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Interaction of bistable neurons leading to the complex network dynamics

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ABSTRACT

We investigate the dynamics of the networks of 100 identical bistable Hodgkin-Huxley neurons with scale-free, small-world and random topologies. For all of them, we discover a phenomenon when one part of the neurons are in the resting state, while the other one is in the oscillatory regime in a certain area of coupling strength and external current amplitude. We investigate this phenomenon and explain it by neuron interaction similar to the short pulse of external current which is able to switch the neuron regime from resting to oscillatory one and vice versa. We find the differences on this phenomenon for different topologies and investigate the evolution of it with increasing of external current.

Keywords: Complex network, Hodgkin-Huxley neuron, neural network, chimera state, scale-free, small-world

1. INTRODUCTION

The dynamics of complex networks has attracted much attention in recent years.^{1–6} Especially, the networks of spiking neurons or neuron-like elements take a significant part of this area.^{7–11} The interest in neural networks is due it helps to make a contribution to a better understanding of brain functionality, that also is of a grate interest.^{12–19} The most famous mathematical models of neurons are Hodgkin-Huxley (HH),²⁰ FitzHugh–Nagumo (FN),²¹ and Hindmarsh-Rose (HR)²² ones. In our research, we use HH neuron due to its most realistic behavior and biological inspiration.

The coexistence of different brain states is should also be taken into account while studying neuron dynamics.²³ Switches between such coexisting states play an important role in cell signaling and neuronal interactions.^{24–26} Typically, each cell receives inputs from thousands of cells mediated by many different neurotransmitters and consequently modifying the postsynaptic potential by excitation or inhibition.²⁷ Communication between cells takes place at synaptic contacts, where an arriving action potential releases a neurotransmitter, thus affecting the postsynaptic potential of the target cell. It is believed²⁸ that the coexisting dynamical regimes mimic different brain states representing particular objects of perception which can be selected by giving the neural network an input corresponding to an initial condition.^{29–31} Furthermore, the coexistence of multiple states in the brain has been proposed as a basic mechanism for associative content-addressable memory storage and pattern recognition in neural systems.^{28, 32, 33}

Collective dynamics in a neuronal network is usually considered by taking into account that every neuron in the network is monostable, i.e., it has a single stable trajectory.³⁴ However, according to Keener and Sneyd,³⁵ the Hodgkin-Huxley (HH) model exhibits bistability in a narrow range of control parameters near the excitation threshold. The bistability regime in oscillatory systems as known to be of special interest due to a variety of hidden unexpected phenomena. In particular, Nekorkin et al.^{36, 37} found theoretically and experimentally both amplitude and phase chimeras in the network of electronic oscillators constructed on the base of a generic self-excited bistable model. Concerning neuronal models, it is worth mentioning the recent work of Uzuntarla et al.,³⁸ who uncovered a counterintuitive effect in the neuronal network of bistable HH neurons, where a spiking behavior transformed into a steady state under excitatory coupling. We suppose the origin of this lies in the coexistence of

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spiking and silent neural populations in the neuronal network, which can be referred to as a chimera state. Such kind of chimeras may shed light on the unihemispheric brain slow-wave sleep in mammals and birds.^{39,40} The dynamics of the network of bistable HH neurons were recently studied by Esir et al.,⁴¹ who highlighted the role of coupling delays and noise in formation of up and down states in the neuronal network.

We investigate the dynamics of the networks of 100 identical Hodgkin-Huxley neurons in a multistable area where both stable fixed point and stable limit circle coexist. We discover a phenomenon when one part of the neurons are in the resting state, while the other one is in the oscillatory regime in a certain area of coupling strength and external current amplitude.

2. NUMERICAL MODEL

We consider the network of $N = 100$ Hodgkin-Huxley neurons. The time evolution of the transmembrane potential of the HH neurons is given by²⁰

$$C_m \frac{dV_i}{dt} = -g_{Na}^{max} m_i^3 h_i (V_i - V_{Na}) - g_K^{max} n_i^4 (V_i - V_K) - g_L^{max} (V_i - V_L) + I_i^{ex} + I_i^{syn} \quad (1)$$

where $C_m = 1\mu F/cm^3$ is the capacity of cell membrane, I_i^{ex} is an external bias current injected into a neuron in the network, V_i is the membrane potential of i -th neuron, $i = 1, \dots, N$, $g_{Na}^{max} = 120mS/cm^2$, $g_K^{max} = 36mS/cm^2$ and $g_L^{max} = 0.3mS/cm^2$ receptively denote the maximal sodium, potassium and leakage conductance when all ion channels are open. $V_{Na} = 50mV$, $V_K = -77mV$ and $V_L = -54.4mV$ are the reversal potentials for sodium, potassium and leak channels respectively. m , n and h represent the mean ratios of the open gates of the specific ion channels. n^4 and m^3h are the mean portions of the open potassium and sodium ion channels within a membrane patch. The dynamics of gating variables ($x = m, n, h$) are given:

$$\frac{dx_i}{dt} = \alpha_{x_i}(V_i)(1 - x_i) - \beta_{x_i}(V_i)x_i, \quad x = m, n, h \quad (2)$$

