IEICE Proceeding Series

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Vol. 1 pp. 771-774
Publication Date: 2014/03/17
Online ISSN: 2188-5079

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Abstract—Inhibitory synapses regulate synchronous firings, however, the analysis of the inhibitory coupled system is not enough. In this paper we investigate inhibitory coupled five and six Morris-Lecar neurons. This system is an important motif to understand phenomena in a large-scaled small-world network. In this system, we observe all possible cluster synchronizations except for the complete in-phase synchronization. Also, their bifurcations are studied.

1. Introduction

Recently, complex network structures, such as small-world [1] and scale-free [2, 3], have been found in various real neuronal networks [4–6]. Synchronization in neuronal networks is also found and it is considered that synchronous activities play an important role in information processing in the brain [7–9]. On the other hand, they are not desirable for several neurological diseases such as epilepsy and tremor in Parkinson's disease [10, 11]. 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 [12], and Nishikawa and Motter extended it for an asymmetric case [13]. In small-world networks the average path length becomes short, thus it is considered that synchronization is easier achieved than in a regular lattice [14–17]. However, it is not the only condition, synchronizability also depends on a network size, the degree distribution (distribution of a number of links), the clustering coefficient and so on [18–21].

In a previous paper we investigated synchronization in neuronal networks with small-world structure [22]. Inhibitory connected 24 neurons were considered. Inhibitory synapses are considered to regulate synchronous firings [23]. We found many cluster phase synchronizations. However, clustered states corresponding to non-periodic solutions coexist and which one is observed depends on initial states. In this paper, we consider smaller systems (numbers of coupled neurons (n) are five and six). All possible clustered states except for complete in-phase solutions are observed by changing the value of a coupling coefficient and some states coexist in $n = 5$. Studying such a piece of complex networks called "network motifs" [24] is fundamental to understand phenomena in whole complex networks.

2. System Equation

In this paper we consider a system of synaptically coupled Morris-Lecar (ML) neurons [25]. The ML neuron model was proposed as a model for describing a variety of oscillatory voltage patterns of Barnacle muscle fibers. The system equation for synaptically coupled ML neurons with two nearest neighbors is described by

$$\begin{aligned} C\frac{dV_i}{dt} &= -g_L(V_i - V_L) - g_{Ca}M_{\infty_i}(V_i - V_{Ca}) \\ &\quad -g_K N_i(V_i - V_K) + I_{ext} + I_{syn_i} \\ \frac{dN_i}{dt} &= \frac{N_{\infty_i} - N_i}{\tau_{N_i}} \\ \frac{ds_i}{dt} &= \frac{1 - s_i}{1 + \exp(-V_i)}\left(\frac{1}{\tau_r} - \frac{1}{\tau_d}\right) - \frac{s_i}{\tau_d} \\ &\quad (i = 1, \cdots, 5\text{or}6), \end{aligned} \tag{1}$$

where V_i is the membrane potential, $N_i \in [0,\ 1]$ is the activation variable for K^+, I_{ext} is the external current and t denotes the time measured in milliseconds. The system parameters V_{Ca}, V_K and V_L represent equilibrium potentials of Ca^{2+}, K^+ and leakage currents, respectively, and g_{Ca}, g_K and g_L denote the maximum conductance of the corresponding ionic currents. The functions of V_i, M_{∞_i}, N_{∞_i} and τ_{N_i} are given by

$$\begin{aligned} M_{\infty_i} &= 0.5[1 + \tanh(V_i - V_a)/V_b], \\ N_{\infty_i} &= 0.5[1 + \tanh(V_i - V_c)/V_d], \\ \tau_{N_i} &= 1.0/[\phi\cosh(V_i - V_c)/(2V_d)], \end{aligned} \tag{2}$$

where V_a and V_c are the midpoint potentials at which the calcium current and the potassium current is halfactivated, V_b is a constant corresponding to the steepness of voltage dependence of activation, V_d denotes the slope factor of potassium activation and ϕ is the temperature-like time scale factor. In Eq. (1), s_i, τ_r and τ_d are the gating variable for the synapse, the raise and the decay time of the synapse, respectively, and I_{syn_i} is the synaptic current given by

