Excitation Properties of the Biological Neurons with Side-Inhibition Mechanism in Small-World Networks *

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(Received 8 May 2006)

We have studied the excitation properties of biophysical Hodgkin–Huxley neurons with the side-inhibition mechanism in small-world networks. The result shows that the excitation properties in the networks are preferably consistent with the characteristic properties of a brain neural system under external constant stimuli, such as fatigue effect, extreme excitation principle, and the brain neural excitation response induced by different intensity of noise and coupling. The results of the study might shed some light on the study of the brain nerve electrophysiology and epistemological science.

PACS: 87. 18. Sn, 05. 45. −a, 84. 35. +i, 87. 18. Bb

For many years, the neural-response to external stimulus and neural-information processing have been challenging hot topics for the study of neurology. The Hodgkin–Huxley (HH) equations, which describe neuron discharge, are frequently used as node dynamical equations in the coupling model.[1−11] For example, Kim and Lee[4] have studied the mechanisms for synchrony of neural networks based on biophysical HH neurons by using the methods of nonlinear dynamics; Lago-Fernández *et al.*[5] have shown that the features of both fast response and temporal coherent oscillations of biophysical HH neurons in small-world networks; and Wang *et al.*[6] have studied the coherence resonance and noise-induced synchronization in globally coupled biophysical HH neurons. Although the results of these models can mimic the dynamical properties and discharge features of a neural system to some extent, the side-inhibition mechanism existing in a real neural system is neglected. In this Letter, we propose a new small-world biological neural network model by combining the complex network theory with the latest findings by American scientists: the neural system of a human brain is just like a small-world network in complex networks.[12] In such a complex network model, a side-inhibition mechanism is considered because the study of neurophysiology has verified the mechanism existing in a brain neural system, and HH equations are taken as the node dynamical equations. The connecting strength with side-inhibition mechanism is used to simulate the connecting intensity between neurons. Under the external constant stimulus, these neurons of the network model behave with excitation and rest, and interact with each other. The purpose of this study is to characterize the process of 'stimulating–exciting–conducting effect' of brain neurons via exciting and inhibiting. Simulation results show that the model of biological neural networks has different excitation properties under different intensities of dc stimuli, noise and coupling. These results are quite consistent with the behaviour under the external constant stimuli shown by a brain neural system.

Generally, the study of biological neurons focuses on the electro-activities of neurons. The HH equations are a kind of discharge model[13] of neurons closest to the action potential and shows very complex dynamical properties under different external stimuli as well as environmental noises.[6,10] We adopt the HH equations to govern the dynamical evolution of nodes, employ the side-inhibition mechanism existing in a brain neural system into consideration, and take small-world networks to be the underlying structure. The complex network model is described by the following equations:

$$C_m\dot{V}_i = I_{i(\mathrm{ion})} + I_{i(\mathrm{syn})} + I_{i(\mathrm{ext})} + \frac{c}{N}\sum_{j=1}^{N} S_{ij}a_{ij}V_j, \tag{1}$$

$$\dot{m}_i = \alpha_{m_i}(V_i)(1-m_i) - \beta_{m_i}(V_i)m_i, \tag{2}$$

$$\dot{h}_i = \alpha_{h_i}(V_i)(1-h_i) - \beta_{h_i}(V_i)h_i, \tag{3}$$

$$\dot{n}_i = \alpha_{n_i}(V_i)(1-n_i) - \beta_{n_i}(V_i)n_i, \quad (1\le i\le N), \tag{4}$$

where

$$\begin{aligned} I_{i(\mathrm{ion})} =& -g_{Na}m_i^3h_i(V_i-V_{Na}) \\ & -g_k n_i^4(V_i-V_k) - g_L(V_i-V_L), \end{aligned} \tag{5}$$

$$\tau_c\dot{I}_{i(\mathrm{syn})} = -I_{i(\mathrm{syn})} + \sqrt{2D}\xi_i, \tag{6}$$

* Supported by the National Natural Science Foundation of China under Grant Nos 70571017, 10247005, 10547004 and 10472116, the Guangxi Innovative Fund for the Programme of Graduate Education, and the Key Project of the National Natural Science Foundation of China under Grant No 70431002.