$\alpha_x(V)$ and $\beta_x(V)$ are rate functions, described by⁴²

$$\alpha_m(V) = \frac{0.1(25 - V)}{\exp[(25 - V)/10] + 1} \quad (3)$$

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

$$\alpha_h(V) = 0.07 \exp(-V/20) \quad (5)$$

$$\beta_h(V) = \frac{1}{1 + \exp[(30 - V)/10]} \quad (6)$$

$$\alpha_n(V) = \frac{0.01(10 - V)}{\exp[(10 - V)/10] + 1} \quad (7)$$

$$\beta_n(V) = 0.125 \exp(-V/80) \quad (8)$$

I_i^{syn} is the total synaptic current received by neuron i . We consider coupling via chemical synapses. The synaptic current takes the form⁴³

$$I_i^{syn} = \sum_{j \in \text{neigh}(i)} g_c \alpha(t - t_0^j) (E_{rev} - V_i) \quad (9)$$

where the alpha function $\alpha(t)$ describes the temporal evolution of the synaptic conductance, g_c is the maximal conductance of the synaptic channel and t_0^j is the time at which presynaptic neuron j fires. We suppose $\alpha(t) = e^{-t/\tau_{syn}} \Theta(t)$, there $\Theta(t)$ is the Heaviside step function and $\tau_{syn} = 3ms$. The initial conditions of all neurons correspond to the oscillatory basin of attraction of individual neuron.

3. RESULTS

We investigate 3 different types of network topologies: scale-free, small-world, and random network. Scale-free topology is a well-known and widely-used connectivity paradigm in computational studies of local microcircuits since such connectivity has been observed in many functional brain regions via neuroimaging and electrophysiological studies.^{44,45} Along with the above, it was shown that many areas of the brain have small-world properties.^{46,47}

Scale-free topology was generated by Barabási–Albert algorithm.⁴⁸ Small-world one was generated by Watts–Strogatz algorithm⁴⁹ for $\beta = 0.3$, $K = 5$. Random network was generated the same way as small-world one but for $\beta = 1.0$.

As we investigate the dynamics of the network of neurons, we can expect that not only the external current amplitude but also the coupling strength will control neural dynamics. In order to verify the truthfulness of this statement, we analyze how the number of active neurons depends on both external current and coupling

