

Bifurcations in Class 1 neuron models interconnected by inhibitory and electrical synapses

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Abstract—Electrical coupling has been discovered extensively between FS neurons in the neocortex. They are also coupled by bi-directional or uni-directional inhibitory synapses. However, the relationship between collective activity in interneuronal circuits and different functions of their coupling have not been revealed perfectly. To clarify the above problem, we investigate bifurcation phenomena in coupled neuron models and spatio-temporal dynamics in large scale network, which consist of two-dimensional Hindmarsh-Rose type models connected by gap junction and inhibitory synapses. As a result, we show in- and anti-phase solutions and complex behavior in coupled neurons. By the interaction between electrical and inhibitory synapses, moreover, spatio-temporal complex behavior occurs in large scale network.

1. Introduction

Several groups have investigated fast-spiking (FS) interneurons connected by gap junction (e.g., Ref.[1, 2]). These experimental data suggest that synchronous interneuronal oscillations play important roles in the neocortex[3], since they powerfully respond to synchronous inputs from other networks (e.g., regular spiking (RS) neurons). Moreover, they often coupled by bi-directional or uni-directional inhibitory synapses. The interplay of two different functions, voltage dependency and short-term plasticity, can develop advanced information processing in inhibitory interneuronal networks. However, the relationship between collective activity in interneurons and different functions of their coupling has not been revealed perfectly.

The purpose of this paper is to clarify the relationship between various synchronous phenomena and parameter values of each coupling coefficient, i.e., we discuss the variety of synchronous firing and spatio-temporal dynamics generated by two different functional synapses. Hence, we firstly investigate coupled neurons and thereafter examine the

spatio-temporal behavior in the large scale network, which consist of homogeneous two-dimensional Hindmarsh-Rose (2DHR) type neuron models connected by gap junction and inhibitory synapses.

We firstly investigate synchronization phenomena in coupled neurons by using the bifurcation theory. As a result, we show that in-phase and anti-phase solutions change to chaotic solutions via period-doubling and pitchfork bifurcations, although two neurons are connected by fully and symmetrically coupling. We show an example of spatio-temporal behavior in large scale network. Although we set same values of coupling coefficients and internal parameters, the large scale network shows spatio-temporal complex behavior when initial values of each neuron are chosen randomly. In the parameter region of two coupling coefficients, these phenomena are observed extensively and coexist with synchronous firing. Note that large scale network connected by the only gap junction exhibits synchronization phenomena. By increasing the parameter of coupling coefficient of gap-junction, the population size of neurons exhibiting the firing activity enlarges. Firing patterns of each neuron do not be synchronized in the long time course, but these neurons are divided into some clusters, and the number of these clusters and its population size change dynamically as time go on. This network may be able to switch between synchronous and asynchronous firing due to the input from other network. These results may indicate the additional variety of information representation by the interaction of two different couplings in heterogeneous interneuronal networks.

2. 2DHR-type neuron model

To investigate synchronization phenomena in coupled system interconnected by electrical and inhibitory synapses, we firstly consider a simple neuron model de-

scribed as follows:

$$\begin{cases} \frac{dx}{dt} = c \left(x - \frac{x^3}{3} - y + z \right) \\ \frac{dy}{dt} = \frac{x^2 + dx - by + a}{c} \end{cases} \quad (1)$$

where x and y denote the cell membrane potential and a recovery variable, respectively. z represents the external stimulus. This model is equivalent to the two-dimensional Hindmarsh-Rose model[4, 5], if we consider the substitution of state variable, $y \mapsto -y$.

It is well known that 2DHR-type neuron model shows two kinds of excitability[6], Class 1 and Class 2 excitability associated with saddle-node and Hopf bifurcations, respectively. In fact, this model show Class 1, Class 2 and their subtype excitability by setting certain parameter sets[7]. Hence, this model has the possibility to be able to represent the excitability of some neurons. However, which excitability does FS neuron exhibit? This question has remained elusive. Therefore, in the following section, we hypothesize that FS neuron shows Class 1 excitability, based on some modelling studies[8, 9].

3. Bifurcations in inhibitory 2DHR-type neurons coupled by gap-junction

In this section, we investigate bifurcation phenomena in a fundamental system that two neurons are interconnected by electrical and bi-directional inhibitory synapses as shown in Fig.1.