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$$S_{ij} = \frac{\sin[(i-j)/(N-1)\times 4\Pi]}{(i-j)/(N-1)\times 4\Pi}, \tag{7}$$

where S_{ij} describes the side-inhibition mechanism existing in a brain neural system; N represents the total number of neurons and for simplicity we use $N = 100$ throughout this study because the number of neurons $N = 100$ can be used to describe small-world property;[14] V_i represents the membrane potential of unite i; C_m denotes the membrane capacity per unit area; m_i, h_i, and n_i are the voltage dependent activating and inactivating variables; α_i and β_i are functions of V_i adjusted to physiological data; g_{Na}, g_K, and g_L are the maximal conductances for ion and leakage channels; In addition, V_{Na}, V_K, and V_L are the corresponding reversal potentials. We have used the original functions and parameters employed by in Ref. [13]. $I_{i(\mathrm{ion})}$ denotes the ionic current inside the cell which satisfies Eq. (5); $I_{i(\mathrm{syn})}$ is the noise current in a complex life system which satisfies Eq. (6), where ξ_i is Gaussian white noise with correlation given by $\langle\xi_i(t)\xi_j(t)\rangle = D\delta_{ij}\delta(t-s)$ which satisfies the zero-mean value.[2] D and τ_c are the intensity and the correlation time of the synaptic noise, respectively; $\tau_c = 2.0\,\mathrm{ms}$ is employed throughout this study. $I_{i(\mathrm{ext})}$ is the external stimulating current; $\frac{c}{N}\sum_{j=1}^{N} S_{ij}a_{ij}V_j$ is the coupling term of the complex neurons, where c is the coupling strength; S_{ij} is connection intensity between neuron i and neuron j, which describes the side-inhibition mechanism indicating the excited roles of the neighbouring neurons and inhibition roles of the neurons apart from each other, meanwhile Eq. (7) is introduced. S_{ij} decreases gradually with the increase of the distance between two neurons leading to the weakening of the excitation strength according to Eq. (7). When the distance reaches a certain level, S_{ij} becomes a negative value. The positive value indicates that the two neurons play a role of mutual excitation through the connection of excitation bond, and the negative value denotes that the two neurons play a role of inhibition through the connection of inhibition bond. Here a_{ij} represents the matrix element of the coupling, which takes the following form:[15] $a_{ij} = 1$, when a connection exists between neuron i and j; otherwise $a_{ij} = 0$ and $a_{ii} = -\sum_{j=1,j\neq i}^{N} a_{ij}$. The small-world networks modelled by Watts and Strogatz[16] is adopted with connection-rewiring probability $p = 0.05$ in this study.

Two physical quantities are firstly introduced to describe the properties of the network stimulated by direct current. One is the average transmembrane potential $V_{\mathrm{out}}(t) = \frac{1}{N}\sum_{i=1}^{N} V_i(t)$ as the signal output of the whole neural network.[7] As the output voltage of the network, it represents the excitation strength of the whole network, and the variation rate of its peak value with the change of the time indicates the excitation rhythm. The other is the excitatory neurons number $n_{\mathrm{exc}}(t)$ in the whole network. The neuron is regarded as the excited one on the assumption that its excitation threshold is $5\,\mathrm{mV}$, i.e. $V_i(t) > 5\,\mathrm{mV}$, otherwise it is regarded as the rested one.

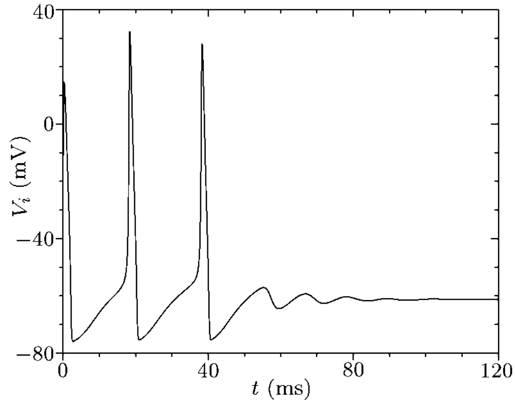

Fig. 1. The membrane potential V_i under the weak dc stimulus at $I = 6.2\mu\mathrm{A\cdot cm^{-2}}$, $D = 1.0$, and $c = 0.1$.

