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Bifurcation in Coupled Fast-Spiking Neurons Model

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Abstract—In this study, we consider a system of coupled two fast-spiking neurons as a motif of an interneuron network. We investigate the bifurcation structure to clarify synchronization phenomenon of the neurons. As a result, we find that unidirectionally coupled neurons with an excitatory or inhibitory synapse, easily achieve synchronization at a higher or lower firing frequency than the fundamental frequency of a post-synaptic neuron. When an electrical synapse is added to above model, the neurons have a wider parameter region in which stable synchronous firing is observed than unidirectionally coupled neurons have. Furthermore, we can observe the coexistence of two synchronized states.

1. Introduction

For complex and large scale networks, studying the behavior of the sub-network(motif) is very important to estimate the phenomena in whole networks. The interneuron networks are categorized into such complex networks. Skinner and coworker investigated an inhibitory two-cell network as a motif of the interneuron networks, and they found that analyzing a basic motif predict the dynamics of the large network[1]. Also, Nomura et al. considered another motif and large scale network consisting of such motifs, and showed that synchronous firing can be observed in both cases at the same value of the parameters [2]. Hence, the investigation of the phenomenon in the motif by using neuron model is very available way to clarify synchronization in the interneurons network.

For the analyses using coupled FS neurons model, it is found that the synchronous firing state can be changed by the strength of the electrical and chemical couplings[2]. In addition, Wang et al. discovered that the synaptic delay of an excitatory chemical synapse also affect the synchronous firing state[3]. In these studies, the external stimuli of the neurons are fixed as the same value. However, in the brain, individual neurons fire at the different frequencies by the various external stimuli. Thus, there is the necessity of researching synchronization when the neurons oscillate in the different firing frequency.

In the previous study, we investigated synchronization in the unidirectionally coupled two Morris-Lecar(ML) neurons with a chemical synapse, when the firing frequency of a pre-synaptic neuron was varied. We found that the neurons have a wide parameter region in which stable synchronous firing is observed as a firing frequency becomes higher or lower than a that of a post-synaptic neuron for the excitatory or inhibitory synapse[4].

In this study, we replace the ML neuron model with FS neuron model to examine more realistic model. We investigate synchronization and bifurcation structure in three coupling cases: 1)an unidirectional chemical synapse (excitatory or inhibitory), 2)an electrical synapse, 3)both (unidirectional inhibitory and electrical synapses), these motifs are observed in actual neocortical interneurons network discovered by Beierlein and coworkers[5]. As a result, in case(1), the neurons easily achieve synchronization at a higher or lower firing frequency than that of a post-synaptic neuron for the excitatory or inhibitory synapse, respectively. In case(2), the neurons show in-phase, anti-phase and other synchronization by the difference of the fundamental frequency of individual neurons. In case(3), the neurons have a wider parameter region in which stable synchronous firing is observed than the coupled neurons with an inhibitory synapse have. Furthermore, in case(3), the neurons easily achieve synchronization at a smaller stimuli and shows a lower firing frequency than in case(1). Therefore, the electrical synapse play the key role the synchronization at a wide range frequency in the inhibitory networks.

2. Neuron Model

Figure 1 is a schematic diagram of coupled two neurons. We use the Erisir's neuron model as a single FS neuron model[6]. The system equation is described as follows:

$$
\begin{aligned}
C_M \frac{dV_1}{dt} &= -g_{Na} m_1^3 h_1 (V_1 - V_{Na}) \\
&\quad - g_{k1} n_{1(1)}^4 (V_1 - V_{k1}) - g_{k2} n_{2(1)}^2 (V_1 - V_{k2}) \\
&\quad - g_l (V_1 - V_l) + g(V_2 - V_1) + I_{ext1} \qquad (1) \\
C_M \frac{dV_2}{dt} &= -g_{Na} m_2^3 h_2 (V_2 - V_{Na})
\end{aligned}
$$

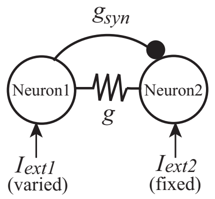


Figure 1: **Schematic diagram of coupled two FS neurons.** g_{syn} and g are maximum coupling conductance of the chemical and electrical synapse, respectively. I_{ext1} and I_{ext2} are varied and fixed external DC current of Neuron 1 and 2.