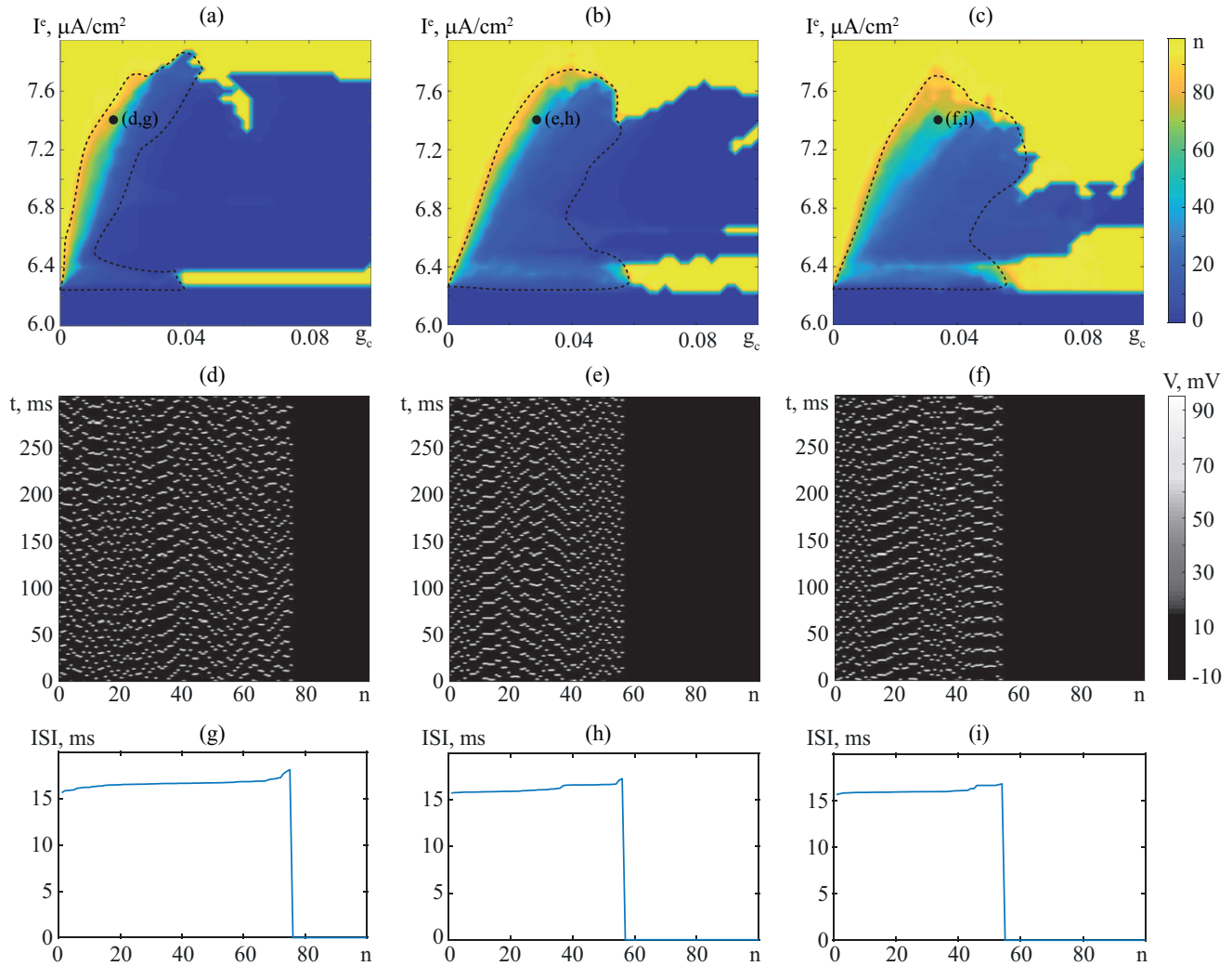


Figure 1. (a-c) Two-parametric dependencies of the oscillating neurons number in the network of $N = 100$ HH neurons from coupling strength g_c and external current I_e , dashed lines correspond to the area of the state when one part of neurons is in oscillatory regime while another one is resting. (d-f) Time series of all neurons and averaged inter-spike intervals (g-i) calculated for different topologies and parameters: (a,d,g) scale-free, (d,g) $g_c = 0.0175$; (b,e,h) small-world, (e,h) $g_c = 0.0275$, (c,f,i) random topology, (f,i) $g_c = 0.0325$. $I_e = 7.4$ for (d-i).

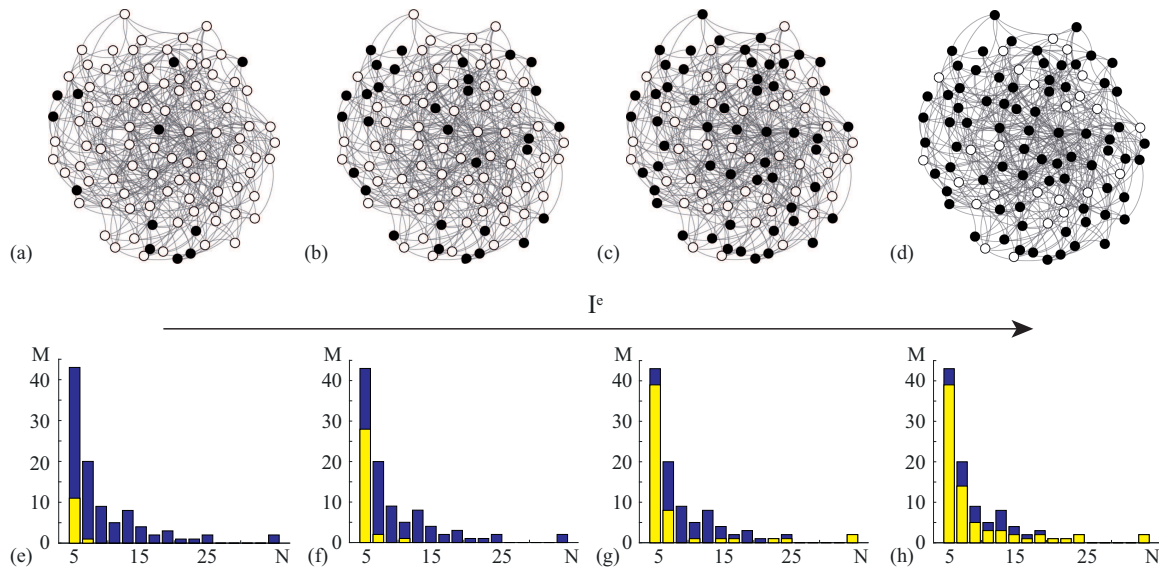


Figure 2. (a-d) Scale-free topologies and (e-h) the corresponding distributions of the number of active (yellow) and silent (blue) neurons M according to the neuron couplings number N for (a,e) $I^e = 7.0$, (b,f) $I^e = 7.2$, (c,g) $I^e = 7.3$, (d,h) $I^e = 7.4$. Black nodes in the networks mean active neurons, white – the silent ones. i -th column on the diagrams (e-h) means the number of neurons coupled to i or $i + 1$ other elements in the network. $g_c = 0.0175$.

