Coherence resonance in globally coupled neuronal networks with different neuron numbers*

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Because a brain consists of tremendous neuronal networks with different neuron numbers ranging from tens to tens of thousands, we study the coherence resonance due to ion channel noises in globally coupled neuronal networks with different neuron numbers. We confirm that for all neuronal networks with different neuron numbers there exist the array enhanced coherence resonance and the optimal synaptic conductance to cause the maximal spiking coherence. Furthermoremore, the enhancement effects of coupling on spiking coherence and on optimal synaptic conductance are almost the same, regardless of the neuron numbers in the neuronal networks. Therefore for all the neuronal networks with different neuron numbers in the brain, relative weak synaptic conductance (0.1 mS/cm^2) is sufficient to induce the maximal spiking coherence and the best sub-threshold signal encoding.

Keywords: coherence resonance, ion channel noise, neuronal network

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1. Introduction

The phenomenon of stochastic resonance (SR) was first discovered by Benzi *et al.*[1] in 1981 in order to explain the periodic recurrence of ice ages. In the subsequent decades, SR has been extensively studied in many systems, such as optical systems,[2] semiconductor devices,[3] nervous systems,[4−6] and so on. The phenomenon is that the weak external signal in a nonlinear system can be amplified and optimized by noise with optimal strength.[3] A decade later, Gang *et al.*[7] found SR-like behaviour in a noisy nonlinear system even without external signal, which is referred to as the autonomous SR or coherence resonance (CR). The phenomenon of CR has been found in a variety of nonlinear systems, such as the FitzHugh–Nagumo model,[8] the Hindmarsh–Rose model,[9,10] the Morris–Lecar model,[11] and the Hodgkin–Huxley (HH) model.[12]

In recent years, many scientists have paid much attention to the SR and the CR in coupled nonlinear systems,[13−16] and found some interesting phenomena, such as the noise enhanced phase synchronization,[17] the noise induced spatiotemporal pattern formation,[18] and the noise enhanced wave propagation.[19] Furthermore, the phenomena that the coupling between nonlinear systems enhances SR and CR has also been found. They are the so-called array enhanced stochastic resonance (AESR) and array enhanced coherence resonance (AECR).[13,20−22] The phenomena AESR and AECR not only have the general features of SR and CR, i.e., there exists an optimal noise strength to induce the maximal coherence, but also have their unique feature, namely there exists an optimal coupling strength to induce the maximal coherence.[13,20−22]

The nervous system is full of noises. There are mainly ion channel noise and synaptic noise in a nervous system.[23] Synaptic noise can induce spontaneous spiking,[23] SR,[24] and CR[12] in single neuron and induce AESR[25] and AECR[26] in the coupled neuronal network. Research results also show that ion channel noise in single neuron can also induce spontaneous spiking,[27,28] SR,[29] and CR.[30] In our previous research,[31] we studied the spiking coherence induced by ion channel noise in globally coupled neu-

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ronal networks and found the phenomenon of AECR and that there is an optimal synaptic conductance among neurons to induce the maximal spiking coherence. Because a brain consists of tremendous neuronal networks with different neuron numbers and the neuron numbers in the neuronal networks of the brain range from tens to tens of thousands,[32−34] in this paper we study the spiking coherence induced by ion channel noise in globally coupled neuronal networks with different neuron numbers. We find that globally coupled neuronal networks with different neuron numbers each demonstrate the phenomenon of AECR and each has the optimal synaptic conductance to cause the maximal spiking coherence regardless of the neuron numbers in the neuronal networks. Furthermore, we also find that the enhancement effects of coupling on the spiking coherence and the optimal synaptic conductance to induce the maximal spiking coherence are almost the same and independent of the neuron number in the neuronal network. If neurons in the network each have a common soma area (500 μm^2), the optimal synaptic conductance is approximately 0.1 mS/cm^2 for all neuronal networks with different neuron numbers. Our research results show that the relative weak synaptic conductance (0.1 mS/cm^2) is enough to cause the maximal spiking coherence and the best sub-threshold signal encoding for all the neuronal networks with different neuron numbers in a brain.

