Synchronization of neuron population subject to steady DC electric field induced by magnetic stimulation

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Abstract Electric fields, which are ubiquitous in the context of neurons, are induced either by external electromagnetic fields or by endogenous electric activities. Clinical evidences point out that magnetic stimulation can induce an electric field that modulates rhythmic activity of special brain tissue, which are associated with most brain functions, including normal and pathological physiological mechanisms. Recently, the studies about the relationship between clinical treatment for psychiatric disorders and magnetic stimulation have been investigated extensively. However, further development of these techniques is limited due to the lack of understanding of the underlying mechanisms supporting the interaction between the electric field induced by magnetic stimulus and brain tissue. In this paper, the effects of steady DC electric field induced by magnetic stimulation on the coherence of an interneuronal network are investigated. Different behaviors have been observed in the network with different topologies (i.e., random and small-world network, modular network). It is found that the coherence displays a peak or a plateau when the induced electric field varies between the parameter range we defined. The coherence of the neuronal systems depends extensively on the network structure and parameters. All these parameters play a key role in determining the range for the induced electric

field to synchronize network activities. The presented results could have important implications for the scientific theoretical studies regarding the effects of magnetic stimulation on human brain.

Keywords Steady DC electric field · Magnetic stimulation · Topology · Synchronization

Introduction

Electrical recordings from the massively parallel brain regions such as the neocortex and cerebellum invariably reveal robust oscillatory activity. These network oscillations are attractive for cellular neurophysiologists interested in understanding network behavior in terms of the underlying biophysical mechanisms. The study of synchronous oscillations has become an area of converging interests across many disciplines in neuroscience.

In the past decades, many experimental and theoretical studies have focussed on synchronous oscillations in neural systems. During the last 20 years, the study of neural rhythms has undergone a major renaissance, we now have far more information about how rhythms are produced, how they are associated with normal function, and how pathologies in rhythms relate to neurological diseases. In pursuit of the idea that synchronous rhythms are actually relevant to adaptive brain functioning, increasingly specific relationships have been proposed between neuronal oscillations and numerous cognitive functions. For instance, evidence from studies of the cortical gamma rhythm suggests that it is associated with temporal binding of sensory stimuli (Kaiser et al. 2009; Tallon-Baudry 2009; Sederberg et al. 2007), information transmission (Gielen et al. 2010; Børgers and Kopell 2008; Li et al. 2011), attentiveness (Lakatos et al.

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2008; Gu and Liljenström 2007), cognitive processing (Rojas-Líbano and Kay 2008), focused arousal (Lee et al. 2001), sensory perception (Correa and Nobre 2008; Schroeder and Lakatos 2009) and movement (Cheyne et al. 2008), memory (Ventriglia 2008). In addition to above evidence for normal function related with gamma oscillatory, more recent results clearly indicate that an altered or aberrant version of normal gamma oscillatory activity may be associated with cognitive and behavioral impairments in schizophrenia (Uhlhaas et al. 2006; Uhlhaas and Singer 2010; Haenschel et al. 2009). Impaired synchronous gamma oscillations was also found in patients with autism (Wilson et al. 2007) and Alzheimer's disease (Koenig et al. 2005; Stam et al. 2007; Yener and Başar 2010). Thus, consensus is building that neuronal oscillations are instrumental rather than incidental to brain function and dysfunction.

More recently, Jiao and Wang (2010) explored the synchronous firing patterns in neuronal population with excitatory and inhibitory connections. Liu et al. (2010) shows the role of inhibitory neurons for network synchronization. The effect of phase synchronization in dynamic transmission of neural information has been investigated (Wang and Zhang 2011; Wang et al. 2008a). Zhang et al. (2010) studied the relationship between variable higher-order coupling and synchronization of neuronal oscillator population. The dependence of synchronization on the information transmission delay has also been investigated (Wang et al. 2008b, 2010a, b).

As is well known, synchronization of complex neural network results from the interplay between the intrinsic properties of individual neuron and the network topology. Traditionally, excitatory principal neurons in the hippocampus are viewed as a major source of rhythmogenesis as well as neuronal synchronization. However, extensive research has demonstrated that the principal neurons usually desynchronizes rather than synchronizes repetitive spike firings of mutually coupled neurons (Hansel et al. 1995; van Vreeswijk et al. 1995). Moreover, there was a large body of evidence converging that pyramidal cell populations may be entrained by a population of GABAergic inhibitory interneurons firing rhythmically and in synchrony (Liu et al. 2010; Buzsaki et al. 1983; Lytton and Sejnowski 1991). The mechanism of synchronization originating from inhibition also have been shown in other computational works (Whittington et al. 1995; Ermentrout 1996; Traub et al. 1996a, b). Above observation supports the notion that whether an interneuronal network could subserve an adequate basis for population rhythm or control the granule neuron activity in the hippocampus. In this study, we consider synchronizing in a network of interconnected GABAergic fast-spiking interneurons by means of numerical simulations.