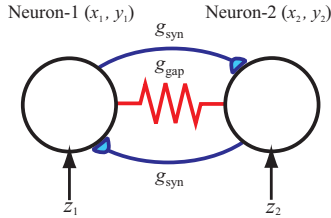


Figure 1: Schematic diagram of coupled neurons connected by both electrical and bi-directional inhibitory synapses.

The equations are

$$\begin{cases} \dot{x}_1 = c_1(x_1 - x_1^3/3 - y_1 + z_1 + g_{\text{gap}}(x_2 - x_1) + g_{\text{syn}}s_1(x_{\text{syn}} - x_1)) \\ \dot{y}_1 = (x_1^2 + d_1x_1 - b_1y_1 + a_1)/c_1 \\ \dot{s}_1 = \alpha(1 - s_1)/(1 + \exp(-x_2/0.1)) - \beta s_1 \\ \dot{x}_2 = c_2(x_2 - x_2^3/3 - y_2 + z_2 + g_{\text{gap}}(x_1 - x_2) + g_{\text{syn}}s_2(x_{\text{syn}} - x_2)) \\ \dot{y}_2 = (x_2^2 + d_2x_2 - b_2y_2 + a_2)/c_2 \\ \dot{s}_2 = \alpha(1 - s_2)/(1 + \exp(-x_1/0.1)) - \beta s_2 \end{cases} \quad (2)$$

where g_{gap} and g_{syn} are the maximal electrical and synaptic conductances, respectively. For the inhibitory

synaptic transmission, we adopt the first-order kinetics equation[10], $s_{1,2}$, with a sigmoidal function. Although this model is not equipped with biophysically meaning, we can qualitatively investigate various synchronous phenomena and the effects generated by some important parameters in coupled system, e.g., the effects of the intensity of each coupling or the variation of firing frequency derived from the decay time constant of synaptic transmission.

Here, we suppose that both single neurons have the same internal parameters, i.e., they exhibit the same excitatory type. We fix the parameter $a_1 = a_2 = 0.42$, $b_1 = b_2 = 1.0$, $c_1 = c_2 = 3.0$, $d_1 = d_2 = 1.8$ as each neuron shows the Class 1 excitability [7]. Additionally, we assume that the same constant current $z_1 = z_2 = 0.5$ is injected to the individual neurons. This situation indicates that the isolated individual neurons show the firing state with same frequency (≈ 35 [Hz]). The synaptic reversal potential is set to $x_{\text{syn}} = -2.5$ less than the resting potential (≈ -2.2), and the rise and decay time constants are set to $\alpha = 1.0$ and $\beta = 0.05$, respectively.

To investigate the interaction between two coupling coefficients, we compute the bifurcation diagram in the $g_{\text{syn}}-g_{\text{gap}}$ plane as shown in Fig.2. In this bifurcation diagram, G_i , I_i and Pf_i represent the tangent, period-doubling and pitchfork bifurcations, respectively. i is a nominal number. S_{in} and S_{anti} indicates the region where the stable in-phase and anti-phase solutions exist, respectively.

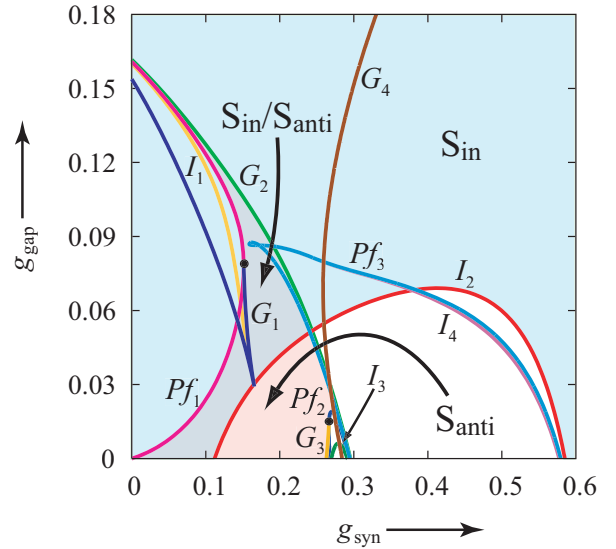


Figure 2: Bifurcation diagram of limit cycles in the $g_{\text{syn}}-g_{\text{gap}}$ plane.