2. Model

2.1. Deterministic Hodgkin–Huxley neuronal network model

In their cornerstone paper, Hodgkin and Huxley[35] first presented a quantitative description of the electrical behaviour of neuronal membranes by a series of first-order ordinary differential equations,[35] which is the famous Hodgkin–Huxley (HH) equation. Because the globally coupled neuronal network is a very popular study model and has abundant theoretical and biological meanings,[26,36,37] in this paper we adopt this kind of neuronal network. The electrical behaviour of the globally coupled neuronal network can be described by the following equation:[35,37]

$$\begin{aligned} C_{\rm m}\frac{{\rm d}V_i}{{\rm d}t} &= -g_{\rm Na}m_i^3h_i(V_i-V_{\rm Na}) \\ &\quad -g_{\rm K}n_i^4(V_i-V_{\rm K})-g_{\rm L}(V_i-V_{\rm L}) \\ &\quad +I_{i({\rm ext})}+\sum_{j=1,j\neq i}^{N} g_{\rm syn}\alpha(t-t_j) \\ &\quad \times(V_{\rm syn}^{ij}-V_i) \end{aligned} \tag{1}$$

with

$$\alpha(t)=(t/\tau)\exp[-t/\tau],$$

where N is the neuron number in the network, V_i is the membrane potential of the i-th neuron, $C_{\rm m}$ is the membrane capacitance per unit area, $V_{\rm Na}$, $V_{\rm K}$, and $V_{\rm L}$ are the reversal potentials of the sodium, potassium and leakage systems respectively, $g_{\rm Na}$ and $g_{\rm K}$ are the maximal conductances of sodium and potassium systems per unit area respectively and $g_{\rm L}$ is the leakage conductance per unit area. Gating variables m_i, h_i, and n_i are the open fractions of the m, h, and n types of ion channel gates in the i-th neuron and have the value from 0 to 1, $I_{i({\rm ext})}$ is the external injection current for the i-th neuron, which is sub-threshold stimulus and is set as 6 $\mu A/cm^2$ in this paper, $g_{\rm syn}$ denotes the synaptic conductance between two neurons and the peak synaptic conductance is $g_{\rm syn}/e$, t_j is the starting interaction time of the synapses of the presynaptic j-th neuron, i.e., the initial firing time of the presynaptic j-th neuron, τ is the character time of synaptic interaction, which is set as 2 ms in this paper, $V_{\rm syn}^{ij}$ is the synaptic potential between the i-th and the j-th neurons, the value of $V_{\rm syn}^{ij}$ determines that the synapse is either excitatory or inhibitory. For excitatory synapse, $V_{\rm syn}^{ij}$ is chosen as 0 mV. For inhibitory synapse, $V_{\rm syn}^{ij}$ is chosen as −80 mV. In our paper, the percentage of excitatory synapses in the total number of synapses is 80%.

Each ion channel gate has two states: open state and closed state. If the open fraction of n type of gates in the i-th neuron is n_i, then the corresponding closed fraction is $1-n_i$. The transition dynamics of one gate between the open and the closed states satisfies the first-order differential equation. The transition rate of n type of gate in the i-th neuron from the closed state to the open state is α_{n_i} and the corresponding transition rate from the open state to the closed state is β_{n_i}. It is similar for m and h types of gates. The dynamics of gating variables m_i, h_i and n_i satisfies the following equations and the parameters and rate functions used in the paper are shown in Table 1.[27,35]

$$\begin{aligned} \frac{{\rm d}m_i}{{\rm d}t} &= \alpha_{m_i}(V_i)(1-m_i)-\beta_{m_i}(V_i)m_i, \\ \frac{{\rm d}h_i}{{\rm d}t} &= \alpha_{h_i}(V_i)(1-h_i)-\beta_{h_i}(V_i)h_i, \\ \frac{{\rm d}n_i}{{\rm d}t} &= \alpha_{n_i}(V_i)(1-n_i)-\beta_{n_i}(V_i)n_i. \end{aligned} \tag{2}$$

Table 1. Parameters and rate functions used in our simulation.