The typical inhibitory network discussed above is Interneuronal Network Gamma (ING), which does not

depend on the participation of excitatory cells. ING can be induced relatively simply in vitro by the application of specific antagonists of the major fast excitatory components of synaptic transmission (Whittington et al. 1996; Traub et al. 1996b), such as ionotropic (i.e., NMDA and AMPA) glutamate receptor blockers. Previous works have found that there may be physiological correlates when examining the afferent input to auditory cortex from subcortical areas (Barth and MacDonald 1996), or tonic excitation of populations of purely inhibitory neurons such as the thalamic reticular nucleus (Pinault and Deschênes 1992). It also has been simulated in large-scale, biophysically realistic computational models (Traub et al. 2000). Recent theoretical study examines the progress in understanding how different hippocampal interneuron networks contribute to feedback and feed-forward inhibition at different timescales (Kullmann 2011). Furthermore, an experiment results not only shows a critical role for hilar GABAergic interneuron activity in controlling spatial learning and memory retrieval, but also provides evidence for the potential contribution of GABAergic interneuron impairment to the pathogenesis of amnesia in Alzheimer's disease (Andrews-Zwilling et al. 2012).

Although synchronous activity in neural networks has been reported extensively in the past years, most of them was mostly devoted to the study of local scale structure of real complex networks, such as random (Strogatz 2001), small-world (Perc 2007; Ozer et al. 2009; Sun et al. 2008) or scale-free network (Perc 2008; Wang et al. 2011). Moreover, some scientific research demonstrates that the brain's structural and functional systems show some common features of complex networks, such as small-world topology, highly connected hubs and modularity (Bullmore and Sporns 2009; Stam and Reijneveld 2007; Meunier et al. 2010; Zamora-López et al. 2010).

The property of a modular community structure is one of important organizational principles for lots of information processing systems in brain network. A module is topologically defined as a subset of highly inter-connected nodes which are relatively sparsely connected to nodes in other modules (Meunier et al. 2010). It is shown that cortical neuronal networks are modular, which composed of certain subnetworks with differential internal and external connectivity in macaque monkeys and cats (Scannell et al. 1995; Hilgetag and Kaiser 2004). Quantitative analysis of (hierarchical) modularity in brain networks has revealed that the cortical hubs form a spatially delocalized, but topologically central module with the capacity to integrate multisensory information in a collaborative manner, by facilitating the communication between the different sensory modalities (Zhou et al. 2006). Thus, investigating synchronization phenomena of neuronal systems in modular networks can extend the works on the understanding of

dynamics. Meanwhile, it also may be meaningful to neuroscientists.

Neurons in nervous system will undergo a variety of physiological processes, under the influence of electrical field, which is induced by external magnetic fields. The effects of induced electric field on the dynamics of the nervous system have been investigated through both experiments and numerical simulation. Clinical evidences point out that magnetic field can induce an electrical field that modulates neuronal activity of special brain tissue (Legros et al. 2010; Cook et al. 2004). For example, transcranial magnetic stimulation (TMS) can disrupt or induce activity in a particular brain tissue (Pashut et al. 2011; Kamitani 2011). It provides a valuable tool to map brain function, such as motor and sensory processes, attention, memory, language, and neuronal plasticity (Di Lazzaro et al. 2004; Lisanby et al. 2000; Terao and Ugawa 2002; Ziemann and Rothwell 2000). Moreover, TMS has been used for promising clinical applications in the treatment for several psychiatric and neurological disorders (Dlabáč-De Lange et al. 2010; George et al. 2010; Kobayashi and Pascual-Leone 2003). Devos and Lefebvre (2006) found the impaired neural rhythms originating the symptoms are re-organized by the magnetic stimulus toward physiological rhythms.

However, the underlying mechanisms supporting the interaction between the electrical field induced by the magnetic stimulus and brain tissue are still not clear. To our knowledge, there are still no corresponding works on studying the effects of induced electric field on synchronization of interneuronal networks. Therefore, in this paper, we will take a first step on this topic by studying the effects of steady DC electric field induced by linear varying magnetic field on the dynamics of neuronal network. The network in this paper consists of fast-spiking interneurons only. Researchers believe that the excitatory cell populations may be entrained by inhibitory rhythm originating from fast-spiking interneurons. The fast-spiking interneuron in this paper adopt single compartment HH model (Hodgkin and Huxley 1952), which is more biologically plausible for modeling the influence induced by electric fields. Different network topologies from simple random and small-world network to complex modular network are considered. The modular network consists of several small-world subnetworks, one of which is taken as central module directly controlling others. Moreover, the effects of network structure and parameters on the coherence of population are also investigated.

The rest of the present study is arranged as follows. Firstly, a one-compartment HH model under an electric field and methods are introduced briefly in “Model and methods” section. Then, the coherence oscillation under the effects of DC electric field in random network are investigated in “Effect of DC electric field in random

network”. The analyses of coherence oscillation in small-world and modular network are presented in “Effect of DC electric field in small-world network” and “Effect of DC electric field in modular network” sections, respectively. Finally, conclusions and discussions are made in “Conclusions” section.

Model and methods

Each interneuron is described by a single compartment and obeys the current balance equation:

$$C_m \frac{dV}{dt} = -g_{Na} m_\infty^3 h (V - E_{Na}) - g_K n^4 (V - E_K) - g_L (V - E_L) - I_{syn} + I_{app}. \quad (1)$$

The units of conductance are mS/cm², those of current are μ A/cm², and capacitance is μ F/cm², where $C_m = 1 \mu$ F/cm² and I_{app} is the injected current. The leak current has a conductance $g_L = 0.1$ mS/cm² and reversal potential $E_L = -65$ mV. The spike-generating Na⁺ and K⁺ voltage-dependent ion currents are of the Hodgkin-Huxley type (Hodgkin and Huxley 1952). The transient sodium current Na⁺ has one activation variable m , which is assumed fast and substituted by its steady-state function m_∞ ; and one inactivation variable h , which obeys a first-order kinetics. $g_{Na} = 35$ mS/cm²; $E_{Na} = 55$ mV, $\emptyset = 5$.

