Vibrational resonance in a randomly connected neural network

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Abstract

A randomly connected network is constructed with similar characteristics (e.g., the ratio of excitatory and inhibitory neurons, the connection probability between neurons, and the axonal conduction delays) as that in the mammalian neocortex and the effects of high-frequency electrical field on the response of the network to a subthreshold low-frequency electrical field are studied in detail. It is found that both the amplitude and frequency of the high-frequency electrical field can modulate the response of the network to the low-frequency electric field. Moreover, vibrational resonance (VR) phenomenon induced by the two types of electrical fields can also be influenced by the network parameters, such as the neuron population, the connection probability between neurons and the synaptic strength. It is interesting that VR is found to be related with the ratio of excitatory neurons that are under high-frequency electrical stimuli. In summary, it is suggested that the interaction of excitatory and inhibitory currents is also an important factor that can influence the performance of VR in neural networks.

Keywords Vibrational resonance · Neural network · Izhikevich neuron model · Weak electric field

Introduction

Signal propagation is one of the most significant issues in neuroscience field (Diesmann et al. 1999; Zhou et al. 2003; Kumar et al. 2010; Guo and Li 2011; Lyamzin et al. 2015; Zhao et al. 2018). The two phenomena, stochastic resonance (SR) and vibrational resonance (VR), which are closely related with signal propagation of neural systems, have been studied intensively in recent years (Stacey and Durand 2002; Li et al. 2007; Sun et al. 2013; Xue et al. 2013). SR is a phenomenon that can be widely observed,

which is closely related with the interaction between noise and low-frequency signal (LFS) (Benzi et al. 1981). As noise is inevitable in neural systems, e.g., the synaptic background activity or the channels stochastic gating, the effects of it on signal propagation are studied based on different network structures (Yu et al. 2014; Qin et al. 2014; Megam Ngouonkadi et al. 2016; Zhao et al. 2017). VR, a phenomenon caused by the interaction of high-frequency signal (HFS) and low-frequency signal, are shown to have similar phenomena with SR, where the optimal high-frequency stimuli can enhance the response of excitable systems to a subthreshold low-frequency signal (Ullner et al. 2003; Chizhevsky 2008; Chizhevsky and Giacomelli 2005; Zaikin et al. 2002). The bichromatic signals with different frequencies can be found in a number of fields, for example, the bursting neurons in local brain areas may display two different time-scales of firing behaviors due to their diverse coupling with neighbouring neurons (Okun et al. 2015). As the high-frequency signal can be easily controlled at each time than the noise signal, it can be more efficiently when applied in related fields. Therefore, its effects are frequently studied based on different network structures, including random network, small-world network, feedforward network and modular network (Deng et al. 2010; Qin et al. 2011; Yu et al.

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2011). By studying the performance of SR or VR with the commonly used network structures, it can give us much inspiration about the mechanism of the two phenomena on signal propagation. But there should be more significant to investigate these phenomena based on a much real network that has similar characteristics as the mammalian brain, i.e., the synaptic delays, the ratio of excitatory and inhibitory neurons and the connection probability between neurons in the constructed network model are similar with the real mammalian brain.

Transcranial electrical stimulation (TES), one therapeutic method frequently studied in recent years, has been found to be useful in many fields, such as curing several kinds of neurological and psychiatric diseases (Fregni et al. 2006; Liebetanz et al. 2006), helping the wound recover (Fraccalvieri et al. 2015), enhancing the sensory perception or cognitive function (Nitsche and Paulus 2000; Iyer et al. 2005; Kirov et al. 2009; Pogosyan et al. 2009; Thomson et al. 2015). But the mechanism of such treatments is still unclear as it is difficult to measure the neuronal activities when the brain is under the treatments. Based on a small group of neurons, it is verified with both experiments and model simulation that electrical stimulation can affect the activities of neurons (Bikson et al. 2004; Deans et al. 2007; Reato et al. 2010; Kim and Lim 2017). As the rhythmic oscillations are often appeared in our brain, it is reasonable to explore the mechanisms of the currents stimulation or the electrical field stimulation with mechanism of VR by simulating a network with similar structure as the mammalian brain.