Neuron number in the network (N)	10∼1000
Specific membrane capacitance ($C_{\rm m}$)	1 μF
Potassium reversal potential ($V_{\rm K}$)	−77 mV
Sodium reversal potential ($V_{\rm Na}$)	50 mV
Leakage reversal potential ($V_{\rm L}$)	−65 mV
Maximal sodium channel conductance ($g_{\rm Na}$)	120 mS/cm^2
Maximal potassium channel conductance ($g_{\rm K}$)	36 mS/cm^2
Leakage conductance ($g_{\rm L}$)	0.3 mS/cm^2
Single potassium channel conductance ($\gamma_{\rm K}$)	20 pS
Single sodium channel conductance ($\gamma_{\rm Na}$)	20 pS
Potassium channel density ($\rho_{\rm K}$)	18/μm^2
Sodium channel density ($\rho_{\rm Na}$)	60/μm^2
α_{n_i}	$\frac{0.01(V+55)}{1-{\rm e}^{-(V+55)/10}}$
β_{n_i}	$0.125\,{\rm e}^{-(V+65)/80}$
α_{m_i}	$\frac{0.1(V+40)}{1-{\rm e}^{-(V+40)/10}}$
β_{m_i}	$4\,{\rm e}^{-(V+65)/18}$
α_{h_i}	$0.07\,{\rm e}^{-(V+65)/20}$
β_{h_i}	$\frac{1}{1-{\rm e}^{-(V+35)/10}}$

2.2. Stochastic Hodgkin–Huxley neuronal network model

When ion channel number in the neuronal membrane is large, the deterministic HH equations are in the good approximation to describe the average electrical behaviour of the ensemble of numerous ion channels. However, each ion channel gate switches stochastically between the open state and the closed state. When the ion channel number is small, the effect due to stochastic gating of ion channels is considerable. In this case, the deterministic HH equation is not efficient and the stochastic HH equation is needed to describe the electrical dynamics of small ion channel clusters. In the stochastic HH equation, the electrical behaviour of small ion channel clusters obeys the following equation:

$$\begin{aligned} C_{\rm m}\frac{{\rm d}V_i}{{\rm d}t} = &-\Bigg(g_{\rm Na}\frac{N^{\rm open}_{{\rm Na}_i}}{\rho_{\rm Na}A}(V_i-V_{\rm Na}) \\ &+g_{\rm K}\frac{N^{\rm open}_{{\rm K}_i}}{\rho_{\rm K}A}(V_i-V_{\rm K})+g_{\rm L}(V_i-V_{\rm L})\Bigg) \\ &+I_{i({\rm ext})}+\sum_{j=1,j\neq i}^{N}g_{\rm syn}\alpha(t-t_j) \\ &\times(V^{ij}_{\rm syn}-V_i), \end{aligned} \tag{3}$$

where $N^{\rm open}_{{\rm Na}_i}$ and $N^{\rm open}_{{\rm K}_i}$ are the open sodium and potassium channel numbers in the i-th neuron, $\rho_{\rm Na}$ and $\rho_{\rm K}$ are the densities of sodium channels and potassium channels in each neuronal membrane respectively and A is the membrane area of each neuron. Therefore $\rho_{\rm Na}A$ and $\rho_{\rm K}A$ are the total numbers of sodium channels and potassium channels in each neuronal membrane respectively. In order to integrate Eq. (3), it is necessary to update $N^{\rm open}_{{\rm Na}_i}$ and $N^{\rm open}_{{\rm K}_i}$ at each instant. For a potassium ion channel, there are gates 0, 1, 2, 3, and 4 and the corresponding states can be denoted as S_0, S_1, S_2, S_3, and S_4. Then the corresponding potassium channel numbers in states S_0, S_1, S_2, S_3, and S_4 can be denoted as $[n_0]$, $[n_1]$, $[n_2]$, $[n_3]$, and $[n_4]$ and stochastic transition can take place between two nearby states. Obviously, $[n_4]$ represents the open potassium channel number. It is assumed that the stochastic transition of potassium channels between two nearby states satisfies the Markov process and the corresponding kinetic scheme is shown in Fig. 1. Similarly, sodium channels exist in eight different states and the corresponding kinetic scheme is shown in Fig. 2. In Fig. 2, $[m_ih_j]$ denotes the sodium channel number with i open gates of m type and j open gates of h type and $[m_3h_1]$ denotes the open sodium channel number.

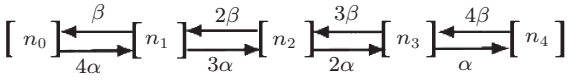


Fig. 1. Kinetic scheme of single potassium channel.