$$I_{syn_i} = (V_{syn} - V_i)\sum_{j=1, j\neq i}^{n} g_{syn_{ij}} s_j \tag{3}$$

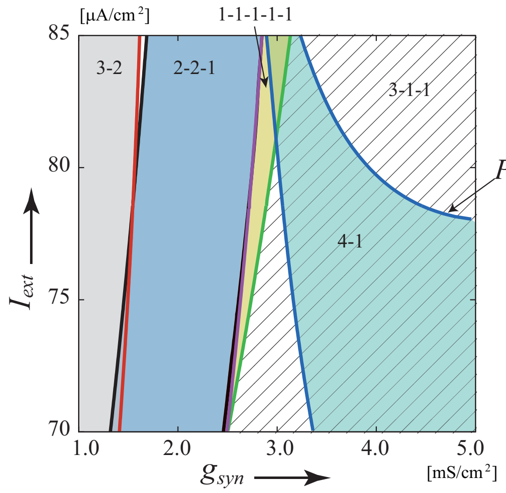


Figure 1: Two-parameter bifurcation diagram. In each colored or hatched region we observe indicated cluster synchronization. Numbers connected by hyphens indicate of neurons with simultaneous firings. All curves indicate pitchfork bifurcation sets except for the curve indicated by *PD* (period-doubling bifurcation sets).

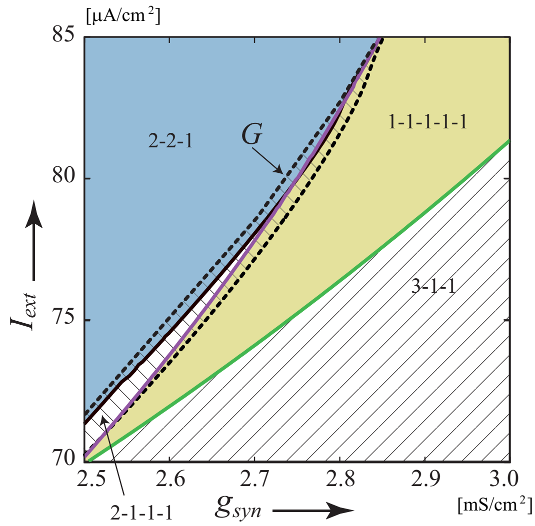


Figure 2: Enlarged diagram of Fig. 1. All curves indicate pitchfork bifurcation sets except for the curve indicated by *G* (tangent bifurcation sets).

where $g_{syn_{ij}}$ is the maximum synaptic conductance between neurons i and j, and V_{syn} is the reversal potential. Here, we consider two-way coupling ($g_{syn_{ij}} = g_{syn_{ji}}$) and two-nearest neighbors coupling ($g_{syn_{ij}} = 0$ if i-th and j-th neurons are not two-nearest neighbors). 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 [26]. The values of the other parameters in the ML neuron are fixed as follows:

$$
\begin{array}{rclrcl}
C & = & 20\ [\mu\mathrm{F/cm^2}], & g_K & = & 8\ [\mathrm{mS/cm^2}],\\
g_L & = & 2\ [\mathrm{mS/cm^2}], & g_{Ca} & = & 4\ [\mathrm{mS/cm^2}],\\
\phi & = & 1/15\ [\mathrm{sec^{-1}}], & V_{Ca} & = & 120\ [\mathrm{mV}],\\
V_K & = & -80\ [\mathrm{mV}], & V_L & = & -60\ [\mathrm{mV}],\\
V_a & = & -1.2\ [\mathrm{mV}], & V_b & = & 18\ [\mathrm{mV}],\\
V_d & = & 17.4\ [\mathrm{mV}]. & & &
\end{array}
$$

3. Results

3.1. $n = 5$

The values of all synaptic conductances are the same ($g_{syn_{ij}} = g_{syn}$) in $n = 5$. We obtain bifurcation sets on the parameter plane (g_{syn}, I_{ext}) using Kawakami's method [27]. Figure 1 shows a two-parameter bifurcation diagram. Numbers in the figure are of clustered neurons with synchronous firing. Figure 2 shows an enlarged diagram of Fig. 1.

