic path length and the clustering coefficient at $p = 0$.

moment $\langle \xi_{m_i}(t) \rangle, \langle \xi_{h_i}(t) \rangle, \langle \xi_{n_i}(t) \rangle$ is set as 0. The noise correlations have the following form:

$$\langle \xi_{m_i}(t)\xi_{m_i}(t') \rangle = \frac{2}{N_{\mathrm{Na}}x_{\mathrm{Na}}} \frac{\alpha_{m_i}(V_i)\beta_{m_i}(V_i)}{\alpha_{m_i}(V_i) + \beta_{m_i}(V_i)} \delta(t - t'),$$
(7a)

$$\langle \xi_{h_i}(t)\xi_{h_i}(t') \rangle = \frac{2}{N_{\mathrm{Na}}x_{\mathrm{Na}}} \frac{\alpha_{h_i}(V_i)\beta_{h_i}(V_i)}{\alpha_{h_i}(V_i) + \beta_{h_i}(V_i)} \delta(t - t'),$$
(7b)

$$\langle \xi_{n_i}(t)\xi_{n_i}(t') \rangle = \frac{2}{N_{\mathrm{K}}x_{\mathrm{K}}} \frac{\alpha_{n_i}(V_i)\beta_{n_i}(V_i)}{\alpha_{n_i}(V_i) + \beta_{n_i}(V_i)} \delta(t - t'), \quad (7c)$$

where N_{Na}, N_{K} indicate the number of sodium and potassium ion channels on an excitable membrane patch, respectively. While the overall numbers of working potassium and sodium ion channels are re-scaled by x_{Na} and x_{K}, respectively, in order to disregard the blocked channels which do not contribute to the channels noise. With an assumption of homogeneous ion channel densities, $\rho_{\mathrm{Na}} = 60~\mu\mathrm{m}^{-2}$ and $\rho_{\mathrm{K}} = 18~\mu\mathrm{m}^{-2}$, the ion channel numbers are given by $N_{\mathrm{Na}} = \rho_{\mathrm{Na}}S$, and $N_{\mathrm{K}} = \rho_{\mathrm{K}}S$, where S is the size of the membrane patch. When S is large the stochastic effects related to the channel noise are negligible due to large numbers of ion channels, and the intrinsic channel noise appearing in equations (2)–(4) for gating variables vanishes. Accordingly, the stochastic model then approaches the deterministic HH version which takes channel-blocks into account in the sodium and potassium conductances [7]. However, when the number of ion channels (or the membrane patch size S) is small, stochastic effects of channel noise could have some significant influences on the neuronal dynamics [3,7–9,11,17–20,26]. Furthermore, numerical integration of equations (1)–(7) is carried out by an explicit Euler method with a time step of 0.001.

Underlying interaction topology for HH neurons is taken as Watt-Strogatz network [12]. The generation of the Watt-Strogatz network starts from a regular ring with periodic boundary conditions comprising N vertices, each vertex bidirectionally connecting to its k nearest neighbors (see Fig. 1a), and subsequently all the existing connections are randomly rewired with probability p (see Fig. 1b). In this paper, N and k are taken as 100 and 8,
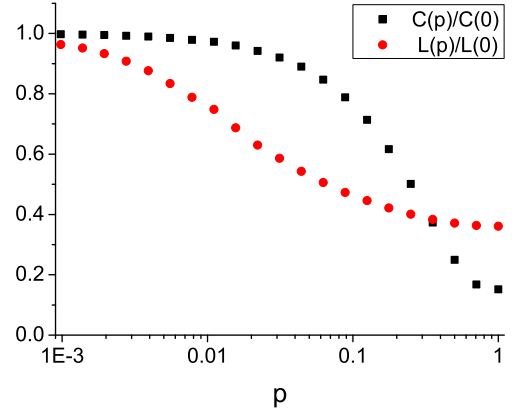
respectively. Considering that the resulting network may not have small-world properties for $0 < p < 1$, we calculate the characteristic path length $L(p)$ and the clustering coefficient $C(p)$ in dependence on the rewiring probability p, as shown in Figure 2. According to Figure 2, we can see that there is an interval $p \in [0.05, 0.1]$, in which the generated networks have prominent small-world properties.

