

Bifurcation in Neurons Driven by Synaptic Currents with Multiple Frequencies

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Abstract—In our previous study, we considered a model of unidirectionally coupled driven and driving neurons, and obtained that the neurons are synchronized in low or high firing frequency by the inhibitory or excitatory coupling, respectively. In this study, we add the third neuron unidirectionally connected to the above two neurons. This neuron drives other neurons. We study synchronization observed in a system consisting of driving and driven neurons. When the synapse is inhibitory or excitatory, the neurons have a wide parameter region in which stable synchronous firing is observed as the external DC current of the driving neuron becomes small or large, respectively.

Moreover, we discovered that this phenomenon depends on the only synapse types.

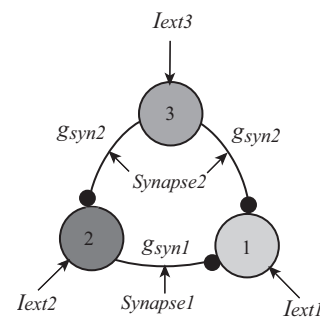


Figure 1: Schematic diagram of the coupled neuron model. g_{syn1} and g_{syn2} are maximum coupling conductance of the chemical synapses. Neuron3 drives Neuron1 and Neuron2 by Synapse2. Neuron2 drives only Neuron1 by Synapse1.

1. Introduction

Neurons have repetitive firing patterns by external stimulus. Neurons are classified into two types : class I and class II neurons, by the onsets of firing [1]. The oscillation of the former is associated with a saddle-node bifurcation that shows zero frequency at the bifurcation point. On the other hand, that of the latter is related to an Andronov-Hopf bifurcation exhibiting a finite frequency at the bifurcation point.

For synchronization of the class I and class II neurons, systems consisting of the same class neurons have been investigated. Izhikevich and Ermentrout showed that the class II neurons easily achieve synchronization [2,3]. However, Tsuji and coworkers indicated that class I neurons also have various bifurcation states and many periodic solutions [4].

However, the combination of different class neurons exists in real neuronal networks. The interneurons in the neocortex show class I or class II excitabilities. In the networks of the interneurons illustrated by Beierlein and coworkers, there are various coupling units of the class I and II neurons with chemical and electrical synapses [5]. According to White, coupled the same class neurons with an asymmetrical external DC current have various synchronization states [6,7]. Hence we studied the synchronization in two unidirectionally coupled neurons with different classes and whit asymmetrical inputs, and found that the neurons with an excitatory or inhibitory synapse have a wide parameter region of synchronization when external DC current of the driving neuron becomes large or small, respectively [8].

In this study, we add the third neuron unidirectionally connected to the above two neurons. This neuron drives other neurons as shown in Fig. 1. We study synchronization observed in the neurons driven by synaptic currents with multiple frequencies. Thomas and coworkers found that the firing of the neuron with the multiple sinusoidal inputs is affected by not only their frequencies but also the powers and phases [9]. However, generically, it is difficult to analyze synchronization of the neurons driven by external forces with multiple frequencies, because the Poincaré mapping cannot be defined. In our model, we fluctuate the firing frequency of the neurons by changing the value of external DC currents of driving neurons. As a result, this system behaves like a forced system in which external forces' frequencies are different. We find that when Synapse2 is inhibitory or excitatory, the neurons have a wide parameter region in which stable synchronous firing is observed as the external DC current of the Neuron3 becomes small or large, respectively.

2. Neuron Model

We consider the model as shown in Fig. 1. The Morris-Lecar equation [10] is applied to the dynamics of a single

neuron. The membrane potentials of each neuron are described as follows:

$$C_M \frac{dV_1}{dt} = -g_l(V_1 - V_l) - g_{Ca}M_{\infty 1}(V_1 - V_{Ca}) - g_k N_1(V_1 - V_k) + I_{ext1} + g_{syn1}\alpha_2(V_{syn} - V_1) + g_{syn2}\alpha_3(V_{syn} - V_1) \quad (1)$$

$$C_M \frac{dV_2}{dt} = -g_l(V_2 - V_l) - g_{Ca}M_{\infty 2}(V_2 - V_{Ca}) - g_k N_2(V_2 - V_k) + I_{ext2} + g_{syn2}\alpha_3(V_{syn} - V_2) \quad (2)$$