$$-g_{k1}n_{1(2)}^4(V_2 - V_{k1}) - g_{k2}n_{2(2)}^2(V_2 - V_{k2})$$
$$-g_l(V_2 - V_l) + g(V_1 - V_2) + I_{syn} + I_{ext2} \quad (2)$$

$$\frac{dx_i}{dt} = a_x(V_i)(1 - x_i) - b_x(V_i)x_i \quad (3)$$
$$(i = 1, 2, x = m, h, n_1, n_2)$$

where, $V_{1,2}$ is the membrane potential of each neuron. m and h are activation and inactivation variables for sodium ion, respectively, and n_1 and n_2 are activation variables for $K_{v1.3}$ and $K_{v3.2-3.3}$ potassium ions, respectively. g is the maximum coupling conductance of electrical synapse. I_{ext1} and I_{ext2} are varied and fixed external DC current, respectively. The synaptic current I_{syn} is denoted as follows:

$$I_{syn} = g_{syn}\alpha(V_2 - V_{syn}) \quad (4)$$

where, g_{syn} is the maximum coupling conductance of chemical synapse. V_{syn} is the reversal potential of the chemical synapse fixed as 0[mV](excitatory) or -75[mV](inhibitory). The open channel of chemical synapse α is given by Eqs.(5) and (6).

$$\frac{d\alpha}{dt} = \frac{\beta}{\tau_d} \quad (5)$$
$$\frac{d\beta}{dt} = -\frac{\alpha}{\tau_r} - (\frac{1}{\tau_r} + \frac{1}{\tau_d})\beta \quad (6)$$

The solution $\alpha(t)$ of Eqs.(5) and (6) with initial condition $(\alpha, \beta) = (0, 1)$ at $t = 0$ is calculated as $\alpha(t) = \frac{\tau_r}{\tau_r - \tau_d}(e^{-\frac{t}{\tau_r}} - e^{-\frac{t}{\tau_d}})$. τ_r and τ_d are the raise and decay time constants of synaptic current. For the excitatory (resp. inhibitory) synapse, $(\tau_r$[msec]$,\tau_d$[msec]$) = (0.5, 2.0)$ (resp.$(0.5, 7.0)$)[7]. In this study, we fix a synaptic delay as 1[msec]. The values of the other parameters are shown in Table 1.

3. Result

We investigate the bifurcation structure in three coupling cases ;1) a chemical synapse, 2) an electrical synapse, 3) both. In this study, the external DC current of Neuron2 is fixed as 80[pA] corresponding to the fundamental frequency denoted by $f_2 = 31.77$[Hz]. The firing frequency of Neuron1 can be varied by changing the value of the external DC current of Neuron1.

Table 1: **The values of the parameters**

$g_{Na} = 900$[nS]
$g_{k1} = 1.8$[nS]
$g_{k2} = 1800$[nS]
$g_l = 4.0$[nS]
$V_{Na} = 60$[mV]
$V_{k1} = -90$[mV]
$V_{k2} = -90$[mV]
$V_l = -70$[mV]
$C_M = 8.04$[pF]

3.1. Chemical Synapse

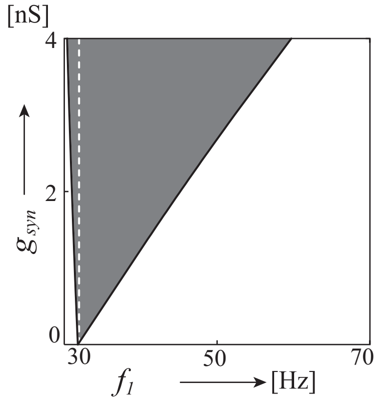
We obtain two-parameter bifurcation diagrams Fig.2(a) and 2(b) for respectively excitatory and inhibitory synapses, by using algorithms in [8, 9]. The horizontal axis is the firing frequency of Neuron1 f_1, and the vertical axis is the synaptic conductance g_{syn}. In this case, f_1 corresponds to the synchronous firing frequency of coupled neurons because Neuron1 is not affected by Neuron2. In these figures, the solid and dashed curves indicate the saddle-node and period-doubling bifurcation, respectively. The white dashed lines show the value of the fundamental frequency of Neuron2 f_2. In the shaded regions, we can observe the stable synchronous firings. We can find the Arnold's tongue structure formed by the saddle-node bifurcation in the both synapses.