The interaction of excitatory neurons and inhibitory neurons is found to play key roles in affecting the network activities (Haider and McCormick 2009a; Renart et al. 2010). There are many studies about the interaction effects of two types of neurons based on different network structures. Based on a feedforward network, Men et al. found that the optimal firing regularity of neurons in the output layer is decreased with the increase of inhibitory neurons in each layer (Men et al. 2012). Kreuz et al. verified that coherence resonance of a FitzHugh-Nagumo (FHN) neuron model can be modulated by the balance of excitatory and inhibitory currents in the high-input regime (Kreuz et al. 2006). Recently, the interaction of excitatory and inhibitory synaptic currents is suggested to be related with the sensory perception and attention as it can modulate the rapidly changing neocortical dynamics (Haider and McCormick 2009b; Gravier et al. 2016). But how the interaction of excitatory and inhibitory currents affects the VR in a randomly connected network is still unknown.

Therefore, the rest of the paper is organized as follows: In “The neural network model” section, the construction of the randomly connected neural network model is presented. It also introduces how the electric fields are applied to the

neurons and how the Fourier coefficient Q is used for evaluating the vibrational resonance. “Results” section investigates several factors that may influence VR phenomena, such as the parameters of two signals and the network characteristics. The interaction effects of excitatory and inhibitory currents on VR are also studied here. Finally, brief discussion and conclusion of this paper are given in “Discussion and conclusions” section.

The neural network model

In this investigation, the network is constructed by the Izhikevich neuron model (Izhikevich 2003)

$$\begin{aligned}\dot{v} &= 0.04v^2 + 5v + 140 - u + I \\ \dot{u} &= a(bv - u)\end{aligned}\quad (1)$$

which has an auxiliary after-spike resetting as

$$\text{if } v \geq 30\text{mv, then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases} \quad (2)$$

Here, variables v and u are dimensionless variables. v represents the membrane potential of the neuron and u represents a membrane recovery variable, which accounts for the activation of K^+ ionic currents and inactivation of N_a^+ ionic currents. The variable u also provides negative feedback to v . The variable I is used to represent the synaptic currents and the injected currents, and the parameters a , b , c and d are dimensionless. a describes the time scale of the recovery variable u , b describes the sensitivity of the recovery variable u to the subthreshold fluctuations of the membrane potential v , c describes the after-spike reset value of the membrane potential v caused by the fast high-threshold K^+ conductances and d describes after-spike reset of the recovery variable u caused by slow high-threshold N_a^+ and K^+ conductances. From Eq. (2), it is known that the membrane voltage and the recovery variable are reset when the spike reaches its apex at +30 mV. By changing the values of these parameters, the model can exhibit many properties of biological neurons (Kawaguchi et al. 2011). The model does not have a fixed threshold and its resting potential is between -70 and -60 mV according to the value of b . We use $(b, c) = (0.2, -65)$ for all neurons in the network. The values $(a, d) = (0.02, 8)$ are used for excitatory neurons, which makes them behave as regular spiking neurons. For inhibitory neurons, the values $(a, d) = (0.1, 2)$ are set, which makes them behave as fast spiking neurons.

An anatomically realistic network model is simulated here, which is composed by excitatory (80%) and inhibitory (20%) neurons with conduction delay between neurons. The ratio of excitatory to inhibitory cells is 4–1, as in

the mammalian neocortex. The connection probability between neurons is 0.1, again as in the neocortex. Each neuron is described by the simple spiking model (Eq. 1). The connections of the neurons in the network belong to the pulse-coupled type, where the firing of the presynaptic neuron instantaneously changes the membrane potential v of the postsynaptic neurons by the synaptic weight s_{ij} . Here, we assign excitatory synaptic weights to distribute randomly in the range of [0, 6] mV and inhibitory weights in the range of [0, 8] mV except mentioned additionally. The synaptic connections among neurons have fixed conduction delays, which are random integers between 1 and 20 ms. In detail, 1 ms delay is assigned to all inhibitory connections, and 1 to 20 ms delay is assigned to all excitatory connections.