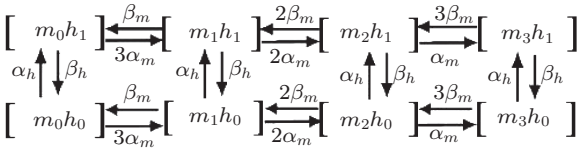


Fig. 2. Kinetic scheme of single sodium channel.

In a specific time, if the transition rate from state 1 to state 2 is γ, then in time interval δt the transition probability of each channel switching from state 1 to state 2 is $\gamma\delta t$. The transition channel number δn_{12} from state 1 to state 2 satisfies the following binomial distribution:[27,38−40]

$$P(\delta n_{12}) = \begin{pmatrix} n_1 \\ \delta n_{12} \end{pmatrix} p^{\delta n_{12}} (1-p)^{(n_1 - \delta n_{12})}, \quad (4)$$

where n_1 is ion channel number in state 1 and p is equal to $\gamma\delta t$. Therefore the switching channel numbers between two nearby states are determined sequentially from the binomial distribution in each step and the channel numbers in each state are updated subsequently. According to the updated channel number in each state, we can integrate the stochastic HH equation, i.e., Eq. (3) and simulate the electrical behaviours of small ion channel clusters.

In order to check the accuracy of our simulation, we calculate the electrical behaviour of single neuron, which is described by Eq. (1) (deterministic) and Eq. (3) (stochastic) without the last coupling term. We have checked that the results obtained by the stochastic HH equation match those acquired by the deterministic HH equations when the ion channel number in the neuronal membrane is large and our results accord with the previous results in Refs. [27], [30], and [38]. We have compared the results from the deterministic and stochastic HH equations in two cases: without external injection current and under suprathreshold injection current ($I_{i(\mathrm{ext})} = 10.0\ \mu\mathrm{A/cm}^2$). In the case without external injection current, the deterministic HH equation cannot generate any spike, but the stochastic HH equation can generate some spontaneous spikes induced by ion channel noises. We can imagine that if the effect of ion channel noise is weak, the spontaneous spiking frequency will be small. The corresponding results are shown in Fig. 3. If the potassium channel number N_{K} is 1000, the spontaneous spiking frequency is as high as 21 Hz. If N_{K} is 10^4, the spontaneous spiking frequency decreases to 0.16 Hz. If N_{K} is 10^5, the spontaneous spiking frequency is as low as 0.0018 Hz. In the case under suprathreshold injection current ($I_{i(\mathrm{ext})} = 10.0\ \mu\mathrm{A/cm}^2$), the deterministic H-H equation can generate regular spikes, but the spikes generated by the stochastic HH are not so regular. In this case, we measure the spikes generated by the stochastic HH equation in two aspects: percentage error of the average interspike interval versus interspike interval of the deterministic HH equation and the standard deviation (SD) of the interspike intervals. We can imagine that if the effect of ion channel noise is weak, the percentage error of the average interspike interval and the SD of the interspike intervals are small. The corresponding results are shown in Fig. 4. If N_{K} is 1000, the percentage error is as high as 11% and the SD is as large as 4 ms. If N_{K} is 10^4, the percentage error decreases to 2% and the SD decreases to 0.7 ms. If N_{K} is 10^5, the percentage error is as low as 0.2% and the SD is as small as 0.1 ms. According to the results in Figs. 3 and 4, we can find that the results from the stochastic HH equation approach to those from the deterministic HH equations as the ion channel number increases, thereby leading to a conclusion that the effect of ion channel noise is strong for 1000 potassium channels, but weak for 10^5 potassium channels and it is very small for 10^5 potassium channels. Therefore 10^4 potassium channels in the neuronal membrane are large enough to use the deterministic HH equations.

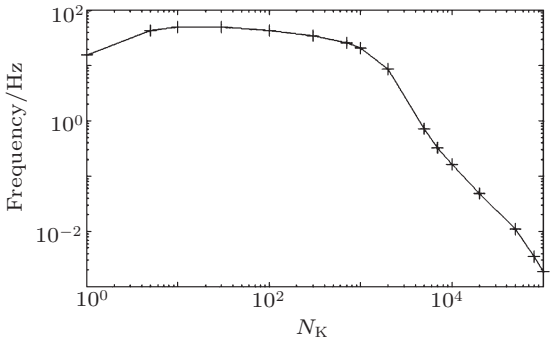


Fig. 3. Spontaneous spiking frequency versus potassium channel number N_{K} in the neuronal membrane.