strength. By active neurons we mean the ones generating spikes. On figure 1(a-c) one can see the two-parametric dependencies for corresponding topologies. $I^e = 6.24$ is the threshold value for a single neuron and for current amplitudes lower than that value a neuron can be only in a “silent” regime. That’s why for all topologies one can see the area $I^e < 6.24$ for all values of coupling strength where all neurons in the network are inactive.

For $I^e > 6.24$ the number of active neurons depends on coupling strength. As one can see on Fig.1(a), there is an area for $6.3 < I^e < 6.35$ and $0.04 < g_c < 0.1$ where all elements of the network are active. For small-world topology (b) this area is wider in current amplitude, but shorter in coupling strength. And for the random network (c), it is mostly like for small-world but it’s wider for $g_c > 0.075$.

One can see that for low external current amplitude there is a narrow coupling strength range when all neurons in the network generate spikes. Increasing the external current leads to its expansion, and for big values of it (for (a) it’s $I^e > 7.8$) the range corresponds to all coupling strength values we analyze. We should note that the transition from “all neurons are active” to “all neurons are silent” regime is smooth, and there is an area where only a part of network elements are active. That area is highlighted by the dashed line, and we can call it the area of the chimera state because we have a part of spiking neurons and another part of resting ones. For scale-free topology that transition is the sharpest and the area is the smallest. For small-world one (b) the transition is smoother, and the dashed area is bigger and includes higher g_c . Random topology is characterized by the smoothest transition and the biggest chimera area.

It is easy to see that in Fig.1(a) the area when all neurons are in the resting state occupies most of the considered parameter values, and moving from (a) to (c) one can see how this area decreases for $g_c > 0.4$.

The situation when in a complex network one part of the elements is in the resting state while another one generates spikes is of interest. And it is not so clear why the system behaves this way, because all connections in the network are excitatory, and at the first blush excitatory synapses shouldn’t suppress neuron oscillations and external current is above the threshold.

In order to figure it out, at first, we investigate the dynamics of all neurons in the system. Figs.1(d-f) illustrate the time series of them after transient sorted by inter-spike interval (ISI) (g-i) for scale-free, small-world and random topologies. $ISI = 0$ corresponds to the resting neurons. As one can see all elements have not only slightly different inter-spike intervals, but also the phase delays relative to each other for both topologies. Even when the external current value corresponds to oscillation dynamics but the steady-state coexists in the phase plane,

a short external pulse is capable to switch the neuron dynamics to the resting one. And the excitatory synapses are similar to the external pulses, so in turn, they can perform the same role. For sure they should come to the neuron approximately at the same time to make the pulse amplitude is high enough, but as we can see in Fig.1, many neurons are synchronized, so together they can switch the neuron dynamics to the resting one.

At second, we investigate how the external current influences the number of active neurons. The top row (a-d) on Fig.2 illustrates which neurons are in the oscillatory regime (black) or in the resting one (white) for different values of external current, but for one coupling strength. One can see that most neurons which are already active stay at the oscillatory regime with increasing I^e while the new neurons start to oscillate. From the node order distributions, one can see that the neurons with the lowest number of connections start to oscillate first [5 and 6 for Fig.2(e)], while the rest of them are in the resting regime. With the increasing of external current, the number of active neurons with the lowest order rapidly increases, and it slowly makes the neurons with higher order start to oscillate too [7 and 8 for Fig.2(f,g)]. And for high external current (h), the most of each group of neurons (each column in the distributions) oscillate, but not all of them. We should note that the more neurons have the same number of connections, the more of them start to oscillate.

4. CONCLUSION

We have investigated the dynamics of the networks of 100 identical Hodgkin-Huxley neurons with 3 different topologies: scale-free, small-world and a random one. We have discovered the existence of a specific state in such networks in a certain area of coupling strength and external current amplitude, when one part of the neurons are in the resting state, while the other one is in the oscillatory regime. We have investigated this phenomenon and explained it by a neuron interaction similar to the short pulse of external current which is able to switch the neuron regime from resting to oscillatory one and vice versa. So as all neurons in the network oscillate initially, the dynamics of the neurons with a high number of input connections can be easily switched to the resting one, while other ones having a small number of connections continue to generate spikes. We also show that for scale-free topology the chimera state area is the smallest one when for the random topology the chimera state takes the most area of the parameters.

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