3 Results

In this paper, we aim to discuss the effects of channel noise on firing coherence of the studied neuronal network. Here, we consider sodium and potassium channel noise. As shown by equation (7), the intensity of sodium(potassium) channel noise is determined mainly by the total number of non-blocked channels, which equals $N_{\mathrm{Na}}x_{\mathrm{Na}} = S\rho_{\mathrm{Na}}x_{\mathrm{Na}}$ ($N_{\mathrm{K}}x_{\mathrm{K}} = S\rho_{\mathrm{K}}x_{\mathrm{K}}$). Because $\rho_{\mathrm{Na}}, \rho_{\mathrm{K}}$ are assumed to be constants, thus, we take the fractions $x_{\mathrm{Na}}, x_{\mathrm{K}}$ and the membrane patch size S as control parameters to investigate the effects of channel noise on firing coherence of the studied neuronal network.

The population coherence measure κ is applied to quantify firing coherence of the neuronal network. It is defined as an average of the normalized cross-correlation of all neuron pairs [27–29]. The normalized cross-correlation $\kappa_{ij}(\tau)$ of neuron i and neuron j is defined as

$$\kappa_{ij}(\tau) = \frac{\sum_{l=1}^{m} Y_i(l)Y_j(l)}{\sqrt{\sum_{l=1}^{m} Y_i(l) \sum_{l=1}^{m} Y_j(l)}},$$
(8)

where τ is a time bin, by which a long time interval T is divided into small bins. τ is chosen to make sure that there is no or only one spike in each time bin. $\{Y_i(l),\ l = 1, 2, \ldots, m\}$ (here $m = T/\tau$) is a spiking event

train with $Y_i(l) = 1$ if the onset of a spike occurred at the lth time bin, otherwise $Y_i(l) = 0$. For the currently studied stochastic HH neuron, τ is set as 1 ms. Accordingly, the population coherence measure κ can be expressed as

$$\kappa = \frac{1}{\frac{N(N-1)}{2}} \sum_{i,j=1; i \neq j}^{N} \kappa_{ij}(\tau). \tag{9}$$

We can see that κ is between 0 and 1, and large κ indicates high coherence of the neuronal firings. The measure κ has also been used to quantify synchronization of firing activities of neuronal networks [21,22,30]. Moreover, if the neuronal network does not generate spikes, there is no much meaning in asking questions about firing coherence. Thus, we should calculate the mean firing rate of the studied neuronal network to ensure neurons inside the neuronal network do generate spikes. The mean firing rate of the neuronal network is defined as

$$r = \left\langle \frac{1}{N} \sum_{i=1}^{N} \theta[V_i(t) - V_{th}] \right\rangle_T. \tag{10}$$

$\theta(x)$ is a heaviside function with $\theta(x) = 1$ if $x \geq 0$ and $\theta = 0$ if $x < 0$. The bracket $\langle \rangle$ indicates the average over the whole time span T. $V_{th} = -20.0$ mV is the firing threshold determined by the action potential of HH neuron. And the results presented below were obtained as averages over 10 independent realizations of the network.

Variations of the population coherence measure κ with respect to the fractions of working sodium ion channels x_{Na} are depicted in Figure 3a. Inset shows variations of the mean firing rate r with respect to x_{Na} accordingly. From the inset, we can see that $r = 0$ when $x_{Na} \leq 0.2$ and $r > 0$ when $x_{Na} > 0.2$ for various x_K. This implies that more than 20% sodium ion channels should be involved to excite the currently discussed neuronal network. For $x_{Na} > 0.2$, the population coherence κ increases with x_{Na} increasing from 0.2 to 1.0, as exhibited in Figure 3a. Namely, firing coherence of the neuronal network is enhanced by the fraction of working sodium ion channels x_{Na}. Because the intensity of sodium channel noise decreases as x_{Na} increasing, thus, increasing the intensity of sodium channel noise will make the population coherence decrease. In other words, sodium channel noise reduces firing coherence of the studied neuronal networks. Meanwhile, variations of the population coherence measure κ with respect to the fractions of working sodium ion channels x_K are depicted in Figure 3b. Inset shows variations of the mean firing rate r with respect to x_K accordingly. As shown in Figure 3b, the mean firing rate r and the population coherence κ both decrease with x_K. This means that increasing the intensity of potassium channel noise could increase the coherence of neuronal firings, which is contrary to the above obtained results for sodium channel noise. Thus, with the intensity of channel noise increasing, firing coherence of neuronal networks can be either enhanced or reduced, depending on the source of the channel noise-sodium channel noise reduces the firing coherence while potassium channel noise enhances it.
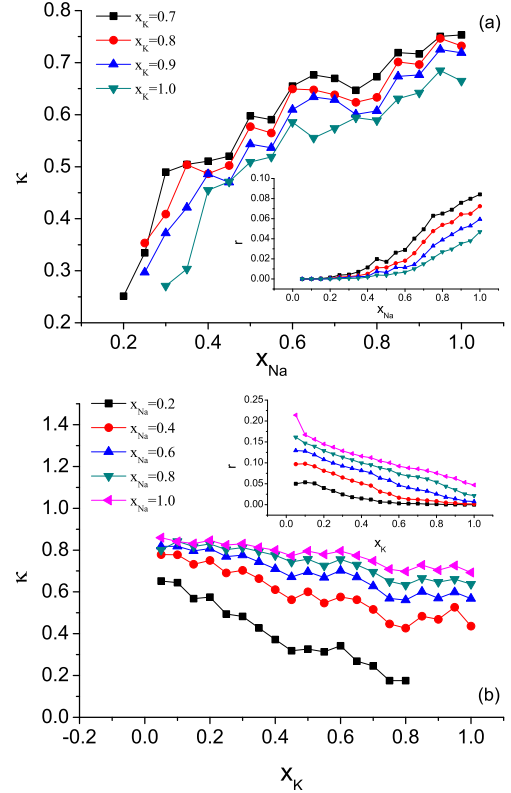