Figures 2(a) and 2(b) show that the neurons have a wide parameter region in which stable synchronous firing is observed as the synchronous firing frequency becomes higher or lower than f_2 for the excitatory or inhibitory synapse, respectively. This synchronization phenomenon is also found in coupled ML neurons model[4]. However the period-doubling bifurcation is observed in $g_{syn} \geq 2.7$ only for the inhibitory coupling in this study.

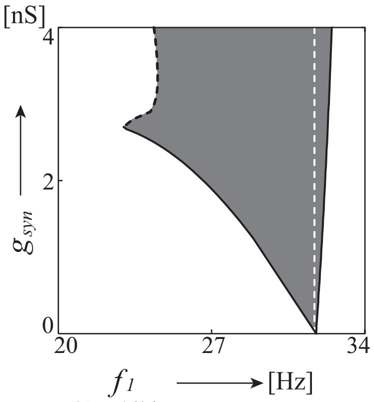
3.2. Electrical Synapse

Figure 3 is the two-parameter bifurcation diagram in an electrical coupling case. The horizontal axis is the firing frequency of the coupled neurons, and the vertical axis is the electrical synaptic conductance g. In this figure, we can observe stable synchronous firing in the shaded region. This figure shows that when $g < 0.4$, the neurons easily achieve synchronization at a higher firing frequency than f_2. However, when $g \geq 0.4$, the neurons synchronize at not only a higher firing frequency but also a lower that than f_2.

Figures 4(a)-4(d) are lissajous curves at the points(a)-(d) in Fig.3. The vertical and horizontal axes are the membrane potentials of Neuron1 and Neuron2, respectively. From Fig.4(b), the neurons synchronize at in-phase because the neurons have the same fundamental frequency at the point(b). At the points(a) and (d), the neurons show the anti-phase synchronization (Figs.4(a) and 4(d)). At these points, the difference of the fundamental frequency of in-



(a) Excitatory synapse.



(b) Inhibitory synapse.

Figure 2: **Two-parameter bifurcation diagrams in the case of excitatory(a) and inhibitory(b) synapse coupling.** In these figures, the solid and dashed curves indicate the saddle-node and period-doubling bifurcation, respectively. The white dashed lines denote the value of the fundamental frequency of Neuron2(= 31.77[Hz]). We can observe stable synchronous firing in shaded regions.

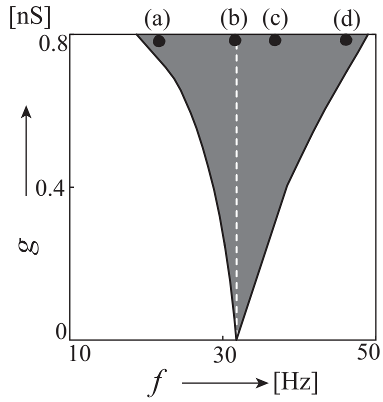


Figure 3: **Two-parameter bifurcation in the case of an electrical synapse coupling.** Symbols are the same as those of Fig.2.

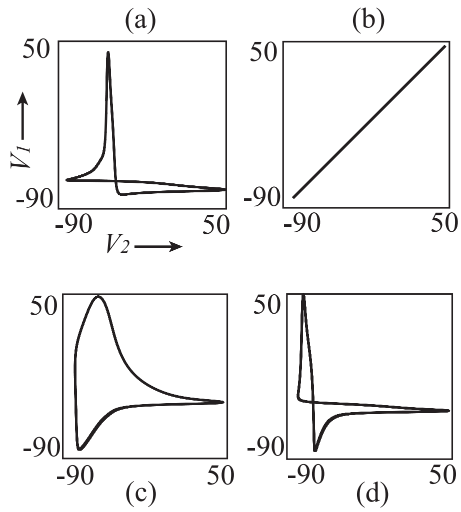


Figure 4: **Lissajous curves at the points(a)-(d) in Fig.3.** (a)f_1=14.88, (b)f_1=31.77, (c)f_1=38.55, (d)f_1=31.77.

dividual neurons becomes larger than that at point(c). At the point(c), the neurons show the near anti-phase synchronization (Fig.4(c)).