Inhibitory neurons were not polarized by the weak electric field, assuming a typical symmetric morphology (Radman et al. 2009). For excitatory neurons and weak uniform electric fields, the change of membrane voltage is linear with the magnitude of the applied field and the polarization of the single-neuron model of Izhikevich to a current injection exhibits low-pass characteristics (Deans et al. 2007; Reato et al. 2010). So the electrical stimulation in the model is implemented as low-pass-filtered current I_E that is proportional to the applied electrical field:

$$\tau_E \frac{\partial I_E}{\partial t} = -I_E + k_E E(t), \quad (3)$$

where k_E is the sensitivity of the membrane to the field and depends on cell geometry and field orientation. Here, the electrical stimulation includes two types of electrical field, the low-frequency electrical field ($E_L(t) = A_s \sin(2\pi f_s t)$) and high-frequency electrical field ($E_H(t) = B_s \sin(2\pi f_{hs} t)$). In order to achieve a better match with experimentally obtained magnitude response, the sensitivity $k_E = 0.1 \text{ m/V}$ and time constant $\tau_E = 10 \text{ ms}$, the same as in Ref. (Reato et al. 2010). Thus, the variable I in Eq. (1) has the form as $I = I_{EL}(t) + I_{EH}(t) + I_{syn}(t)$, where $I_{EL}(t)$ represents the low-frequency current (the currents produced by the low-frequency electrical field), $I_{EH}(t)$ represents the high-frequency current (the currents produced by the high-frequency electrical field), and $I_{syn}(t)$ is the neuron's presynaptic currents.

To evaluate the effects of the vibrational resonance on the neural network, we calculate the Fourier coefficient Q for the input frequency. We use the Q parameter instead of the power spectrum because we are interested in the transport of the information by the neural network. For this task the Q parameter is a much more compact tool than the power spectrum (Gammaitoni et al. 1998),

$$\begin{aligned} Q_{\sin} &= \frac{\omega}{2n\pi} \int_0^{2\pi n/\omega} 2x(t) \sin(\omega t) dt, \\ Q_{\cos} &= \frac{\omega}{2n\pi} \int_0^{2\pi n/\omega} 2x(t) \cos(\omega t) dt, \\ Q &= \sqrt{Q_{\sin}^2 + Q_{\cos}^2}, \end{aligned} \quad (4)$$

Here, n is the number of periods, and $\omega = 2\pi f_s$ where f_s is the frequency of the filtered low-frequency signal I_{EL} . The maximum of Q shows the best phase synchronization between input signal and output firing rate of the network. It is to be noted that in the case of phase synchronization one could expect a response of the Q measure but not vice versa. Also, as information in the neuron system is carried through large spikes instead of subthreshold oscillations, we are more interested in the frequency of spikes. So the firing rate of the network ($x(t)$) is used in Eq. (4), which is calculated as $x(t) = \frac{Nn}{t}$ and Nn is the firing times of the network during t s. Other parameters used in this paper are given in each case.

Results

Network responses to high-frequency signal with different intensities

The effects of amplitudes of HFS on neuronal activities are studied firstly based on the neural network constructed above. In Fig. 1, it can be easily found that the spike raster of neurons changes with the increase of the amplitude of the HFS. When the signal's amplitude is lower, all of the neurons fire randomly. When the signal's amplitude is increased to a certain intensity (here, $B_s = 6 \text{ mV}$), the network is firing regularly where most of the neurons in the network have similar rhythm. When the signal's amplitude is increased further, the neurons are firing more frequently than before, but it is not as rhythmic as the case with medium amplitude, and the spiking rhythms of excitatory and inhibitory neurons also differ apparently. Considering that the LFS has a frequency of 5 Hz, it is obvious that the neuron activities are much synchronous with the low-frequency signal when the amplitude of high-frequency signal has a suitable intensity (Fig. 1b). This is consistent with the previous results where the amplitude of high-frequency signal can modulate the synchronization between the network activity and subthreshold low-frequency signal (Deng et al. 2010).

Fig. 1 Spike raster diagrams of randomly coupled 600 neurons under the stimulation of the same subthreshold LFS and different HFSs. Red dots represent inhibitory spikes and blue dots represent excitatory spikes. LFS has the frequency and amplitude as $f_s = 5$ Hz and $A_s = 0.2$ mV, and the HFS has the frequency as $f_{hs} = 50$ Hz and the amplitudes as **a** $B_s = 2$ mV; **b** $B_s = 6$ mV; **c** $B_s = 8$ mV. (Color figure online)

The effects of high-frequency and low-frequency signals on network activities

As the amplitude of the high-frequency signal above plays strong roles on the propagation of low-frequency signal, the interaction between the two kinds of signals and the neural network is studied in detail. In Fig. 2, the response Q is calculated as the function of amplitude of high-frequency signal. It can be found that there is a maximal Q value in each line corresponding to the optimal

vibrational resonance state. With the increase of the amplitude of low-frequency signal, the optimal amplitude of high-frequency signal is also shifted towards the right. In addition, the maximal Q value is increased with the increase of amplitude of low-frequency signal, which means the vibrational resonance phenomenon is more obvious than the cases with low amplitude of low-frequency signal.