$$m_\infty = \frac{\alpha_m}{\alpha_m + \beta_m}$$

$$\alpha_m(V) = \frac{-0.1(V + 35)}{\exp(-0.1(V + 35)) - 1} \quad (2)$$

$$\beta_m(V) = 4 \exp(-(V + 60)/18)$$

$$\frac{dh}{dt} = \phi(\alpha_h(1 - h) - \beta_h h)$$

$$\alpha_h(V) = 0.07 \exp(-(V + 58)/20) \quad (3)$$

$$\beta_h(V) = \frac{1}{\exp(-0.1(V + 28)) + 1}.$$

The activation variable n of the delayed rectifier potassium current K⁺ also obeys a first-order kinetics, $g_K = 9$ mS/cm²; $E_K = -90$ mV.

$$\frac{dn}{dt} = \phi(\alpha_n(1 - h) - \beta_n n)$$

$$\alpha_n(V) = \frac{-0.01(V + 34)}{\exp(-0.1(V + 34)) - 1} \quad (4)$$

$$\beta_n(V) = 0.125 \exp(-(V + 44)/80).$$

First, the electric field induced by magnetic field should be determined, when a time-varying magnetic field is applied to the brain, a time-varying electric field is induced according to Faradays' law:

$$E(t) = \frac{r}{2} \frac{dB(t)}{dt}, \quad (5)$$

where r is the radius of exposure. In this paper, we assume that magnetic field varies linearly, and then a steady DC electric field E_0 will be induced.

Second, the effect of induced electric field on membrane depolarization will be considered. It is known that the membrane potential V results from the differential of ions concentrations between the extra- and intra- cellular medium, and it can be described by the GHK equation (Goldman 1943; Hodgkin and Katz 1949). A movement of charges carried by ions is possible under the electric force exerted by the induced electric field. Therefore, charges may accumulate in parts of the membrane under the effect of induced electric field. Membrane depolarization will be greater with the increase of charges accumulation. The relationship between the field-induced membrane depolarization ΔV and a steady DC electric field with amplitude E_0 can be described by following differential equation:

$$\frac{d\Delta V}{dt} + \frac{1}{\tau} \Delta V = \frac{\lambda}{\tau} E_0. \quad (6)$$

Complex geometry of real neuron cell and their polarisability have been considered in Eq. (6), λ is the polarization length (Radman et al. 2009) and τ is the Maxwell–Wagner time constant, which indicates the “speed” of charges accumulation on the cell membrane (Bédard et al. 2006).

Moreover, the solution to Eq. (6) was derived by Schwan in the case of assuming spherical cell geometry in 1957 (Schwan 1957):

$$\Delta V = 1.5 RE_0 \cos \theta, \quad (7)$$

where R is the cell radius and θ the angle between the axis of the DC electric field and normal vector in somewhere of the membrane, $\cos \theta = 1$ in the ideal case. Then the membrane depolarization ΔV is proportional to the DC electric field with amplitude E_0 .

Recently, the transmembrane voltage component ΔV induced by DC electric field (Kotnik et al. 1998 and Kotnik and Miklavcic 2000) takes the following form:

$$\Delta V(t) = K_c E_c R \cos \theta \left[1 - \exp\left(-\frac{t}{\tau_c}\right) \right]. \quad (8)$$

R is the cell radius, E_c is the amplitude of electric field, θ is the polar angle measured with respect to the direction of the electric field. K_c is a constant parameter (Kotnik et al. 1997) determined by the geometric structure and electrical properties of the cell, τ_c is the membrane time constant (Pauly and Schwan 1959). The induced voltage caused by DC electric field E_c , it gradually decays to steady-state value with time increased according to Eq. 3:

$$\Delta V(t) = K_c E_c R \cos \theta \quad (9)$$

Equation (9) also shows that the membrane depolarization ΔV is proportional to the DC electric field. Overall consideration, for simplicity, we make E_0 equal to ΔV in this paper.

Third, to include the field-induced membrane depolarization in the model, we considered the ΔV acts as an additive perturbation to the membrane potential V (Gianni et al. 2006). In this study, V_E stands for ΔV , and $C_m dV_E/dt = 0$ when V_E is a DC electric field. Thus, the Eq (1) could be rewritten as:

$$C_m \frac{dV}{dt} = -g_{Na} m_{\infty}^3 h [(V + V_E) - E_{Na}] - g_K n^4 [(V + V_E) - E_K] - g_L [(V + V_E) - E_L] - I_{syn} + I_{app}. \quad (10)$$

In real neural network with a large amount of neurons, it is unnecessary and impossible to add external signals to all involved individuals. Only weak and local input is reasonable. So, the induced electric field will be applied to a fraction PN ($0 < PN < 1$) of elements in the neuronal population in this paper.

The synaptic current $I_{syn} = g_{syn} s (V - E_{syn})$, where g_{syn} is the maximal synaptic conductance and E_{syn} is the reversal potential. We set $g_{syn} = 0.1 \text{ mS/cm}^2$, $E_{syn} = -75 \text{ mV}$ (Buhl et al. 1995). The gating variable s represents the fraction of open synaptic ion channels and obeys a first-order kinetics (Perkel et al. 1981; Wang and Rinzel 1993):

$$\frac{ds}{dt} = \alpha F(V_{pre})(1 - s) - \beta s$$

$$F(V_{pre}) = \frac{1}{1 + \exp(-(V_{pre} - \theta_{syn})/2)}, \quad (11)$$

where $F(V_{pre})$ is assumed to be an instantaneous and sigmoid function of the presynaptic membrane potential; $\theta_{syn} = 0 \text{ mV}$, it is high enough so that the transmitter release occurs only when the presynaptic cell fires a spike. We take the channel opening rate $\alpha = 12 \text{ ms}^{-1}$ and the channel closing rate $\beta = 0.1 \text{ ms}^{-1}$.