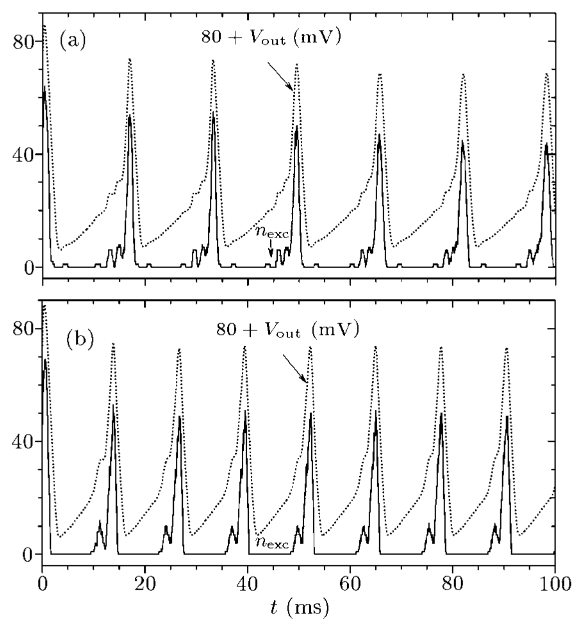

Fig. 2. The excitation measurement, V_{out}, and the number of excitatory neurons, n_{exc}, under $D = 1.0$ and $c = 0.1$ at $I_{i(\mathrm{ext})} = 8\,\mu\mathrm{A\cdot cm^{-2}}$ (a) and $15\,\mu\mathrm{A\cdot cm^{-2}}$ (b).

Figure 1 indicates that the neuron exhibits the fatigue effect under weak dc stimulus. The excitation and the rest occur alternatively until it rests completely and reaches a stable equilibrium state. In this case, all of the neurons are in the state of fatigue. The membrane potential $V_i(t)$ changes from strong to weak when the network is excitatory. Higher excitation strength at the beginning stage complies well with the extreme excitation principle in the biomedicine. Disappearing of the fatigue effect with the gradual increase of the dc stimulus indicates that a stimulating threshold $I_{i(\mathrm{thd})}$ exists. A short period of response occurs in the region $I_{i(\mathrm{ext})} < I_{i(\mathrm{thd})}$, while for

$I_{i(\mathrm{ext})} > I_{i(\mathrm{thd})}$ all the time response comes into being, which leads to the alternative occurrence of excitation and rest. Under this circumstance, the duration of excitation is extremely short compared with the duration of rest, which complies with the practical response of a brain neural system under the external constant stimulation. Further analysis indicates that the excitation strength and rhythm are different[7,9] under different dc stimuli, thus the output potential and the number of excited neurons are also different. The change of the values along with the change of the dc stimulus is shown in Fig. 2. It is shown that the excitation rhythm speeds up with the increase of $I_{i(\mathrm{ext})}$, while the rhythms of V_{out} and n_{exc} are the same (in Fig. 2, V_{out} has been shifted 80 units upwards in order to compare these two rhythms easily). It is also indicated that both V_{out} and n_{exc} can be used to describe the strength of excitation, where V_{out} indicates the excitation strength quantitatively, and n_{exc} indicates the excitation strength qualitatively.

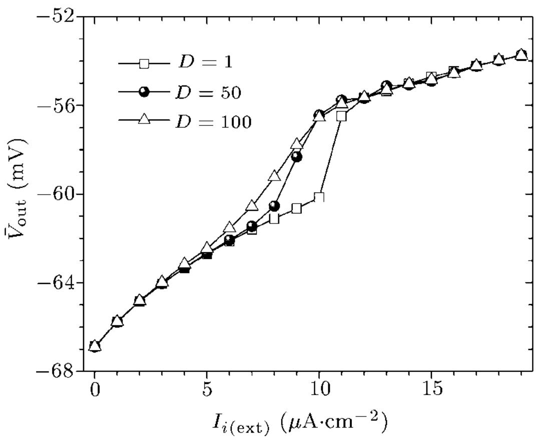

Fig. 3. Average excitation measure, $\bar{V}_{\mathrm{out}}$, versus dc stimulus, $I_{i(\mathrm{ext})}$, at $c = 0.5$ for noise intensity $D = 1$, 50, 100.