By the effect of gap-junction, an in-phase solution (Fig.3-(a)) exists extensively in this diagram. However, the inhibitory coupling destabilizes the in-phase solution via period-doubling bifurcation I_2 , but its effect is decreased by increasing the intensity of the electrical coupling. On the other hand, the anti-phase solution (Fig.3-(b)) is generated by both gap-junction and inhibitory synapses. The re-

gion exhibiting the anti-phase solution is shrank by increasing the parameter g_{gap} . Moreover, in the right-side region than G_4 curve, odd firing solutions (Fig.3-(c)) generated by strong inhibitory coupling exist, independent of the intensity of the electrical coupling. Although two neurons are connected by fully and symmetrically coupling and have the same internal parameters, the in-phase and anti-phase solutions are destabilized by each pitchfork bifurcation Pf_1 and Pf_2 , and then two sets of solutions located at a symmetrical position occur simultaneously. Additionally, they change to chaotic phenomena (e.g., Fig.3-(d)) via a period-doubling cascade, but such regions are very small. As a future work, we will investigate the transition of these regions divided by some bifurcation curves when z and β are changed.

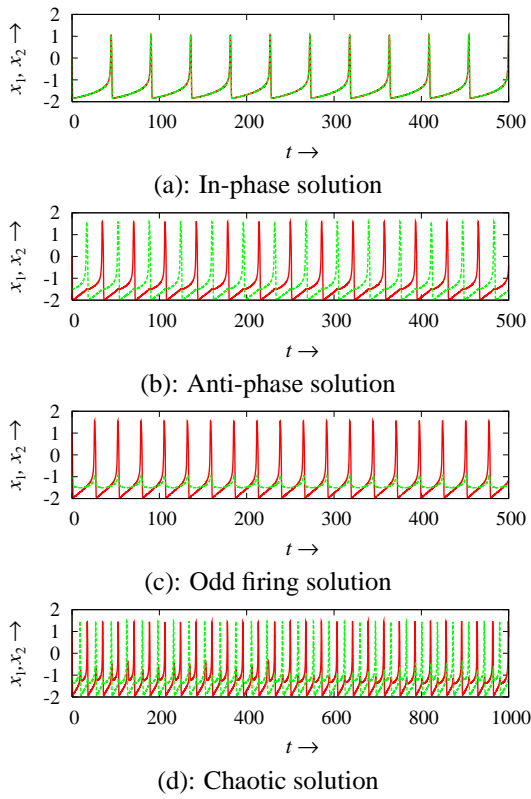


Figure 3: Wave forms in Fig.2.

4. Spatio-temporal dynamics in large scale network

Finally, we study the dynamical behavior in large scale network of 2DHR-type neurons interconnected by electrical and inhibitory synapses. This system is two-dimensionally lined up with four neighbors coupling (50×50) and defined with a periodic boundary condition. We show an example of spatio-temporal dynamics in large scale network as shown in Fig.4. Initial values of each neuron are chosen randomly, and the values of each coupling coefficient are the same in this network. Large scale network connected by only gap junction exclusively exhibits

synchronous firing mode (data not shown). On the other hand, in the case of only inhibitory coupling, the fluctuation of each initial value decreases gradually, and each neuron finally shows a periodic firing state independently as shown in Fig.4 and Fig.5-(a). However, this network shows complicated spatio-temporal behavior by increasing the parameter g_{gap} as shown in Fig.4. This complicated phenomena are observed extensively in the parameter sets of two coupling coefficients, although coupled neurons have small regions where chaotic phenomena are shown in. In Fig.5-(b), firing patterns of each neuron do not be synchronized in the log time course, but these neurons seem to be divided into some groups, and the number of them and its population size change dynamically as time go on (Fig.5-(b)). By increasing the parameter g_{gap} , the population size of neurons exhibiting the firing activity enlarges as shown in Fig.4.

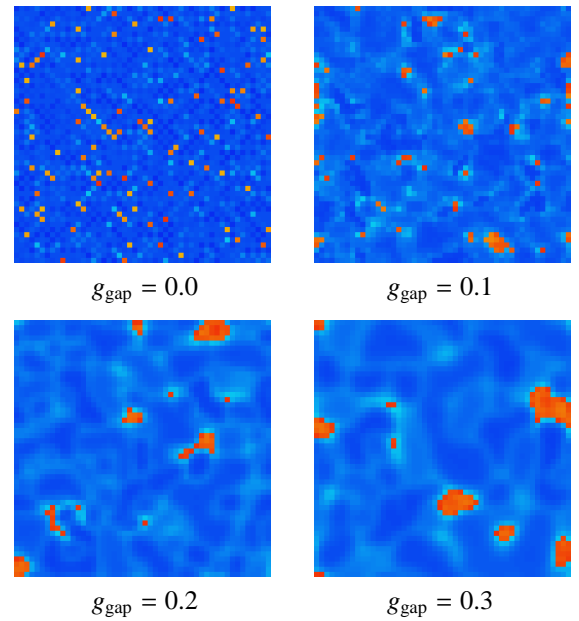


Figure 4: Snapshots of contours of membrane potentials of 50×50 neurons. Note that we fix the inhibitory coupling coefficient $g_{\text{syn}} = 0.1$.