In order to quantify the synchronization of interneurons under the influence of DC electric field, we introduce a coherence measure based on the normalized cross-correlations of the neuronal pairs in the network (Wang and Buzsáki 1996). The coherence between neurons i and j is measured by their cross-correlation of their spike trains. A long time interval T is divided into small bins of τ_T , so the two spike trains can be given by $X(l) = 0$ or 1 , $Y(l) = 0$ or 1 , $l = 1, 2, \dots, m$ ($T/m = \tau_T$). The small time constant $\tau_T = 1 \text{ ms}$. The definition of coherence for the pair as following:

$$k_{ij} = \frac{\sum_{l=1}^m X(l)Y(l)}{\sqrt{\sum_{l=1}^m X(l) \sum_{l=1}^m Y(l)}}. \quad (12)$$

The population coherence measure K is defined by the average of k_{ij} over each pair of neurons in the network. It

not only can be used to quantify the synchronization of the network, but also could be applied to quantify the synchrony of nonoscillatory neuronal firings. The degree of synchrony of the network can be quantified by how $K(\tau_T)$ behaves as function of τ_T . Therefore, $K(\tau_T)$ varies between 0 and 1 for all τ_T . In the present study, the coherence index K is calculated with $\tau_T = 0.1/f$, where f represents the mean firing rate of the network.

The network model was integrated using the Modified Euler method, with integration step 0.01 ms. As initial conditions, the membrane potential is uniformly distributed between -70 and -55 mV and the other channel-gating variables are set at their corresponding steady-state values. The population coherence was calculated after 1,000 ms transients.

Effect of DC electric field in random network

After the construction of the model, we investigate the firing patterns induced by the DC electric field. The bifurcation diagram of membrane voltage V for different amplitudes of electric field V_E is shown in Fig. 1. Thick solid lines indicate stable fixed points and thin lines represent unstable fixed points. Solid and open circles represent stable and unstable periodic solutions, respectively.

The cells can fire spikes periodically when V_E varies between $[-28 \text{ } -2]$ mV. Different firing patterns corresponding to DC electric field with different values of V_E are shown in Fig. 2. Once the amplitude of V_E becomes larger

Fig. 1 Bifurcation diagram of the single model versus induced electric field. It shows the single neuron from rest to tonic firing and then decays to rest versus the induced electric field V_E . Lines and circles indicate fixed points and periodic solutions, respectively. Thick solid lines indicate stable fixed points; thin lines are unstable fixed points. Solid circles are stable periodic solutions and open circles are unstable periodics. When V_E varies between $[-28 \text{ } -2]$ mV, the cell can fire spikes

than the threshold (1.5 mV), the neuron begins to fire a spike. The firing rate increases with the amplitude of V_E . The voltage decays to rest when V_E has grown to exceed an extreme value (28.5 mV).

Now we consider the network which consists of interconnected GABAergic fast-spiking interneurons. First of all, the coherence of a random network has been

Fig. 2 The action potential of the single model with different values of V_E . The fire rate increases with V_E in (a–e). But when $V_E < -28.5$ mV, the voltage decays to rest in (f)

Fig. 3 Example of considered random network topologies. Given 100 isolated nodes, one connects every pair of nodes with probability p_r , **a** 0.01, **b** 0.1

investigated. The random networks are characterized by asymmetric structures and capture in an idealized way in many real systems. These networks have a short average path length which drives from the fact that, starting from each node, any other node of the network can be reached in a small number of links (Strogatz 2001). Starting from a population of N interneurons the random network has been built by using the following rule. Given a probability p_r of connections, each pair of neurons is connected by a link with probability p_r , so the topology structure of a random network is determined by the probability, as shown in Fig. 3.

First, we fix $p_r = 0.5$ which means that each pair of neurons is connected by a link with probability 0.5. The effects of induced DC electric field in a random network of interneurons have been characterized with respect to different values of the number of interneuron units. The result is shown in Fig. 4, where it is evident that increasing the

Fig. 4 The dependence of coherence coefficient K on the induced electric field for different size of the random network. The parameters is $p_r = 0.5$. This figure is the average result of ten trials

size of the network, the maximum of the coherence coefficient K shifts up. The number of synaptic inputs received from the other neurons increases with the size of the network. In other words, the mutual connections inside the network become intensified. Furthermore, two peaks of the coherence K appear with larger network size $N = 200$ and $N = 500$. The right peak may be as a result of the imbalance between the synaptic inhibitory received from the other neurons and the induced DC electric field stimulation. Notice that the firing frequency of the neuron increases with the amplitude of applied DC electric field drive in Fig. 2. Then, the action of individual cell in the network will not response strongly to the induced electric field with small amplitude in the case of inhibitory synapse involved. It also means that the high coherence of the network will not appear in such case. But this could happen when the mutual inhibition among the neurons of the network become weaker, as a result of the increasing network size. Here, g_{syn} is the maximal synaptic conductance of each neuron, Num is the number of synaptic input from the other neurons in the network. In this paper, the maximal synaptic conductance g_{syn} is divided by Num , so that when the number of synapses Num is varied, the total synaptic drive per cell in average remains the same. With the increase of the network size, Once the ratio g_{syn}/Num becomes smaller enough, the positive effect of the induced DC electric field occupies a dominant position in competition with the negative effect of the inhibitory synaptic conductance. Then the right peak appears. It is also shown that the amplitude of V_E corresponding to the transition from the peak value of K to zero does not change notably for different network size.