Then we fix the amplitude of low-frequency signal and change its frequency, and the results are shown in Fig. 3. It

Fig. 2 Response Q of the neural network versus the amplitude of HFS for different intensities of LFS. The frequencies of the LFS and HFS are $f_s = 5$ Hz and $f_{hs} = 50$ Hz respectively

Fig. 3 Response Q as a function of the amplitude of HFS for different frequencies of LFS. The amplitude of the LFS is $A_s = 0.2$ mV, and the frequency of the HFS is $f_{hs} = 50$ Hz

is shown that the response Q is increased with the increase of LFS's frequency. Moreover, with the increase of frequency of LFS, the optimal amplitude of high-frequency signal for vibrational resonance shifts right slightly, indicating that the network needs high-frequency signal with higher amplitude to attain an optimal vibrational resonance state.

In Fig. 4, we fix the amplitude and frequency of LFS and calculate the Q values corresponding to the changes of frequency of HFS. Interestingly, it is found that the frequency of HFS is also an important factor that can strongly influence the activities of the neural network. With the increase of frequency of LFS, the optimal amplitude of high-frequency signal corresponding to the maximal Q value shifts right obviously, which indicates that the network needs high-frequency signal with higher amplitude to attain an optimal vibrational resonance state.

To gain more insights into the effects of the two signals on vibrational resonance, the response Q is calculated as a function of both the frequency and amplitude of high-frequency signal (Fig. 5). It can be seen that the optimal vibrational resonance relates to both of the HFS's parameters, where the maximal Q values corresponding to different frequencies of HFS are almost unaltered but the optimal amplitude of HFS for VR is increased with the increase of HFS's frequency.

In Fig. 6, the response Q is calculated as a function of the frequency of low-frequency signal and amplitude of high-frequency signal. It can be found that the optimal amplitude of high-frequency signal corresponding to the maximal Q is increased slightly with the increase of the frequency of low-frequency signal. By comparing Fig. 6a and b, it is also found that the optimal amplitude of LFS is increased obviously with the increase of the frequency of HFS, but the variation trend of Q is still consistent in the two cases.

Fig. 4 Response Q as a function of the amplitude of HFS for different frequencies of HFS. Here, $A_s = 0.2$ mV, $f_s = 5$ Hz

Fig. 5 Response Q as a function of the amplitude of amplitudes of the HFS. Here, $A_s = 0.2$ mV, $f_s = 5$ Hz

Fig. 6 Response Q as a function of the frequency of LFS and amplitude of HFS with $A_s = 0.2$ mV and $f_{hs} = 50$ Hz. **a** $f_{hs} = 50$ Hz; **b** $f_{hs} = 80$ Hz

The effects of network properties on signal propagation

In this part, several network properties that may influence the signal propagation are studied in detail. Figure 7 shows the response Q as a function of the amplitude of high-frequency signal under different neuron populations. It can be found that the maximal Q increases firstly with the

increase of neuron population, then it decreases when the neuron population is large enough. Moreover, the amplitude of high-frequency signal corresponding to the maximal Q has a decreasing trend with the increase of neuron population. As the percentage of excitatory neurons is larger than that of the inhibitory neurons in the network, increased neuron population should lead to an increase in the summation of excitatory currents compared with the increase of inhibitory currents, which further influences the excitability of the network. Specially, it should be noted that the more excitatory currents in the network do not always mean a better signal propagation. The intrinsic frequency of a neuron also plays important roles in the network firing activities here because the neurons are likely to fire at a certain frequency although much more excitatory currents are existed in the network than the excitatory currents of network with smaller neural population.

The synaptic strength is also studied here as it is the key factor that determines the presynaptic neurons' influences on their postsynaptic neurons. In Fig. 8, it is shown that the maximal Q is increasing with the increase of the synaptic strength, but the amplitude of high-frequency signal corresponding to the maximal Q is decreased when the synaptic strength is increased. This result should be related with the balance of the excitatory and inhibitory currents in the network. As the network is constructed with pulse-coupled synaptic connections, increasing the synaptic strength can result in the increase of postsynaptic currents for the spiking neurons. Considering the larger proportion of excitatory neurons in the network, it can easily noticed that more excitatory currents are generated with the increase of the synaptic strength than inhibitory currents, which makes the network more active and its firing activities are more easily to be consistent with the frequency of the low-frequency signal. The results are also consistent with the previous investigations where they found the