Statistical method is used to describe the average excitation strength of the network within a long period of time. Two average excitation measures, $\bar{V}_{\mathrm{out}}$ and $\bar{n}_{\mathrm{exc}}$, are introduced as expressed in Eqs. (8) and (9). The calculation starts from t_1 without the consideration of transient process in order to reflect the average strength of the excitation in the stable state after being stimulated. Here $t_1 = 400\,\mathrm{ms}$ and $t_2 = 600\,\mathrm{ms}$ are selected for the following calculation and discussion.

$$\bar{V}_{\mathrm{out}} = \frac{1}{t_2 - t_1}\int_{t_1}^{t_2} V_{\mathrm{out}}(t)dt, \tag{8}$$

$$\bar{n}_{\mathrm{exc}} = \frac{1}{t_2 - t_1}\int_{t_1}^{t_2} n_{\mathrm{exc}}(t)dt. \tag{9}$$

The changing trend of $\bar{V}_{\mathrm{out}}$ and $\bar{n}_{\mathrm{exc}}$ under different noise intensity D and coupling strength c are calculated and analysed when the network response reaches the stable state (as shown in Figs. 3–6).

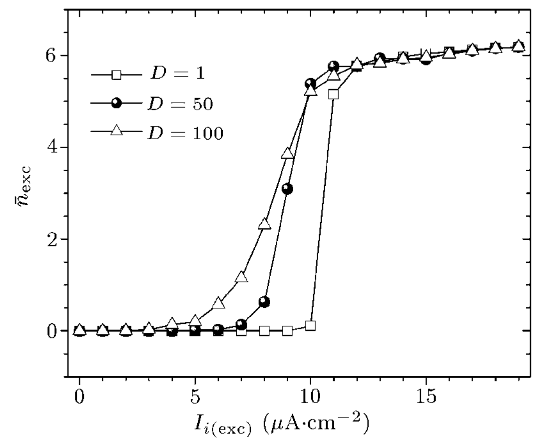

Fig. 4. Average number of excitatory neurons, $\bar{n}_{\mathrm{exc}}$, versus dc stimulus, $I_{i(\mathrm{ext})}$, at $c = 0.5$ for noise intensity $D = 1$, 50, 100.

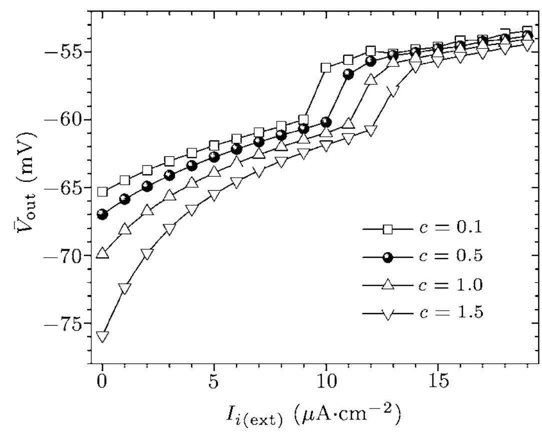

Fig. 5. Average excitation measure, $\bar{V}_{\mathrm{out}}$, versus dc stimulus, $I_{i(\mathrm{ext})}$, at $D = 1.0$ for coupling strength $c = 0.1$, 0.5, 1.0, 1.5.