In the large scale network of Class 2 neuron, an irregular synchrony is generated by the effect of two couplings as shown in Fig6. However, synchronization of this network is promoted than Class 1 neurons, because they have the different subthreshold property, “integrate” (Class 1) and “resonate” (Class 2) firing. Hence, to emphasize intrinsic frequency (e.g., gamma frequency), Class 2 neuronal network might be more effective.

5. Conclusions

We investigate bifurcation phenomena in coupled Class 1 neurons interconnected by inhibitory and the electrical coupling, and clarify that many firing patterns, including

both the in-phase and anti-phase solutions, are generated by the interaction of each coupling. In the large scale network, however, the spatio-temporal dynamics irregular switching the synchronous and asynchronous firing are observed extensively in the parameter sets of two coupling coefficients. From these results, gap-junctional coupling can produce partially synchronous firing via the propagation of subthreshold oscillations, while this coupling can also promote the effect of inhibition when inputs from neighbor cells have a certain time lag. Hence, this network may be able to switch between synchronous and asynchronous firing due to the input from other network, e.g., regular-spiking (RS) neurons. Moreover, interneurons may switch synchrony and asynchrony between these neurons in other network, effectively. These results may indicate the additional variety of information representation by the interaction of two different couplings in interneuronal networks.

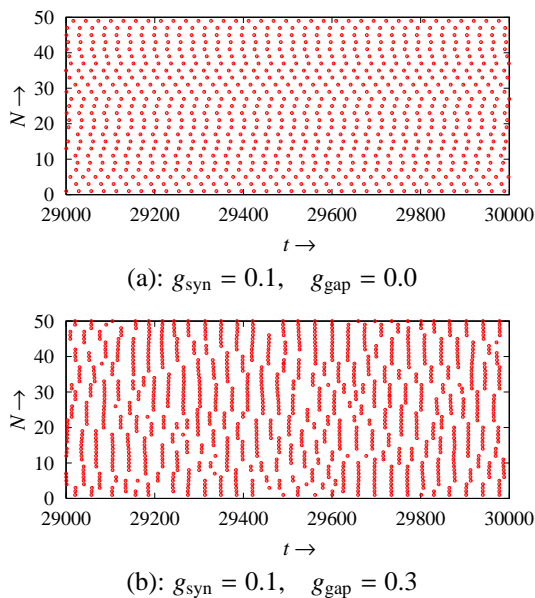


Figure 5: The raster plots representing the activity of 50 neurons.

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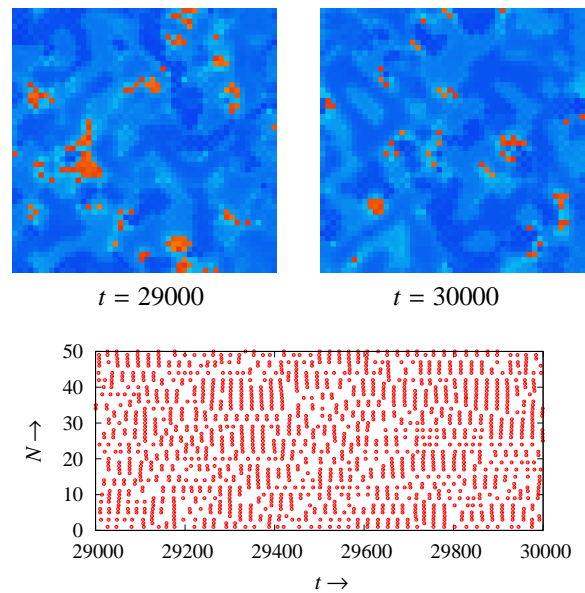


Figure 6: Snapshots of contours of membrane potentials of 50×50 Class 2 neurons and the raster plots representing the activity of 50 neurons. We set the internal parameters and the coupling coefficients as follows: $a = 0.88, b = 1.0, c = 3.0, d = 2.2, z = 0.5, x_{\text{syn}} = -2.0, g_{\text{syn}} = 0.1$ and $g_{\text{gap}} = 0.07$.

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