Because of Num is determined by the network size N and the probability p_r of connections. In following studies, we will show that the right peak in larger network size can be controlled by varying parameter g_{syn} and p_r .

Second, the effects of induced DC electric field in a random network consists of interneurons have been investigated with respect to different values of connection probability p_r . As shown in Fig. 5a, the coherence coefficient K increase with p_r with fixed network size $N = 100$. But the increment of the peak value shows a downward trend with the increasing p_r . That is because that all the cells in the population could be connected with each other when the connection probability p_r increases to a certain threshold. Then the coherence coefficient K will not increase notably.

If p_r increases further ($p_r > 0.5$), then the number of synaptic input for each neuron becomes larger than the critical value which is necessary for network synchronization. Therefore, the right peak will appear again when the

Fig. 5 The dependence of coherence coefficient K on the induced electric field for different values of probability p_r of connections in the random network. The parameters are $N = 100$ in (a), $N = 200$ in (b). This figure is the average result of ten trials

ration g_{syn}/Num becomes excessively small. Simulation with $N = 200$ is performed in Fig. 5b. The threshold for p_r to induce the right peak ($p_r < 0.4$) is smaller than the one in Fig. 5a. The results of numerical simulation validate our hypothesis before. It is also found that the critical value of V_E corresponding to the transition from the peak value of K to zero does not have notable change for different values of p_r .

Third, the effects of induced DC electric field in a random network have been investigated with respect to different values of maximal synaptic conductance g_{syn} of each neuron. Simulation with $N = 100$ in Fig. 6a show that the coherence coefficient K decreased rapidly with the increasing g_{syn} . The right peak will appear once g_{syn} drops below 0.1. Similar conclusion also can be drawn with $N = 200$ in Fig. 6b. The right peak appears when $g_{syn} < 0.2$. Therefore, we could have concluded that the threshold for g_{syn} inducing the

Fig. 6 The dependence of coherence coefficient K on the induced electric field for different values of maximal synaptic conductance g_{syn} each neuron has in the random network. The parameters are $N = 100$ in (a), $N = 200$ in (b), $p_r = 0.5$. This figure is the average result of ten trials

appearance of the right peak increases with network size N . In the two cases above, we both find that the critical value of V_E corresponding to the transition from the peak value of K to zero increased with g_{syn} .

It is unnecessary and impossible to add external signals to all involved individuals in neural systems. Local input is reasonable and possible in large neural networks. The induced DC electric field applied to a different fraction PN ($0 < PN < 1$) of elements in the neuron population also have been investigated. Simulations with $N = 100$ in Fig. 7a and $N = 200$ in Fig. 7b are performed.

When $PN < 0.1$, the coherence coefficient K nearly remained the same and is close to zero; while $PN > 0.1$, the coherence coefficient K increased with the amplitude of DC electric field and reached a maximum, then decreased to zero quickly. The peak value also increased with PN , and reached its historical maximum when all individuals

receiving electric field stimulation ($PN = 1$). The critical value of V_E corresponding to the transition from the peak value of K to zero does not change notably for different values of PN .

Effect of DC electric field in small-world network

In this section, we investigate the effects of induced DC electric field in a network of interconnected interneurons with small-world topology. The property of small-world network is characterized by a relatively short average path length between all pairs of nodes in the network, comparable with a regular network; at the same time show a high clustering coefficient (Watts and Strogatz 1998) due to the presence of both short-range and long-range links, just like a regular network. Evidences show that small-world networks are widespread in neural systems. Small-world topology architectures have been found in several empirical studies of structural and functional brain networks in humans and other animals (Sporns et al. 2004; Bassett and Bullmore 2006; Reijneveld et al. 2007). Quantitative analysis also shows that neural networks in some areas of the brain cortex present the small-world property (Bullmore and Sporns 2009). Experimental studies suggested that a small-world topology might be a general organization principle of the human brain (Honey et al. 2007; Van der Van den Heuvel et al. 2008). Models of neural systems with small-world coupling exhibit enhanced signal-propagation speed, computational power, and synchronization (Perc 2005, 2007).

In order to model small-world network, we can refer to the concept which Strogatz and Watts proposed. Starting from a ring-like network with regular connectivity, each neuron is connected to its k nearest neighbors on each side of the ring, and replacing some links with new random ones with probability p . By increasing the probability p the architecture of the neuron population is tuned between the two extremes, regular ($p = 0$) and random networks ($p = 1$). Small-world networks are characterized by intermediate value of the probability $0 < p < 1$, as exemplified in Fig. 8.

Topology structure is another important factor affecting the spatiotemporal patterns of spiking oscillations of the network.