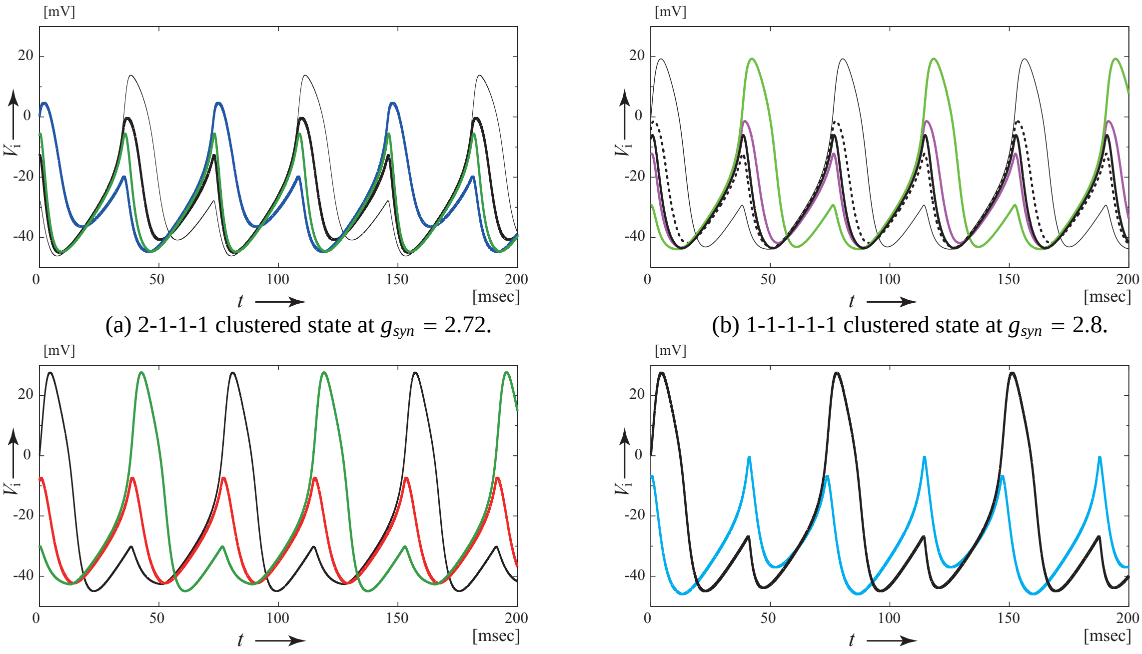
Increasing the value of g_{syn} from 1.0 we observe several cluster synchronizations:3-2, 2-2-1, 2-1-1-1, 1-1-1-1-1, 4-1 and 3-1-1, where numbers connected by hyphens indicate of neurons with simultaneous firings. Moreover, some regions are overlapped. All possible clustered states except for a complete in-phase solution are observed. Boundaries of parameter regions in which stable clustered states are formed by mainly pitchfork bifurcation sets except for one period-doubling bifurcation set and one tangent bifurcation set. Roughly speaking, which clustered state is observed stably depends on mainly the value of the synaptic conductance (or coupling strength) rather than the external current (controlling the firing frequency).

The waveforms of typical clustered states are shown in Fig. 3. They are classified into two types: suppressed by fired neurons (e.g. green and black ones in Fig. 3(c)) and non-suppression (e.g. red one in (c)).

On the boundary of 1-1-1-1-1 and 3-1-1 shown by the green curve in Figs. 1 and 2. the supercritical pitchfork bifurcation occurs and in-phase three membrane potentials bifurcate to non-in-phase three potentials. Two characteristic multipliers become one at this bifurcation point. Thus, this pitchfork bifurcation is degenerate by the symmetrical property (the system equation is invariant under interchange of any two neurons). Comparing Fig. 3(b) with 3(c) we can see that the red waveform in Fig. 3(c) (three waveforms are overlapped) bifurcates to three distinct waveforms shown in Fig. 3(b) (purple, solid black and dashed black waveforms). All other pitchfork bifurcations are subcritical.