Figures 3 and 4 show the influence of the noise on excitation. It is obvious that the noise almost has no influence on the excitation properties in the region $I_{i(\mathrm{ext})} < I_{i(\mathrm{thd})}$ because the neurons are in the 'fatigue' state and the network hardly responds to the external noises under weak dc stimulus. When $I_{i(\mathrm{ext})}$ exceeds a certain level of $I_{i(\mathrm{thd})}$, the influence of the noise on the excitation properties becomes remarkable. The stronger the noise strength is, the higher the average excitation strength of the network is, due to the coherence resonance induced by the noises.[6] When $I_{i(\mathrm{ext})}$ continuously increases, the curves of different noise intensities tend to overlap, which indicates that the noise almost has no influence again on the excitation properties. The reason is that the influence of the noise can be ignored since the signal-to-noise ratio of the stimulation imposed on the network is higher under stronger dc stimulus. Figures 5 and 6 reveal the influence of the coupling strength on the excitation properties among neurons. Clearly, the coupling strength imposes remarkable influence on the excitation properties under weak dc stimulus. It also shows that the higher the coupling strength is, the lower the average excitation of the network is, which is because the rest period lasts longer compared with the excitation period, thus most of the coupling period occurs in the rest state of the neurons during the alternative occurrences of the excitation and rest. In addition, as $I_{i(\mathrm{ext})}$ continuously increases, the curves of different noise strengths tend to overlap, which illustrates that the excitation properties of the neurons under strong constant stimulating signals are almost independent of the coupling strength. This phenomenon is consistent with the excitation reflects of different human brains (different coupling strengths of different brain neurons) occurring under strong constant stimulating signals. Figures 4 and 6 show that the phase transition of the average number of the excitatory neurons occurs (jumps from rest phase to excitation phase), and the network gradually reaches saturation with the increase of the dc stimulus strength. The phase transition exhibits the ON- and OFF-excitation effect of the stimulating threshold.

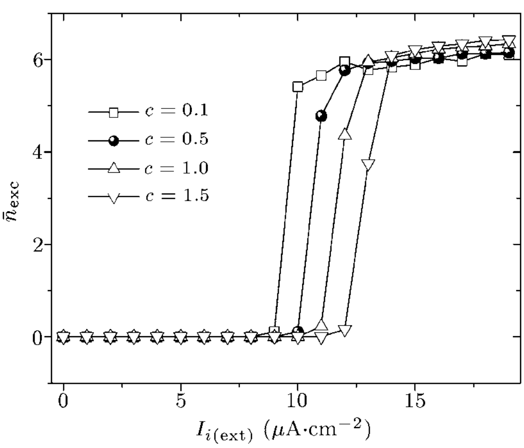

Fig. 6. Average number of excitatory neurons, $\bar{n}_{\mathrm{exc}}$, versus dc stimulus, $I_{i(\mathrm{ext})}$, at $D = 1.0$ for coupling strength $c = 0.1$, 0.5, 1.0, 1.5.

Here we would like to further discuss the influence on the stimulating threshold, which reaches the phase transition, imposed by the change of the strength of noise and coupling. According to Fig. 4, the stimulating threshold decreases with the increase of the noise strength because the strong noise, as an additional interfering stimulus, is equivalent to the increasing strength of external stimulus, which is called the beyond-phase of excitation. In Fig. 6, the stimulating threshold increases with the increase of the coupling strength because the rest period of the neurons is longer compared with the excitation period and the duration of its action is longer than that of the excitation period, which is called the lag-phase of excitation.

In conclusion, we have studied excitation properties of the neurons with the side-inhibition mechanism under the stimuli of different strengths of dc and intensity of noise and coupling, based on small-world networks. According to the simulation of the model described above, the biological neuron model built up in this study shows many characteristics, such as fatigue effect, extreme excitation principle, the rapid alternation of excitation and inhibition are similar to the workings of the brain neural system in real life. Moreover, this model has some features as follows. (1) Under weak dc stimulus, the coupling strength has stronger influence on the excitation properties. This shows that the higher the coupling strength is, the lower the average excitation of the network is, and the higher the stimulating threshold is. (2) When the dc stimulation strength exceeds a certain level of the stimulating threshold, the noise intensity has stronger influence on the excitation properties. This shows that the higher the noise intensity is, the higher the average excitation of the network is, and the lower the stimulating threshold is. In addition, the phase transition of $\bar{n}_{\mathrm{exc}}$ occurs (jumps from rest phase to excitation phase along with increase of $I_{i(\mathrm{ext})}$). (3) Under the strong dc stimulus, the average excitation of the network almost reaches the saturation and the strength of noise and coupling has little effect on the excitation properties. These features are preferably consistent with the functional features of the real brain neural system. The model brought forward by this study possesses the side-inhibition mechanism of a real brain neural system and the biological basics of the small-world neuron-connecting networks. Therefore, the outcome of this study is expected to provide a theoretical insight to the study of the learning process of a human brain towards the information processing, memory and abnormal discharge of the brain neurons (for instance, the falling sickness caused by the synchronization discharge of the neurons), and generate useful reference to the brain nerve electrophysiology and epistemological science.[17]

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