First, we investigate the effects of induced DC electric field in small-world network with different network size, which is obtained from a regular ring ($k = 4$) with random rewiring probability $p = 0.5$. As shown in Fig. 9, the curve of the coherence K displays a plateau in macro-perspective views. It increased along with V_E rapidly when V_E exceeded certain threshold, and reached its maximum value ($K = 1$), which means that the network becomes complete

Fig. 7 The dependence of coherence coefficient K on the induced electric field for different fraction PN of elements in the neuron population receiving stimulation. The parameters are $N = 100$ in (a), $N = 200$ in (b), $p_r = 0.5$. This figure is the average result of ten trials

Fig. 8 Example of considered small-world network topologies. Given 20 isolated nodes. **a** Regular ring characterized by $p = 0$. Each node is connected to its $k = 4$ nearest neighbors. **b** Realization of small-world topology via random rewiring of a certain fraction $p = 0.1$ of links

synchronization. It is found that the threshold of V_E for the network synchronization becomes higher with the increase of network size. It means that different network size need different energy cost to obtain synchronization. Larger amplitude of the induced DC electric field is need for larger network size to obtain synchronous state. However, it decreased significantly when the induced DC electric field V_E exceeded -28 mV.

Second, the effects of induced DC electric field have been investigated with respect to different number of nearest neighbor k , in small-world network with network size $N = 100$ and rewiring probability $p = 0.5$. As can be seen in Fig. 10, there is a sudden transition from asynchrony to synchrony as V_E exceeded a threshold and the threshold decreases with the increasing k . It is shown that less energy is need to synchronize a small-world network with more local connections. But the critical value of V_E corresponding to the transition from the peak value of K to zero nearly remains the same for different values of k .

Third, the effects of induced DC electric field have been characterized with respect to different rewiring probability

Fig. 9 The dependence of coherence coefficient K on the induced electric field for different size of the small-world network. The parameters is $p = 0.5$, $k = 4$. This figure is the average result of ten trials

Fig. 10 The dependence of coherence coefficient K on the induced electric field for different number of nearest neighbors in the small-world network. The parameters is $p = 0.5$, $N = 100$. This figure is the average result of ten trials

p , in a small-world network with network size $N = 100$ and nearest neighbor $k = 4$. As can be seen from Fig. 11, when $p < 0.2$, the coherence coefficient K of the network started to go up gradually, and reached the highest value before beginning to fall. When $p > 0.2$, the coherence coefficient displays a plateau with $K = 1$ as V_E exceeded a threshold. The threshold value decreased with larger value of p . Similarly, the critical value of V_E corresponding to the transition from the peak value of K to zero nearly remains the same.

As the analysis in the random network, the maximal synaptic conductance g_{syn} should also be an important

Fig. 11 The dependence of coherence coefficient K on the induced electric field for different values of rewiring probability in the small-world network. The parameters is $k = 4$, $N = 100$. This figure is the average result of ten trials

factor affecting the network activities. Therefore, the effects of induced DC electric field are investigated with respect to different maximal synaptic conductance, in a small-world network with network size $N = 100$, nearest neighbor $k = 4$ and rewiring probability $p = 0.5$.

As shown in Fig. 12, when $g_{\text{syn}} < 0.05$, the coherence coefficient K of the network increased quickly with V_E , and displayed a plateau in a range of V_E . When $0.05 < g_{\text{syn}} < 0.2$, the coherence coefficient K also displayed a plateau, but with highest value ($K = 1$). When $g_{\text{syn}} > 0.2$, the coherence coefficient K of the network increased with V_E slowly and reached a small peak value, but never get to the

Fig. 12 The dependence of coherence coefficient K on the induced electric field for different values of maximal synaptic conductance g_{syn} each neuron has in the small-world network. The parameters are $N = 100$, $k = 4$, $p = 0.5$. This figure is the average result of ten trials

Fig. 13 The dependence of coherence coefficient K on the induced electric field for different fraction PN of elements in the neuron population receiving stimulation in the small-world network. The parameters are $N = 100$, $k = 4$, $p = 0.5$. This figure is the average result of ten trials

value of 1. The critical value of V_E corresponding to the transition from the peak value of K to zero firstly increased with g_{syn} , and then decreased.

Finally, the induced DC electric field applied to a different fraction PN of elements in the network also has been investigated. We fix $N = 100$, $k = 4$, $p = 0.5$ in the small-world network. As shown in Fig. 13, the coherence coefficient K of the network increased with V_E slowly and can only get to a small peak value when $PN < 1$; but it increased with V_E rapidly, then displayed a plateau with highest value ($K = 1$) when $PN = 1$.

Effect of DC electric field in modular network

As mentioned in this introduction, we will further extend our work and investigate the effects of induced DC electric field in a modular network of small-world subnetworks. The topology structure and the mathematical description of the modular network should be introduced briefly. A modular neural network is a neural network characterized by a series of independent neural networks moderated by some intermediary.

Let us suppose that there are M subnetworks, with each subnetwork consisting of NI ($I = 1, 2, 3, \dots, M$) cells. The first subnetwork may be considered as a central module, and then some pairs of cells from the first and i th ($i = 2, 3, \dots, M$) subnetwork will be chosen randomly. Those selected cell pairs are linked to each other with synapses connect. By doing so, a modular network with a central module is generated, as show in Fig. 14. In this paper, each subnetwork has the same number of cell, $NI = N$, and the

Fig. 14 Schematic presentation of the considered modular network architecture. The modular network consists of $M = 4$ small-world subnetworks, each containing $N_I = 20$ neurons with rewiring probability $p = 0.05$. The subnetwork 1 is taken as a central module connected to other modules. There are three connections among neurons between the central module and any other module

topology structure exhibits small-world property, as introduced in “Effect of DC electric field in small-world network”.

The interconnections between the central module and other subnetworks are distributed with the probability P_{inter} . It represents the proportion of the connections between different subnetworks to total links in the modular network. Then the number of links between different subnetworks can be expressed as $P_{\text{inter}}N^2M$. So, the number of interlinks in the modular network is dependent of parameter P_{inter} .