3.3. Inhibitory chemical and Electrical Synapses

Figure 5 is the bifurcation diagram in coupled neurons with the both synapses. The vertical axis is the external DC current of Neuron1 I_{ext1} and the horizontal axis is the coupling conductance of the chemical synapse. We fix coupling conductance of the electrical synapse as 0.8[10]. In the shaded area, we can observe stable synchronous firing, and the white dashed line indicates the value of the external DC current of the neurons when $I_{ext1} = I_{ext2} = 80$ corresponding to $f_1 = f_2 = 31.77$. The firing frequencies of coupled neurons at the point(a) and (b) in this figure are about 18.8[Hz] and 47.3[Hz], respectively. Hence, the neurons have a wider band of synchronous firing frequency than unidirectionally coupled neurons have.

Figure 6 is the enlarged figure around $I_{ext1} = 84.8$ of Fig.5. In the dark shaded region the coexistence of the synchronized states is observed, so the bifurcation structure becomes complicated. Figure 7 shows the schematic one-parameter bifurcation diagram along the line l in Fig.6. Closed circles represent the saddle-node bifurcations. We can see that a unstable solution and two stable solutions exist at the same value of the external DC current of Neuron1. By the changing the value of I_{ext1}, these stable solutions disappear with unstable one by the saddle-node bifurcation.

4. Conclusion

In this study we investigate the bifurcation structure and synchronization phenomena of coupled two fast-spiking neurons with unidirectional chemical and electrical synapses, when we change the values of the firing fre-

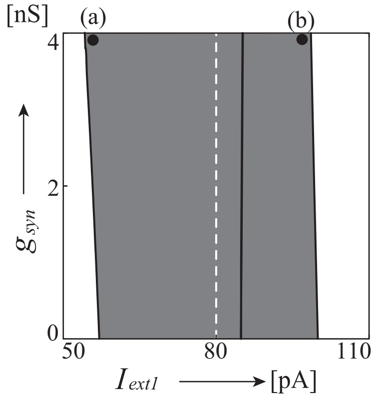


Figure 5: **Two-parameter bifurcation diagram in both chemical and electrical coupling.** Symbols are the same as those of Fig.2

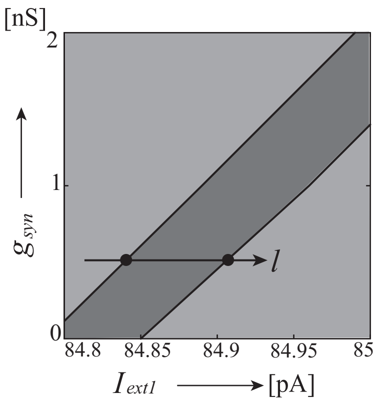


Figure 6: **Enlarged bifurcation diagram of Fig.5.**

quency of the pre-synaptic neuron and the coupling conductance. In the case of coupled neurons with only unidirectional chemical synapse, we find that the neurons easily achieve synchronization at a lower or higher firing frequency than the fundamental frequency of the post-synaptic neuron. On the other hands, in the case of an electrical coupling, by changing the value of the firing frequency of one of coupled neurons, the various synchronized states(in-phase, anti-phase and near anti-phase) are observed at the same value of the coupling conductance. In the case of both unidirectional inhibitory and electrical couplings, the neurons have a wider parameter region in which stable synchronous firing is observed than in the above cases. Furthermore, we discover the coexistence of the synchronized states in only this case.

In the future works, we should clarify the mechanism of generating these phenomena, and consider the physiological meaning of the phenomena.

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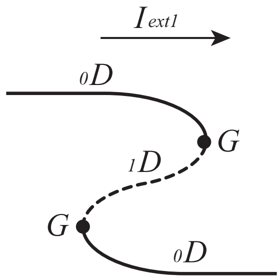

Figure 7: **Schematic one-parameter bifurcation diagram along the line l in Fig.6.** Solid and dashed curves indicate stable and unstable periodic solutions, respectively. Subscript of D means unstable dimension of the periodic solutions. G denote the saddle-node bifurcation.

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