$$C_M \frac{dV_3}{dt} = -g_l(V_3 - V_l) - g_{Ca}M_{\infty 3}(V_3 - V_{Ca}) - g_k N_3(V_3 - V_k) + I_{ext3} \quad (3)$$

where, I_{ext1} - I_{ext3} are external DC currents for Neuron1-Neuron3. In this research, I_{ext1} is fixed as 78.55. g_{syn2} and g_{syn3} are the maximum coupling conductance of the chemical synapses, V_{syn2} and V_{syn3} are the reversal potentials of the chemical synapses. α_2 and α_3 are the open channels of the chemical synapses and their dynamics is described by:

$$\frac{d\alpha_i}{dt} = \frac{\beta_i}{\tau_2} \quad (4)$$

$$\frac{d\beta_i}{dt} = -\frac{\alpha_i}{\tau_1} - \left(\frac{1}{\tau_1} + \frac{1}{\tau_2}\right)\beta_i. \quad (5)$$

$(i = 2, 3)$

The solution $\alpha^{[i]}(t)$ of Eqs. (4) and (5) with the initial condition $(\alpha^{[i]}, \beta^{[i]}) = (0, 1)$ at $t = 0$ is calculated as $\alpha^{[i]}(t) = \frac{\tau_1}{\tau_1 - \tau_2} (e^{-\frac{t}{\tau_1}} - e^{-\frac{t}{\tau_2}})$. τ_1 and τ_2 are respectively the raise and the decay time constants of the synapse. We fix the values of τ_2 as 2.0[msec](excitatory) and 7.0[msec](inhibitory) [11]. This synapse model has a synaptic delay fixed as 1[msec]. M_{∞} and N_{∞} as functions of the membrane potential V are described as follows:

$$\frac{dN_i}{dt} = \frac{N_{\infty i} - N_i}{\tau_{N_i}} \quad (6)$$

$$M_{\infty i} = 0.5[1 + \tanh\{(V_i - V_a)/V_b\}] \quad (7)$$

$$N_{\infty i} = 0.5[1 + \tanh\{(V_i - V_c)/V_d\}] \quad (8)$$

$$\tau_{N_i} = 1/[\phi \cosh\{(V_i - V_c)/2V_d\}]. \quad (9)$$

$(i = 1, 2, 3)$

The M-L model can be changed between class I and class II excitabilities by varying the value of the parameter V_c ; the critical point is about $V_c = 4.6$ [12]. We fix V_c as 2 to obtain the property of class II. The values of the other parameters are shown in Table 1.

Table 1: Fixed values of system parameters

$g_{Ca} = 4.0[\text{mS}/\text{cm}^2]$
$g_K = 8[\text{mS}/\text{cm}^2]$
$g_L = 2[\text{mS}/\text{cm}^2]$
$V_{Ca} = 120[\text{mV}]$
$V_K = -80[\text{mV}]$
$V_L = -60[\text{mV}]$
$V_a = -1.2[\text{mV}]$
$V_b = 18[\text{mV}]$
$V_d = 17.4[\text{mV}]$
$C_M = 20[\mu\text{F}/\text{cm}^2]$
$\phi = 1/15[\text{s}^{-1}]$
$g_s^{[1]} = 20[\text{mS}/\text{cm}^2]$
$\tau_1 = 0.5[\text{msec}]$

3. Result

In this research, we assume that the coupling conductance of Synapse2 g_{syn2} is $0 \leq g_{syn2} \leq 5$. We change the external DC current of Neuron3 I_{ext3} . The coupling conductance of Synapse1 g_{syn1} is fixed as 5. The external DC current of Neuron2 I_{ext2} is fixed as 76 or 80, these are a little smaller or larger value than I_{ext1} . We use the algorithms in [13] and [14] for calculation of bifurcation sets.

3.1. Synapse2 is inhibitory

Figures 2(a) to 2(d) are two-parameter bifurcation diagrams when Synapse2 is inhibitory. The horizontal axis is the external DC current of Neuron3 I_{ext3} , and the vertical axis is the synaptic conductance g_{syn2} . In these figures, the solid curves denote the saddle-node bifurcation, and we can observe stable synchronized firing in the shaded areas. In Figs. 2(b)-2(d), the shaded regions called Arnold's tongue touch the horizontal axis at the value of I_{ext2} . In Figure 2(a)($I_{ext1}=78.55$ and $I_{ext2}=76$), a parameter region does not touch the horizontal axis. In $g_{syn2}=0.0$, Neuron1 and Neuron2 easily achieve synchronization as $I_{ext1} \leq I_{ext2}$, because of the excitatory coupling between these neurons[8]. Hence, the neurons cannot be synchronized when the value of the coupling conductance of Synapse2 is small.