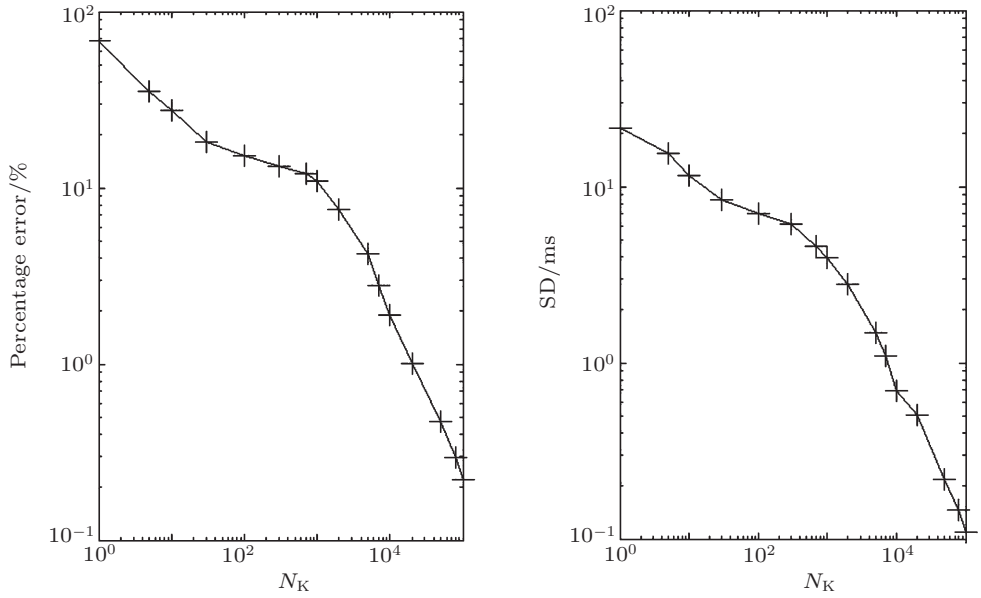


Fig. 4. Percentage error of average interspike interval and the SD of interspike intervals versus the potassium channel number N_K.

3. Results

We set the external injection current as subthreshold stimulus, which is $I_{i(\mathrm{ext})} = 6.0\ \mu\mathrm{A/cm}^2$,[26] change the neuron number in the neuronal network from 10 to 1000, and then study the effect of neuron number on the spiking coherence of the neuronal network. The electrical behaviour of the neuronal network is simulated by the fourth Runge–Kutta method with the time step $\Delta t = 0.01$ ms. In order to reduce the statistical error, 10^4 action potentials for each neuron in each case are obtained. The temporal coherence is calculated as a quantitative measure of coherence resonance, which is calculated by the following formula:[13,41]

$$S_i = \frac{\langle \tau_i \rangle_t}{\sqrt{\mathrm{var}(\tau_i)}}, \quad i = 1, 2, \ldots, N, \tag{5}$$

where τ_i is the interspike interval of the i-th neuron, $\langle\ \rangle_t$ is the average over time and S_i is the coherence factor of the i-th neuron. The average of S_i over the whole neuronal network is the coherence factor S of the network.

We calculate the values of coherence factor S of neuronal networks with different neuron numbers and plot the results in Fig. 5. From Fig. 5, we can find the same phenomena as those obtained by Jung and Shuai[30] and Schmid *et al.*,[42] and the intrinsic coherence resonance induced only by ion channel noise—there is an optimal neuronal membrane area for the maximal spiking coherence.[27,30,42] We can explain the interesting phenomena by different evoking mechanisms of the small ion channel cluster and the large ion channel cluster.[27] If the ion channel cluster is small enough, only one sodium channel opening is sufficient to evoke an action potential. In this case, with the increases of the neuronal membrane area and the ion channel number, the certainty of opening one sodium channel will increase and then the spiking coherence will increase subsequently. If the neuronal membrane area and the ion channel number increase continually, only one sodium channel opening is not sufficient to evoke an action potential and then the membrane potential and the open fraction of sodium channels need to exceed their corresponding critical values. In this case, as the neuronal membrane area and the ion channel number increase, the certainty for the open fraction of sodium channels exceeding a critical value due to stochastic gating will decrease and then the spiking coherence will decrease subsequently. Due to the interaction between the two mechanisms, there is an optimal membrane area for the maximal spiking coherence.