Each neuron in the modular network is also HH (Hodgkin and Huxley 1952) type. We first investigate the coherence activity in a modular network with four small-world subnetwork, namely, $M = 4$. We will take the intercoupling strength g_{inter} , the intracoupling strength g_{intra} , and the probability P_{inter} with which the random links between different subnetworks exist, as control parameters in the following.

First, we set the parameter values $N = 100$, $k = 4$, $p = 0.5$, just like in the single small-world; $P_{\text{inter}} = 0.1$; $g_{\text{intra}} = 0.02$, $g_{\text{inter}} = 0.01$. As in “Effect of DC electric field in small-world network”, the induced DC electric field is applied to a fraction $PN = 0.5$ of elements of the network.

The influences of network structure and parameters on the coherence oscillation of the modular network will be systematically investigated in the next step. We examined the dependence of the population synchrony on V_E . The effects of the induced electric field V_E on the coherence of a modular network with respect to different values of intra- or inter- synaptic conductance are shown in Fig. 15a, b respectively. The population coherence K increased gradually with V_E , and reached the maximum before beginning to fall. From this figure, we also see that, the maximal K decreased along with the increase of the intra- or inter-

synaptic conductance, but the amplitude of V_E corresponding to the peak value does not change noticeably. Similar results are obtained by increasing the nearest neighbors on each side of the ring k in each small-world subnetwork in Fig. 16, meanwhile the amplitude of V_E corresponding to the peaks also increased with k . The magnified panel in Fig. 17 shows that the increasing rewiring probability p only affects the maximal K values. The coherence of the modular network first increased with p , and then declined. Two different results are obtained by increasing the interconnection probability P_{inter} between subnetworks. With the increasing P_{inter} , the maximal K value first increased and then decreased, but it does not display a marked change in the modular network with small inter- synaptic conductance between subnetworks in Fig. 18a; while, the maximal K decreased obviously as P_{inter} grow in the network with larger inter- synaptic conductance between subnetworks in Fig. 18b.

Then, we examined the effects of induced DC electric field applied to a different fraction PN of elements in the modular network. Similarly, the coherence coefficient K in the modular network performs similarly as in the single small-world in “Effect of DC electric field in small-world network”, but it never reached the maximum $K = 1$ even in the case of ($PN = 1$) all the neurons receiving the external drive (Fig. 19).

Finally, we investigated the effects of the subnetworks number on the coherence coefficient K of the modular network with each subnetwork size fixed. Simulations are performed with $M = 1, 2, 4, 6, 8$, in Fig. 20, other parameters remain unchanged. It was found that the coherence coefficient K reached its maximum at the suitable amplitude of induced electric field. However it decreased with the increasing subnetwork number. It means that it is hard to become synchrony in very large networks.

Fig. 15 The dependence of coherence coefficient K on the induced electric field for different values of **a** inter-synaptic conductance g_{inter} between the subnetworks, **b** intra-synaptic conductance g_{intra} in the subnetworks within the modular network. The parameters are $M = 4$, $NI = 100$, $k = 4$, $p = 0.5$, $P_{\text{inter}} = 0.1$, $PN = 0.5$. This figure is the average result of ten trials

Fig. 16 The dependence of coherence coefficient K on the induced electric field for different number of nearest neighbors k in the subnetwork within the modular network. The parameters are $M = 4$, $NI = 100$, $g_{\text{intra}} = 0.02$, $g_{\text{inter}} = 0.01$, $p = 0.5$, $P_{\text{intra}} = 0.1$, $PN = 0.5$. This figure is the average result of ten trials

Fig. 17 The dependence of coherence coefficient K on the induced electric field for different values of rewiring probability p in the subnetwork within the modular network. The parameters are $M = 4$, $NI = 100$, $g_{\text{intra}} = 0.02$, $g_{\text{inter}} = 0.01$, $k = 4$, $P_{\text{intra}} = 0.1$, $PN = 0.5$. This figure is the average result of ten trials

Conclusions

We examined the coherence response of neuronal systems to steady DC electric field induced by magnetic field exposure using theoretical approaches and computer simulations. Bikson et al. (2004) has already shown that the effects of uniform steady state (DC) extracellular electric fields on neuronal excitability in rat hippocampal slices using field intracellular and voltage-sensitive dye recordings. They

found that the relationship between applied field and induced polarization of CA1 pyramidal cells was linear with small electric fields applied to the somato-dendritic axis. In addition, Deans et al. (2007) found that the sinusoidal AC extracellular fields resulted in sinusoidal fluctuations in the somatic transmembrane potential at the same frequencies. Although we do not show the effects of AC electric field on the transmembrane potential, similar conclusion could be

Fig. 18 The dependence of coherence coefficient K on the induced electric field for different values of inter-connection probability P_{intra} between the subnetworks within the modular network. The parameters are $M = 4$, $NI = 100$, $g_{\text{intra}} = 0.02$, $g_{\text{intra}} = 0.005$ in (a) and $g_{\text{intra}} = 0.010$ in (b), $k = 4$, $p = 0.5$, $PN = 0.5$. This figure is the average result of ten trials

Fig. 19 The dependence of coherence coefficient K on the induced electric field for different fraction PN of elements in the neuron population receiving the external drive in the modular network. The parameters are $M = 4$, $NI = 100$, $g_{\text{intra}} = 0.02$, $g_{\text{intra}} = 0.01$, $k = 4$, $P_{\text{intra}} = 0.1$. This figure is the average result of ten trials

Fig. 20 The dependence of coherence coefficient K on the induced electric field for different number M of the subnetworks within the modular network. The parameters are $NI = 100$, $g_{\text{intra}} = 0.02$, $g_{\text{intra}} = 0.01$, $k = 4$, $p = 0.5$, $PN = 0.5$. This figure is the average result of ten trials

drawn from the solution to Eq. 6. Therefore, the way describing the effects of induced DC electric field on neuron transmembrane potential should be reasonable, and it could be used for other related research.

