Bifurcations in a system of inhibitory coupled neurons

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Abstract—We investigate firing patterns in mutually coupled two neurons with inhibitory synapses. In a previous study, we found clustered states: two groups with distinct firing rates and one group with subthreshold oscillations. We study its generation mechanism in the smallest system. As a result, we obtain that the firing frequency and the synaptic conductance are important parameters to generate the clustered states.

1. Introduction

Recently, complex network structures, such as small-world [1] and scale-free [2,3], have been found in various real neuronal networks [4,5]. Synchronization in neuronal networks is also found and synchronous activities play an important role in information processing in the brain [6]. On the other hand, they are not desirable for several neurological diseases such as epilepsy and tremor in Parkinson's disease [7]. Thus the studies of synchronization in complex networks are very important and have attracted much interest. Barahona and Pecora developed the MSF(Master Stability Function) analysis to study synchronizability in complex networks [8], and Nishikawa and Motter extended it for an asymmetric case [9]. Since the average path length becomes short in small-world networks, synchronization is achieved more easily than in a regular lattice [10–13]. However, it is not the only condition, synchronizability also depends on network size, the degree distribution (distribution of a number of links), the clustering coefficient and so on [14–17]. These studies mainly come from the idea that the connections between cells promote in-phase synchronization. Thus, short-cuts in small-world networks can enhance synchronizability. However, in general it is said that the inhibitory connection generates anti-phase synchronization. Although inhibitory networks in the brain are important to generate complicated firing patterns [18–27], the studies of such inhibitory networks are not enough as far as we know.

In the previous study [28], we observed an interesting solution in small-world networks composed of only inhibitory neurons, which has clustered three states: firing with frequencies A and B (A/B is irrational), and subthreshold oscillations. In the full dimension, this solution is quasi-periodic, however, just watching the time series of the oscillatory solution with firing frequency A or B, it is almost periodic. In this paper, we try to clarify the generation mechanism of such a solution when a number of coupled neurons is two.

2. Model Equations

We consider mutual coupled Morris-Lecar (ML) neurons with inhibitory synapses. The ML neurons [29] with synaptic coupling are described by

$$
\begin{aligned}
C\frac{dV_i}{dt} &= -g_L(V_i - V_L) - g_{Ca}M_{\infty_i}(V_i - V_{Ca}) \\
&\quad -g_K N_i(V_i - V_K) + I_{ext_i} + I_{syn_i}, \\
\frac{dN_i}{dt} &= \frac{N_{\infty_i} - N_i}{\tau_{N_i}}, \\
\frac{ds_i}{dt} &= \frac{1 - s_i}{1 + \exp(-V_i)}\left(\frac{1}{\tau_r} - \frac{1}{\tau_d}\right) - \frac{s_i}{\tau_d}, \\
&\quad (i = 1, 2),
\end{aligned}
\tag{1}
$$

where V_i, N_i and s_i are the membrane potential, the activation variable for K$^+$ and the gating variable for the synapse, respectively. τ_r and τ_d are the raise and the decay time of the synapse, respectively. N_{∞_i} and τ_{N_i} are functions of V_i. I_{syn_i} is the synaptic current given by

$$
I_{syn_i} = G_{syn_{ji}}(V_{syn} - V_i)s_j, \tag{2}
$$
$$
(\,j = 1 \text{ and } 2 \text{ for } i = 2 \text{ and } 1, \text{ respectively})
$$

where $G_{syn_{ij}}$ is the maximum synaptic conductance from ith to jth neurons, and V_{syn} is the reversal potential. We define the threshold value for firing is $V_i = 0$. The values of $(\tau_r, \tau_d, V_{syn})$ are fixed as (0.5, 7.0, −60.0) for the inhibitory synapse [30]. The schematic diagram of our model is shown in Fig. 1. One of bifurcation parameters is the firing frequency for the single neuron, which is controlled by the value of the external input I_{ext_i} (direct current).

3. Results

We fix the parameter values as $f_2 = 20$ and $G_{syn_{21}} = 3.0$ [28] for Figs. 2 and 3 which show bifurcation diagrams on the parameter plane $(f_1, G_{syn_{12}})$ when $f_1 \leq f_2$ and $f_1 \geq f_2$,

respectively. The waveforms of membrane potentials V_1 and V_2 in the regions with circled numbers are presented in Figs. 4(a) to 4(f). We explain the synchronized states in each region. In region ①, V_1 and V_2 are synchronized at anti-phase (Fig. 4(a)). We observe this firing pattern in a wide parameter region because these waveforms are typically observed in a system of inhibitory coupled neurons. From this state, as f_1 is decreased when $G_{syn_{12}}$ is larger than 3.0, the firing of neuron 1 is completely suppressed by neuron 2 (Fig. 4(e)), which is observed in region ⑤. On the other hand, as f_1 is increased, neuron 1 suppresses neuron 2 (Fig. 4(f) is observed in region ⑥). Next, we decrease the value of $G_{syn_{12}}$ from the closed circle in Fig. 2. After transition from region ① to ②, we obtain neurons synchronized with a phase lag, see Fig. 4(b). The reasons of generating this solution are as follows:

(1) the amplitude of the synaptic signal from neuron 1 to neuron 2 is not enough to suppress neuron 2,

(2) because of (1), the firing frequency of neuron 2 becomes higher, (suppression of V_2 in Fig. 4(a) disappears)

(3) because of (2), the synaptic input from neuron 2 to neuron 1 is injected when the membrane potential of neuron 1 is low, (($V_{syn} - V_1$) in Eq. (2) becomes small)

(4) the synaptic input from neuron 2 to neuron 1 is also not enough to suppress neuron 1.

Thus, the suppression of neurons 1 and 2 disappears and Fig. 4(b) is observed in region ②. This solution meets the period-doubling bifurcation by decreasing the value of f_1 from region ② to ③, and two-periodic solutions shown in Fig. 4(c) appear in region ③. In region ④, we observe nonperiodic states, however the firings of neurons 1 and 2 are almost in-phase.

Figure 5 shows a bifurcation diagram on the parameter plane (f_1, f_2) when $G_{syn_{12}} = G_{syn_{21}} = 3.0$. From this figure, we can see that subthreshold oscillations appear by changing the firing frequency of each neuron.

4. Discussion and Conclusion

In the previous study [28], we observed an interesting quasi-periodic solution. It contains three clustered groups: two groups consisting of fired neurons with distinct firing frequencies (in the same group, neurons produce synchronized firings with a phase lag or anti-phase), and one group with only subthreshold oscillations (no firings). Identical neurons showed different firing frequencies as a transient state, and a number of the synaptic inputs is not uniformly distributed [28].

In this study, we consider the simplest case (a number of coupled neurons is 2) and clarify the basic mechanism of generating the clustered states. The values of two parameters (frequency and synaptic conductance) are changed because the former and latter correspond to the different firing
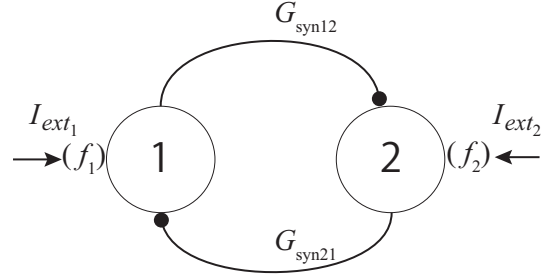

Figure 1: Schematic diagram of our model. f_1 and f_2 indicate frequencies of single neuron.

frequencies and different number of synaptic inputs in the previous study, respectively. As a result, we obtain anti-phase synchronization without changing the values of the parameters. Moreover, we find the existence of subthreshold oscillations and synchronization with a phase lag by changing the values of the frequency and the synaptic conductance, respectively. These can explain three clustered states: anti-phase synchronization, synchronization with a phase lag and subthreshold oscillations. Subthreshold neuronal oscillations were observed in the experiments [31,32] and they are related to the oscillation with θ rhythm which promotes LTP (long-term potentiation) [33–35]. Our previous results showed the importance of the subthreshold oscillation to produce complicated firing patterns. Here, we clarify that the generation of the subthreshold oscillation is mainly controlled by the firing frequency of the single neuron. Even though we consider a system of coupled identical neurons having the same own firing frequency, the distribution of firing frequencies become nonuniform due to inhibitory synapses when a number of neurons are large. Studying bifurcations of a system of large coupled neurons is one of our open problems.

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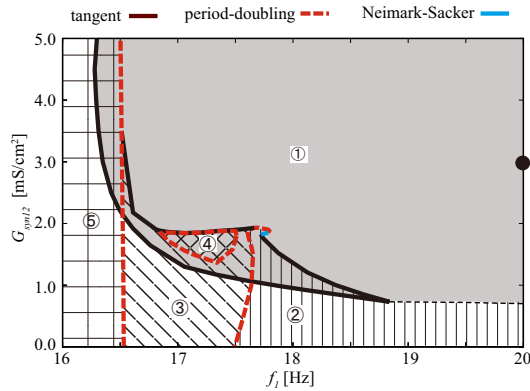[4] D.S. Bassett, A.M. Lindenberg, S. Achard, T. Duke and E. Bullmore, Adaptive reconfiguration of fractal

Figure 2: Bifurcation diagram when $f_1 \leq f_2$. Closed circle indicates the values of the symmetrical case ($G_{syn_{12}} = G_{syn_{21}}$ and $f_1 = f_2$). We observe the same kind of firing patterns in the same colored or hatched regions with circled numbers. Black dotted curves indicate the boundaries between the classified firing patterns, which are not any bifurcations. The other curves indicate the bifurcation sets, and the kind of bifurcation is shown on the top.