These figures show that the neurons have a wide parameter region in which stable synchronous firing is observed when the external DC current of the Neuron3 is less than that of Neuron2. Decreasing the external DC current of Neuron3 means that the system has a low firing frequency. Hence the neurons easily archive synchronization in a low firing frequency.

We show Fig. 3, a bifurcation diagram for $g_{syn1} = 0.0$, to consider the effect of only Synapse2 on synchronization. We can observe that three neurons synchronize in a shaded area. The neurons have a wider parameter region in which stable synchronous firing is observed when the external DC current of the Neuron3 is smaller. We can also observe the similar shape of a parameter region in Fig. 2. Hence, the

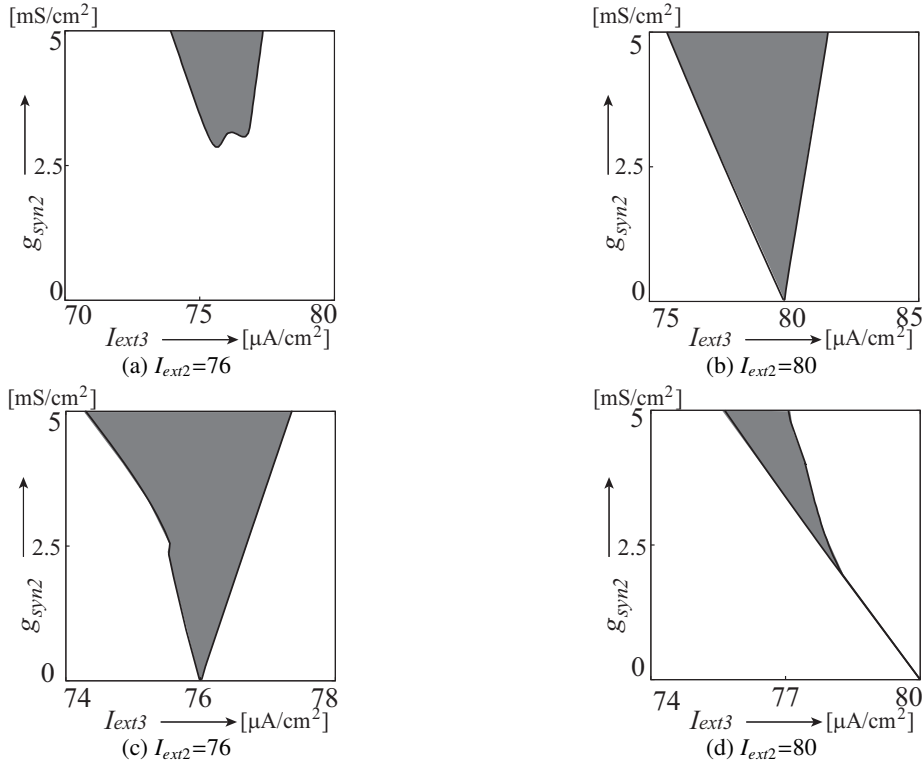


Figure 2: Bifurcation diagrams when Synapse2 is inhibitory. Synapse1 is excitatory ((a) and (b)) or inhibitory ((c) and (d)).

unidirectionally coupling between Neuron 3 and Neuron1 or Neuron3 and Neuron2, is an important factor to decide this synchronization feature. Moreover, in the parameter region as g_{syn2} is small, we observe that the neurons do not synchronize, or that only two neurons synchronize (Neuron3 and Neuron1 or Neuron3 and Neuron2).

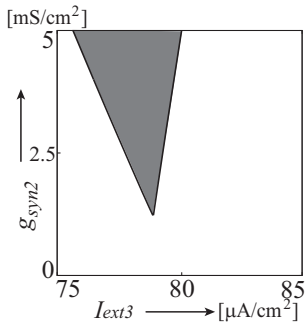


Figure 3: Bifurcation diagram for $g_{syn1} = 0.0$ and $I_{ext2}=80$.