Fig. 3. (Color online) Variations of the population coherence measure κ as a function of the fraction of working sodium ion channels x_{Na} for various values of x_K (a) and potassium ion channels x_K for various values of x_{Na} (b). Insets show variations of the mean firing rate r with respect to x_{Na} (a) and x_K (b). Here the membrane patch size S is taken to be 1.0.

In the following, we discuss effects of membrane patch size S on firing coherence of the studied neuronal network for various x_{Na} with non-blocked potassium channels (i.e., $x_K = 1.0$, shown in Fig. 4a) and various x_K with non-blocked sodium channels (i.e., $x_{Na} = 1.0$, shown in Fig. 4b). From the insets of Figures 4a and 4b, it can be seen that the mean firing rate r decreases to zero when S becomes large enough. Here we discuss the variations of κ with respect to S in the interval $(0, 1]$, within which r is larger than 0, see the insets of Figures 4a and 4b. As shown in equation (7), increasing the membrane patch size S reduces intensities of both sodium and potassium channel noises. According to the results obtained above, reducing sodium channel noise intensity leads to increasing of firing coherence, however, reducing potassium noise intensity results in decreasing of it. Given this competition between these two different effects, it is found that sodium channel noise plays a dominated role and causes an increase in the population coherence with respect to S, see Figure 4.

Finally, in order to investigate whether the obtained results is dependent on the rewiring probability p, we calculate the population coherence κ with respect to x_{Na}, x_K and S for various rewiring probability p, respectively. From Figures 5a–5c, we can see that κ increases with x_{Na}
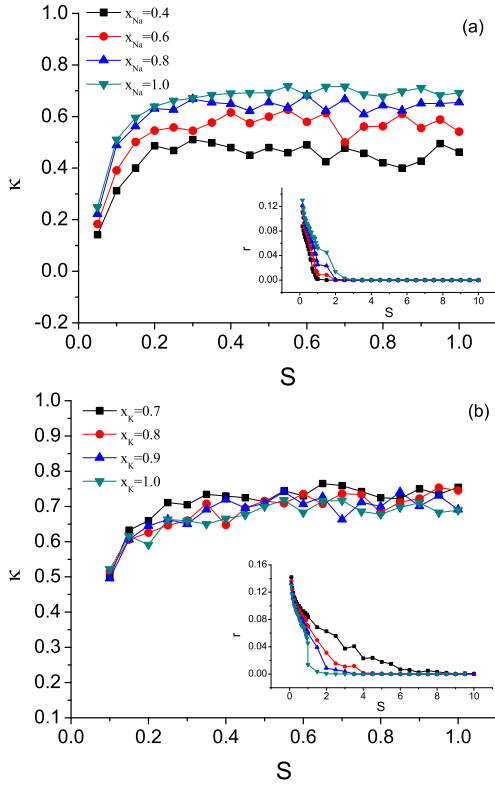
Fig. 4. (Color online) Variations of the population coherence measure κ as a function of the membrane patch size S for various fractions of working sodium ion channels x_{Na} with $x_K = 1.0$ (a) and potassium ion channels $x_K x_{Na} = 1.0$ (b). Insets show variations of the meaning firing rate r with respect to S. Here the rewiring probability p is taken to be 0.05.

and S, while decreases with x_K for various rewiring probability p. This is consistent with the above obtained results: (i) increasing the intensity of sodium channel noise reduces firing coherence of the studied neuronal networks, contrarily, increasing the intensity of potassium channel noise enhances it, see Figures 5a and 5b; (ii) compared with potassium channel noise, sodium channel noise plays a dominant role in affecting firing coherence of the studied neuronal network, see Figure 5c. Thus, the obtained results in this paper are independent of the rewiring probability p.