3.2. $n = 6$

In the previous study [22], we reported interesting nonperiodic clustered states in $n = 24$. Even in $n = 6$ we observe a similar phenomenon. We consider rewiring one connection ($g_{syn_{12}}$ becomes zero and $g_{syn_{14}}$ is not zero). Fig-



(a) 2-1-1-1 clustered state at g_{syn} = 2.72.

(b) 1-1-1-1-1 clustered state at g_{syn} = 2.8.

(c) 3-1-1 clustered state at g_{syn} = 3.0.

(d) 4-1 clustered state at g_{syn} = 4.0.

Figure 3: Waveforms of membrane potentials where I_{ext} = 78.55. Cyan, red and blue curves indicate four, three and two in-phase waveforms, respectively. Other colors are for one neuron.

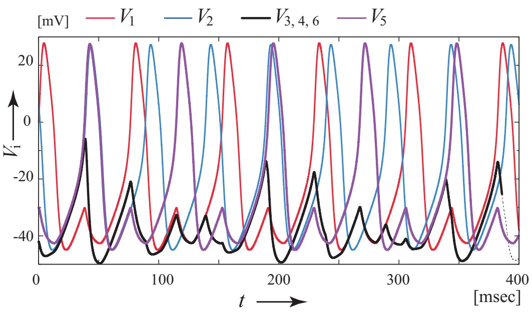


Figure 4: Waveforms of the membrane potentials without periodicity in n = 6, $g_{syn_{12}}$ = 0 and $g_{syn_{14}}$ =3.0.

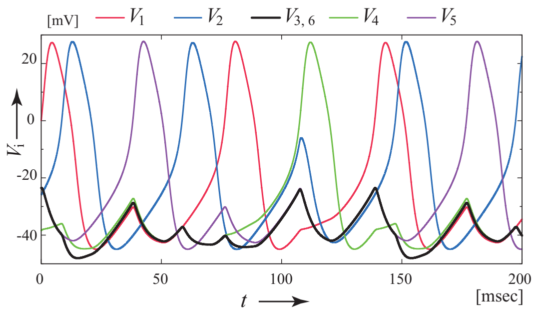


Figure 5: Waveforms of the membrane potentials in n = 6, $g_{syn_{12}}$ = 0 and $g_{syn_{14}}$ =1.1. These waveforms are two-periodic, because considering the point of V_1 = 0 and $dV_1/dt > 0$ same waveforms are repeated at every two points.

ure 4 shows waveforms of V_i. V_1 and V_5 are synchronized at almost anti-phase, and V_3, V_4 and V_6 are in-phase subthreshold oscillations. V_2 is not suppressed by other neurons, thus the firing rate between V_1 and V_2 is irrational.

By numerical bifurcation analysis we find a similar periodic solution. Figure 5 shows waveforms of this periodic solution. In this case V_3 and V_6 are in-phase subthreshold oscillations. V_1 and V_2, and V_4 and V_5 have 1:1 firing, however V_1 and V_4 have 2:1 firing. After disappearance of this periodic solution due to the tangent bifurcation, the non-periodic clustered state as shown in Fig. 4 appears.

4. Conclusion

We investigated a system of inhibitory coupled ML neurons in n (number of coupled neurons) = 5 and 6. This model is minimal realization of a system of coupled two nearest neighbors which is the basis for the small-world network, because usually we construct the small-world network from the two-nearest-neighbors coupling system by changing connections with some probability.

By changing the value of the maximum synaptic conductance, we observed all possible cluster synchronizations except for complete in-phase synchronization in n = 5. When n = 6, we observed the same kind of complicated cluster synchronization as that in n = 24. By numerical bifurcation analysis, we clarified the transition between this synchronized state and the same type of the periodic solution. To confirm the universality of this transition is one of our open problems.

Acknowledgments

This work was supported by JSPS Grant-in-Aid for Scientific Research (C) (No.23500367). We thank Prof. T. Yoshinaga at the University of Tokushima for providing his powerful bifurcation analysis tools. We also thank an anonymous reviewer for his/her valuable comments.

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