Fig. 7 Response Q as a function of the amplitude of HFS for different neuron population N . Here, $A_s = 0.2$ mV, $f_s = 5$ Hz, and $f_{hs} = 50$ Hz

Fig. 8 Response Q as a function of the amplitude of HFS for different ranges of synaptic strength. Here, the excitatory synaptic weights are distributed randomly in the range of $[0, 6 + a]$ mV, and the inhibitory synaptic weights are distributed in $[0, 8 + a]$ mV. $A_s = 0.2$ mV, $f_s = 5$ Hz, $f_{hs} = 50$ Hz

promoting effects of excitatory synapses on the network activities (Bateup et al. 2013; Hånell et al. 2015; Men et al. 2012).

The connection probability of neurons in the network is also one key factor that influences the efficiency of the signal propagation. In Fig. 9, it can be found that the increase of the connection probability leads to the increase of the maximal Q values and the decrease of the optimal amplitude of high-frequency signal. This is similar with the results caused by the changes of the synaptic strength of neurons, but the mechanisms of them should have some differences. The increase of connection probability makes each neuron connected with more neurons than itself before. As the number of excitatory neurons is much more than the number of inhibitory neurons (4:1), more excitatory synapses are appeared in the network, which results in

Fig. 9 Response Q as a function of the amplitude of HFS with different connection probability P . Here, $A_s = 0.2$ mV, $f_s = 5$ Hz, $f_{hs} = 50$ Hz

more excitatory currents and makes the network activities more consistent with the frequency of low-frequency signal than the case with low connection probability. However, increasing the synaptic strength leads to the increased summation of excitatory currents as there are more excitatory neurons than inhibitory neurons that increase their synaptic strength.

Vibrational resonance affected by the interaction of excitatory and inhibitory currents

From the influence of the network parameters on vibrational resonance, it is found that the interaction of excitatory and inhibitory currents in the network plays key roles in determining the performance of VR. To further understand the mechanism underlying the interaction of the two types of currents, the effects of synaptic currents of excitatory and inhibitory neurons are studied by modulating the fraction of excitatory neurons that are under HFS stimulation. The results are shown in Fig. 10, where r is the ratio of excitatory neurons that are stimulated by LFS and HFS. It can be found that the Q values are increasing with the increase of the fraction r , which indicates the interaction between the excitatory and inhibitory currents plays important role in the signal propagation of the network. Neurons under the external electrical stimulation are more likely to spike, which further produces more postsynaptic currents and increases the activities of the whole network. With the increase of the stimulation ratio, more neurons are induced to fire with a relatively high rate, resulting in good performance of vibrational resonance (Fig. 10).

Figure 11 shows the effects of the postsynaptic currents, which includes both the mean currents of excitatory and inhibitory neurons under the changes of stimulation

fraction, and the total currents of excitatory or inhibitory neurons are averaged by the number of neurons in the corresponding type. When the ratio of excitatory neurons under stimulation is low, the mean excitatory currents are similar with the mean inhibitory currents. With the increase of stimulation ratio, both currents are increasing, but the excitatory currents increase much faster than the inhibitory currents. This makes a big gap between the total excitatory currents and inhibitory currents for the network. At the same time, the network displays more consistent activities with the LFS, suggesting the key effects of the currents on the signal propagation. Finally, the results in this part also suggest that the network activities induced by the changes of the network parameters can be modulated by the external stimuli.

Discussion and conclusions

In this paper, VR in a randomly connected neural network is discussed with different stimulation signals and network parameters. The results show that HFS with suitable amplitude can improve the consistency of network firing rates and LFS. Moreover, VR is verified to be related with the network parameters including the neuron population, the synaptic strength, the connection probability and the interaction between excitatory and inhibitory currents.