3.2. Synapse2 is excitatory

We obtain Figure 4 by analyzing the model as shown in Fig. 1 for excitatory Synapse2. The Arnold's tongue structure surrounded by the saddle-node bifurcations can be observe in Figs. 4(b)-4(d). Figures 4(a) to 4(d) show that the neurons have a wide parameter region in which stable synchronous firing is observed when external DC current

of the Neuron3 becomes large. Neuron3 has a high firing frequency by increasing the external DC current, so the neurons easily archive synchronization in a high firing frequency.

Figure 5 is a bifurcation diagram for $g_{syn1} = 0.0$ to explain the effect of only Synapse2 on synchronization. This figure shows that the neurons have a wider parameter region in which stable synchronized firing is observed when external DC current of Neuron3 is large. This shape of a parameter region is similar as shown in Fig. 4.

4. Conclusion

In this study, we have investigated coupled three neurons model as shown in Fig. 1. We find that when Synapse2 is the inhibitory or excitatory chemical synapse, the neurons easily achieve synchronization in a low or high firing frequency, respectively. These synchronization phenomena are depend on the synapse types of a driving neuron (Neuron3), and are similar to the synchronization of unidirectionally coupled system in our previous study. However, in case of small value on the coupling conductance of Synapse2, the type of Synapse1 affects the synchronization.

Studying systems consisting of class I neurons or involving both classes neurons, and considering the physiological meaning of these phenomena will be studied as future problems.

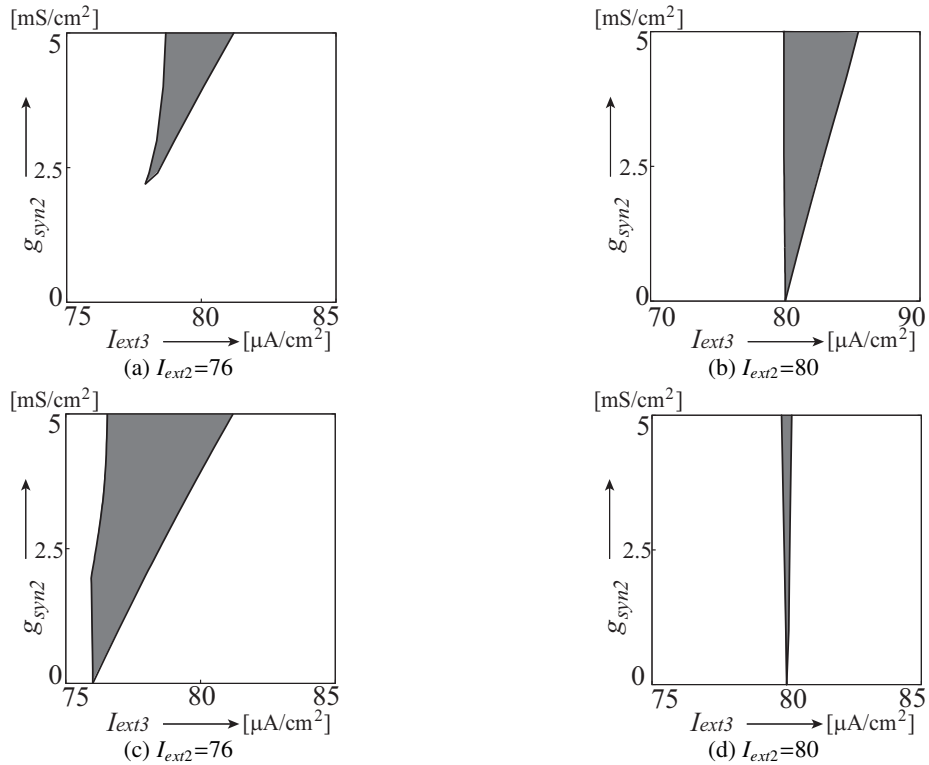


Figure 4: Bifurcation diagrams when Synapse2 is excitatory. Synapse1 is excitatory ((a) and (b)) or inhibitory ((c) and (d)).

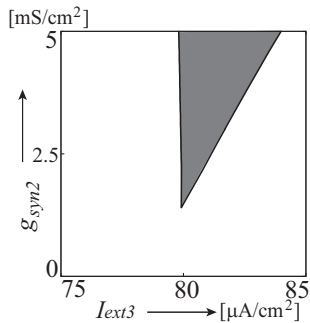


Figure 5: Bifurcation diagram for $g_{syn1} = 0.0$ and $I_{ext2}=80$.

Acknowledgments

This work partly was supported by the Sasakawa Scientific Research Grant from The Japan Science Society.

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