4 Summary

We have studied the effects of intrinsic channel noise on firing coherence of Watts-Strogatz small-world networks that were populated by stochastic HH neurons. The intensity of channel noise is determined by the fraction of working ion channels, the membrane patch size and the ion channel density. In this paper, we assume that the ion channel density is homogeneous on the membrane patches and discuss the effects of channel noise by controlling the fractions of working ion channels x_{Na} and x_K separately, as well as the membrane patch size S. Our
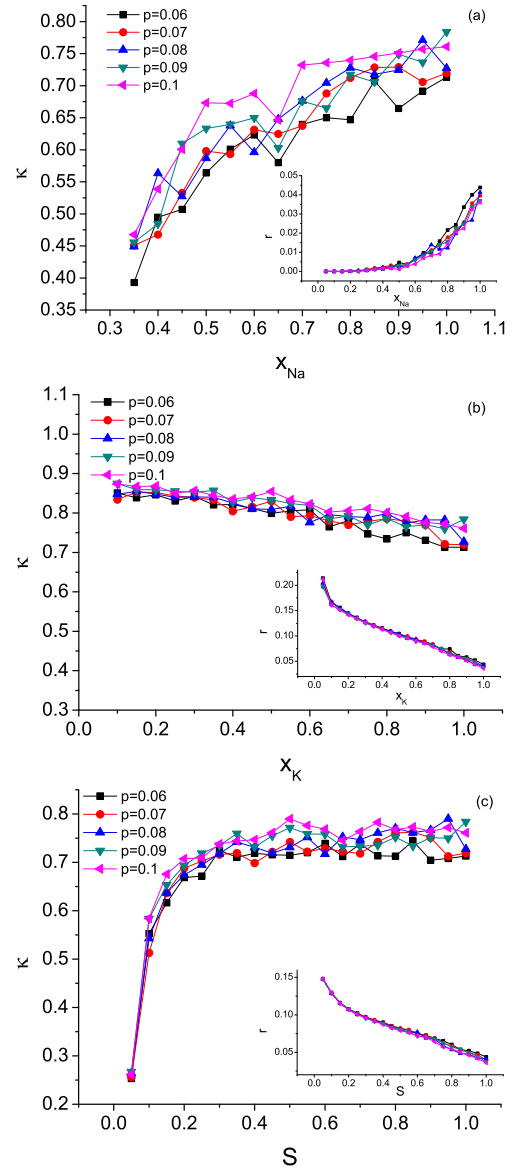

Fig. 5. (Color online) Variations of the population coherence measure κ as a function of the fraction of working sodium and potassium ion channels x_{Na}, x_K are shown in (a) and (b), for various rewiring probability p. Here the membrane patch size S is taken to be 1.0. And $x_K = 1.0$ in (a) while $x_{Na} = 1.0$ in (b). Variations of the population coherence measure κ as a function of the membrane patch size S for various p is shown in (c) with $x_{Na} = x_K = 1.0$. Insets are the corresponding variations of the mean firing rate r.

results indicate that firing coherence is reduced with increasing intensity of the sodium channel noise, while on the other hand, it is enhanced with increasing intensity of the potassium channel noise. Thus, firing coherence of the neuronal network can be either enhanced or reduced, depending on the source of channel noises. In other words, sodium and potassium channel noise have destructive and constructive effects on firing coherence, respectively. By controlling the membrane patch size S with the fractions x_{Na}, x_K fixed, we show that sodium channel noise plays

a dominant role in affecting firing coherence of the neuronal networks. Furthermore, we show that the obtained results are independent of the rewiring probability p of the Watts-Strogatz small-world networks.

The study of firing coherence is vital for several neuronal systems. It has been revealed that neurons can, in a statistical sense, be highly sensitive to the correlations of their input spikes [31]. Correlated firing activities have been found to be important for cortical processes, such as expectation [32] and attention [33]. In this paper, we show that ion channel noises have prominent impacts on firing coherence of the neuronal network, which is averaged over cross-correlation between pairs of neurons. Thus, our results obtained in this paper extend the studies of noise effects on firing correlations, and may have some important implications when investigating the interactions between correlated firing activities and cognitive behaviors in a noisy environment.

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