Different network topologies from single random and small-world network to modular network of subnetworks have been considered. It is shown that the existence of one phenomenon: the coherence of the network displays a peak or a plateau when the induced DC electric field varying between the parameter range we defined. We also have systemically investigated the factors which could affect the behavior of the neuronal systems.

It is found that in single random network, a peak will appear in the curve of coherence. The appearance of the second right peak should be due to the imbalance between the synaptic inhibitory inside the network and the induced electric field drive. In the model, the governable synaptic conductance for each neuron is defined as: $g_{\text{syn}}/\text{Num}$, where g_{syn} is the maximal synaptic conductance for each neuron, and Num is the number of synapses of each neuron. This makes the total synaptic drive per cell in average remains the same. Once the ration $g_{\text{syn}}/\text{Num}$ becomes smaller enough, the positive effect of the induced DC electric field occupies a dominant position in competition with the

negative effect of the inhibitory synaptic conductance. Then the second right peak appears. In addition, we also find that the coherence coefficient in the random network never reached the maximal peak value $K = 1$, even in the case of all individuals receiving the induced electric field drive.

The plateau appears in all simulations of the single small-world network. This presents an obvious contrast against the above results. Moreover, the coherence K can reach the peak value of 1 in all simulations. Compared with random network, the small-world displays enhanced signal-propagation speed and synchronizability. Specifically, a small-world network is defined to be a network where the typical distance L between two randomly chosen nodes (the number of steps required) grows proportionally to the logarithm of the number of nodes N in the network. Because of this more drive is needed to achieve synchronization state for larger network. The simplest and perhaps also the most important characteristic of a single node is its degree. The degree of a node is usually defined to be the total number of its connections with nearest-neighbor nodes. Thus, the larger the degree, the “more important” the node is in a network. The average degree of the network in this study is denoted by k . We found that, synchronization in a network of small-world coupled continuous-time dynamical systems can be achieved with a small value of k . The ability of achieving synchronization in such network can be enhanced by increasing the value of k , which is equivalent to add a small fraction of new connection in the coupled system. The transition between regular ($p = 0$) and random networks ($p = 1$) can be closely monitored by randomly rewiring each edge of the network with probability p . Both the behaviors of the clustering coefficient $C(p)$ and of the average path length $L(p)$ in the WS smallworld model can be considered as a function of the rewiring probability p . It is sufficient to make several random rewirings to decrease the average path length significantly; however, several rewired links cannot crucially change the local clustering property of the network. Therefore, it reveals the transition of the small-world network from asynchrony to synchrony becomes easier by increasing the value of p .

In this paper, we also study synchronization of interneurons in a modular neuronal network, which contains several subnetworks. By means of numerical simulations, we find that the peak value of the coherence decreases notably with the increasing value of the intra- and inter-coupling strengths. It is because the increasing magnitude of inhibitory postsynaptic potential will prevent further action potential generation. As we discussed above, synchronization increases with parameter k (number of nearest neighbors within each subnetwork) in single small-network. Nevertheless, it decreases in the modular network,

probably due to excessive synchronization in each sub-network with increasing value of k . The situation of rewiring probability p is different. It has been shown that the synchronization increases with p in single small-network. Therefore, the coherence of the globally coupled modular network firstly increases with small value of p ; and begins to decrease once p becomes large enough to lead excessive synchronization in each subnetwork. We also find that the maximum of the coherence decreases notably with the increasing interconnection probability between different clusters with larger inter-coupling strength; while no obvious change is observed with smaller inter-coupling strength. Moreover, increasing the subnetwork number also makes the peak value shift down notably.

The way to calculate the coherence is naturally based on cross-correlations, although we use it here to describe coherence of oscillations, it also can be used for data analysis of experimental extracellular multiunit recordings. It can be suitable for the network with any topology type, since it is calculated from spike trains. What you should note here is that it requires relatively small sample sizes. Although we do not introduce the effects of heterogeneity in the induced electric field in present study, we did in our previous study. We investigated that the heterogeneity, using a Gaussian distribution of V_E with standard deviation V_{σ} . It was found the firing frequencies distribution could be wide in a population of uncoupled cells; but when the cells are synaptically coupled, minor differences in intrinsic firing rates overcome by the coupling for small dispersion in V_E . Therefore, it may be tolerated for small deviation V_{σ} , but the network coherence will erode rapidly with larger ones.

In further study, a time-varying electric field should be introduced into the network model in the case of a time-varying magnetic field. In addition, the effect of finite information transmission delays will be considered in our work. Indeed, it is important to note that a biological effect induced by MS exposure is not necessarily an adverse effect. Our study suggests that the induced DC electric field could affect the coherence of the interneuronal network, which may be the basis for population rhythm. This study may be potentially helpful to the scientific theoretical studies regarding the effects of magnetic stimulation on human brain. We also hope that it could be implemented for therapeutic application and normalize brain rhythms associated with specific neurodegenerative diseases.

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Conflict of interest None.

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