From Fig. 5, we can find the AECR and an optimal synaptic conductance causing the maximal spiking coherence for all neuronal networks with different neuron numbers, which accord with the former research results.[13,20−22] For a neuronal membrane with a certain area, we keep all the parameters in Eq. (3) constant and just change the synaptic conductance.

Therefore the change of the coherence factor S is only due to the difference in coupling strength between neurons and the AECR is also induced only by the increase of coupling strength between neurons. If we increase the synaptic conductance, at first the coherence factor S will increase. After the synaptic conductance reaches an optimal value, as it continually increases, the coherence factor S will decrease. We can explain it qualitatively according to our former research results.[31] There are two kinds of effects of coupling between neurons on the spiking coherence. The first one is that coupling between neurons can induce mutual excitation and then can increase the spiking synchronization and the spiking coherence. The other one is that for neurons spending most time in the rest state, coupling between neurons prevents spiking, induces some "missed" spikes, and then reduces the spiking coherence. Due to the interaction between the two kinds of effects, there is an optimal synaptic conductance for the maximal spiking coherence.

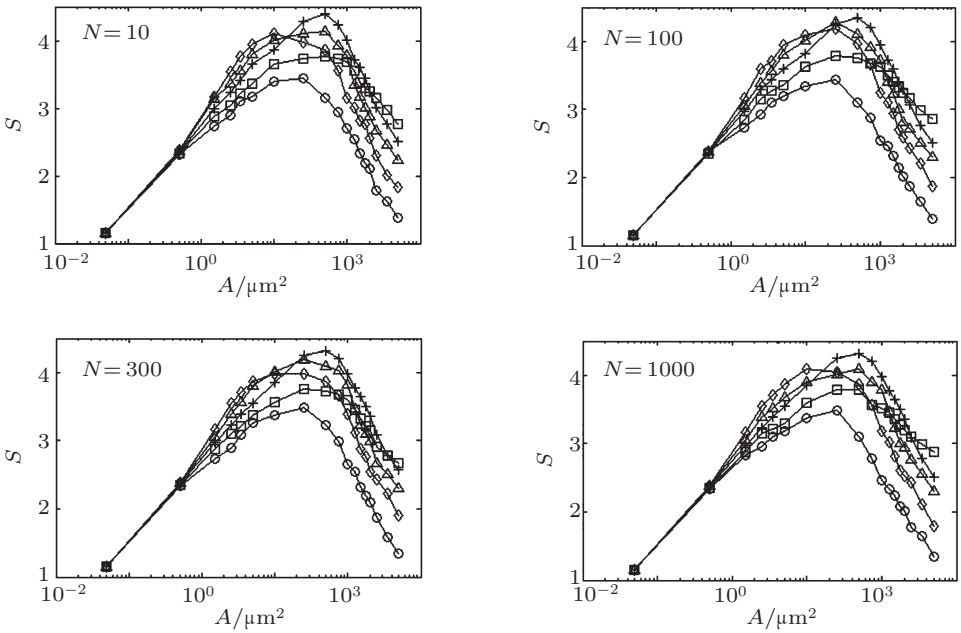


Fig. 5. Values of coherence factor S of neuronal networks with different neuron number N versus the neuronal membrane area A. (◯): $g_{\rm syn} = 0$, (□): $g_{\rm syn} = 0.1$ mS/cm^2, (+): $g_{\rm syn} = 0.2$ mS/cm^2, (△): $g_{\rm syn} = 0.6$ mS/cm^2, (◇): $g_{\rm syn} = 1.0$ mS/cm^2.