The effects of two signals on VR are studied systematically by modulating their amplitudes and frequencies individually. It is consistent with previous investigations that VR is more obvious when the amplitude of LFS is higher (Deng et al. 2010). It is interesting that the noise intensity can also modulate the resonance of the network activity and sub-threshold signal (Qin et al. 2014; Zhao et al. 2017), indicating the similar effects of the amplitude of HFS and noise intensity. The frequencies of two signals

Fig. 10 Response Q as a function of the amplitude of HFS for different ratio (r) of excitatory neurons that are under stimuli. Here, $A_s = 0.2$ mV, $f_s = 5$ Hz, $f_{hs} = 50$ Hz

Fig. 11 Mean synaptic currents of excitatory and inhibitory neurons. Here, $A_s = 0.2$ mV, $f_s = 5$ Hz, $f_{hs} = 50$ Hz

also play essential roles in affecting the VR. When the frequency of HFS is higher, the optimal amplitude of HFS for VR shifts right obviously, indicating that the network needs stronger HFS to attain an optimal state for signal propagation. It is interesting that changing the frequency of LFS can lead to similar variation trends with that resulted from the frequency changing of HFS, but the variation range of the optimal amplitude for VR is much smaller than that resulted from HFS. Moreover, it should be stated that the mechanisms for the frequency change of two signals are different. The change of LFS is related with the natural frequency of the network, where the activity of network will be more easily synchronized with the rhythm of LFS when the signal's frequency is near the natural frequency of the network. But for the effects of HFS's frequency, the changes of optimal amplitude for VR (shifts right) are mainly caused by the reduced amplitude of HFS, that is, the amplitude of HFS applied on the neurons is decreased more when its frequency is higher as the external electrical field is going through a low-pass filter before it is applied on neurons (See Eq. 3).

The factors of the network that may influence the propagation of sub-threshold signal are studied in detail. It is found that the maximal Q values can increase with the neuron population, the coupling strength or the connection probability between neurons. Considering the network structure, it is reasonable that more excitatory currents can be produced in the network with the increase of these parameters, which makes the network more easily excited under the same sub-threshold stimuli. Induced by the effects of these parameters, the effects of the network's currents are studied by modulating the ratio of excitatory neurons that are under HFS stimulation. It can be found that the Q values of the network are increased with the increase of the ratio of excitatory neurons, which means that the network activity can be modulated by the ratio of neurons under external stimulation. VR has been widely studied with different network structures (Yu et al. 2015; Ağaoğlu et al. 2016). Based on a small-world network with spike-timing-dependent plasticity (STDP), it is found that the effects of VR on signal propagation can be weakened by inhibitory synapses (Yu et al. 2015). Interestingly, the mechanisms of theirs are similar with ours where the increase of inhibitory neurons results in the decrease of excitatory currents of synapses in the network, which further reduces the coherence between neural firings and low-frequency signal. But the changes of synaptic currents in their investigations are caused by the interaction of STDP and competition between excitatory neurons and inhibitory neurons, where STDP is not considered in this study. VR is also investigated in a scale-free network consisted of excitatory neurons, and it is found that the optimal amplitude of high-frequency signal for VR is increased

with the increase of synaptic strength (Ağaoğlu et al. 2016). However, the increase of synaptic strength here reduces the optimal amplitude of high-frequency signal for VR. Besides the different network structures, the differences here should also be related with the different synaptic coupling ways as theirs are electrical coupling and ours are pulse-coupled type with time-delay (Ağaoğlu et al. 2016).

TES has been verified its effectiveness in different disciplines although there still lacks clear description about its mechanism. Using the intracellular recording technique, the effects of TES on hippocampal slice of rat are studied, where the TES is verified to polarize somatic membrane potentials and further influences the firing rates and the spiking time of the neurons in the network (Reato et al. 2010; Fröhlich and McCormick 2010). As SR is a possible mechanism for the illustration of TES, various investigations for the effects of weak electrical field on noisy network are studied. Because of the similarity of VR and SR and the controllable property of HFS and LFS, a randomly connected neural network that utilizes the structural parameters of anatomical mammalian cortex is constructed with Izhkevich neural model in this investigation, which is applied to investigate the effects of different parameters of neural networks together with the interaction effects of external electrical fields. The investigation here suggests that the two types of weak electrical fields can play key roles in modulating the cortical activities, and weak LFS with suitable frequency can be effective with a relatively small amplitude when another HFS is applied simultaneously. As the network properties studied above show important effects on the effectiveness of external stimuli, it should also be considered before the application of TES. By knowing the structures of the local area in the brain, the performance of TES applied to a certain brain area should be elevated by modulating the amplitude of stimuli according to the ratio of neurons under stimuli.

The results here should be significant to the field of neuroscience. As the TES usually needs multiple consecutive sessions to become effective (Chavet et al. 2015), it should also be related with the effects of synaptic plasticity. Therefore, further investigations will be focused on the effects of synaptic plasticity on the performance of TES.

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