Figure 3: Bifurcation diagram when $f_1 \geq f_2$. Basic display format is the same as that described in Fig. 2.

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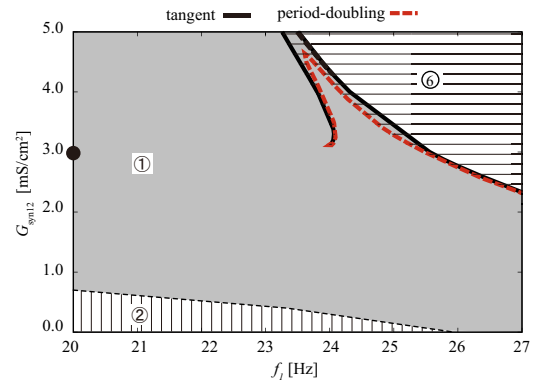[13] A.M. Batista, S.E.S.Pinto, R.L. Viana and S.R. Lopes, Mode locking in small-world networks of coupled circle maps, Physica A, 322:118–128, 2003.

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(a) ① $f_1 = 20$, $G_{syn_{12}} = 3.0$

(b) ② $f_1 = 20$, $G_{syn_{12}} = 0.5$

(c) ③ $f_1 = 17$, $G_{syn_{12}} = 1.0$

(d) ④ $f_1 = 17.3$, $G_{syn_{12}} = 1.6$

(e) ⑤ $f_1 = 16.25$, $G_{syn_{12}} = 3.0$
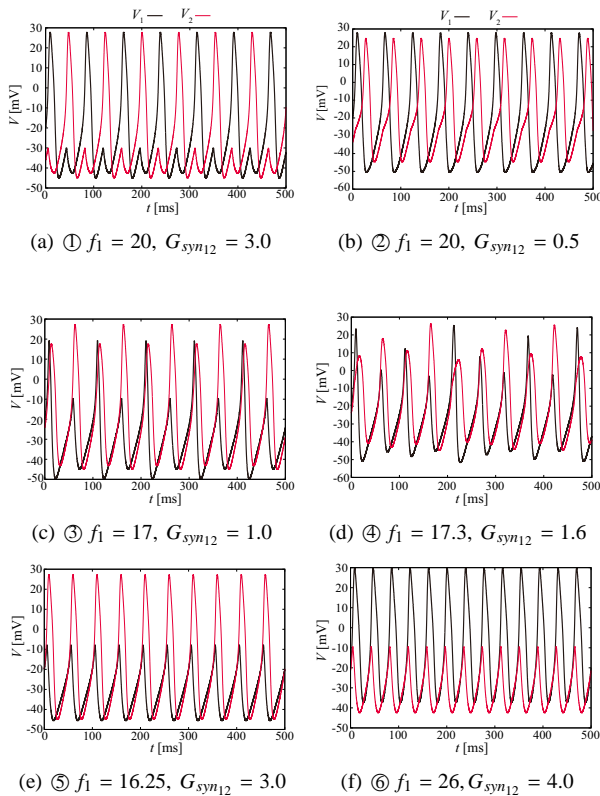
(f) ⑥ $f_1 = 26$, $G_{syn_{12}} = 4.0$

Figure 4: Waveforms in each region in Figs. 2 and 3. Black and red curves indicate membrane potential for neuron 1 and neuron 2, respectively.

Figure 5: Bifurcation diagram on parameter plane (f_1, f_2).

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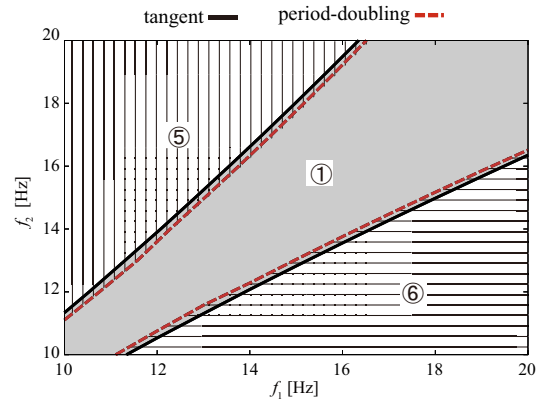
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