We further study the effect of neuron number in the neuronal network on the spiking coherence and focus on two factors: the maximal coherence factor S and the maximal enhancing percentage of the coherence factor S due to coupling. The optimal synaptic conductances inducing the maximal coherence factor S versus the neuron number in the neuronal networks are plotted in Fig. 6. We choose the neuronal membrane areas as 5 μm^2, 50 μm^2, and 500 μm^2 and change the neuronal number from 10 to 1000. As shown in Fig. 6, the optimal synaptic conductances of the neuronal networks with the neuronal membrane areas of 5 μm^2, 50 μm^2, and 500 μm^2 are approximately 1.0 mS/cm^2, 0.3 mS/cm^2, and 0.1 mS/cm^2 respectively. We can also find from Fig. 6 that the optimal synaptic conductance versus the neuron number in the neuronal network is almost a constant and just fluctuates within 10% range due to statistical error. Therefore the neuronal networks with the different neuron numbers have almost the same optimal synaptic conductances. The maximal enhancement percentages of the coherence factor S due to coupling versus the neuronal number in the neuronal network are plotted in Fig. 7. The parameters in Fig. 7 are chosen to be the same as those in Fig. 6. As shown in Fig. 7, the maximal enhancement percentages of the coherence factor S of the neuronal networks with the neuronal membrane areas of 5 μm^2, 50 μm^2, and 500 μm^2 are approximately 20%, 40%, and 100% respectively. It is also demonstrated in Fig. 7 that the maximal enhancement percentages of the coherence factor S versus the neuron numbers in the neuronal networks each are almost a constant and just fluctuate within 10% range due to statistical error. Therefore the neuronal

networks with the different neuron numbers have the same enhancement percentage of the coherence factor S due to coupling.

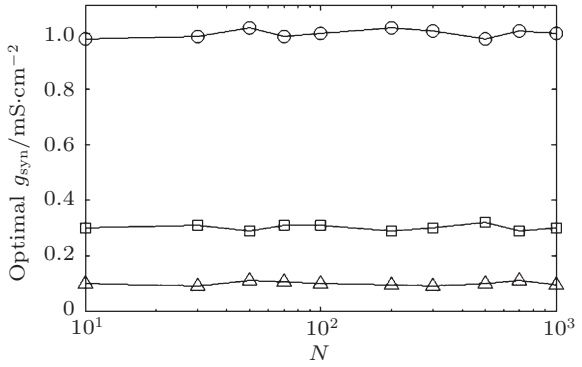


Fig. 6. Values of optimal synaptic conductance $g_{\rm syn}$ versus the neuron number N in the neuronal networks with neuronal membrane area: 5 μm^2 (◯), 50 μm^2 (□), and 500 μm^2 (△).

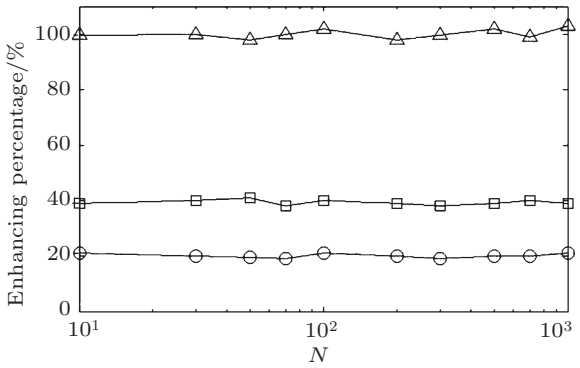


Fig. 7. Maximal enhancing percentages of the coherence factor S due to coupling versus neuron number N in the neuronal networks with neuronal membrane area: 5 μm^2 (◯), 50 μm^2 (□), and 500 μm^2 (△).

4. Conclusion

Excitable nonlinear systems have aroused much interest among researchers during the last decades,[1−12,43−47] and SR and CR are the interesting and important phenomena discovered in these systems.[1−12] Meanwhile, the interesting phenomena referred to as AESR and AECR have also been found.[13,20−22] Because the brain consists of tremendous neuronal networks with different neuron numbers and the neuron numbers range from tens to tens of thousands,[32−34] we studied the CR induced by ion channel noises in coupled neuronal networks with different neuron numbers. Our research results confirm that for all coupled neuronal networks with different neuron numbers there are AECRs and the optimal synaptic conductances to induce the maximal spiking coherences. Our results further show that all coupled neuronal networks with different neuron numbers have the same optimal synaptic conductances to cause the maximal spiking coherences and the same enhancement percentages of the coherence factor S due to coupling. If neurons in the network each have a common soma area (500 μm^2), the optimal synaptic conductance is approximately 0.1 mS/cm^2 and the maximal enhancement percentage of the coherence factor S is approximately 100%. Therefore for all neuronal networks with different neuron numbers in a brain, the relative weak synaptic conductance (0.1 mS/cm^2) is enough to induce the maximal spiking coherence and the best sub-threshold signal encoding.

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