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# Bifurcation in neuronal networks with hub structure

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## ABSTRACT

We investigate bifurcations in neuronal networks with a hub structure. It is known that hubs play a leading role in characterizing the network dynamical behavior. However, the dynamics of hubs or star-coupled systems is not well understood. Here, we study rather subnetworks with a star-like configuration. This coupled system is an important motif in complex networks. Thus, our study is a basic step for understanding structure formation in large networks. We use the Morris–Lecar neuron with class I and class II excitabilities as a node. Homogeneous (coupling the same class neurons) and heterogeneous (coupling different class neurons) cases are considered for both excitatory and inhibitory coupling. For the homogeneous system class II neurons are suitable for achieving both complete and cluster synchronization in excitatory and inhibitory coupling, respectively. For the heterogeneous system with inhibitory coupling, the class I hub neuron has a wider parameter region of synchronous firings than the class II hub. Moreover, the class I hub neuron with the excitatory synapse gives rise to bifurcations of synchronized states and multi-stability (coexistence of a few different states) is observed.

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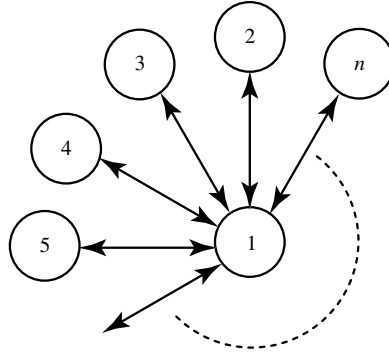
## 1. Introduction

Recently, complex network structures, such as small-world and scale-free, have been found in various real neuronal networks [1–6]. Synchronization in neuronal networks is also found and it is considered that synchronous activities play an important role in information processing in the brain. On the other hand, they are not desirable for several neurological diseases such as epilepsy and tremor in Parkinson's disease [7,8]. 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 [9], and Nishikawa and Motter extended it for an asymmetric case [10]. In small-world networks average path length becomes short; thus it is considered that synchronization is easily achieved than in a regular lattice. However, a heterogeneous distribution of nodes and the number of links of each node are also important for obtaining synchronization [11,12]. In scale-free networks, the existence of hubs (nodes with many connections) is a common feature [13,14]. It is well known that the hubs play a leading role in characterizing the network dynamical behavior [15–21]. However, even the dynamics of a single hub is not well studied, especially when the properties of nodes are not identical. Studying such a piece of complex networks called “network motifs” [22] is fundamental to understand the phenomena in whole complex networks.

In this paper, we investigate neuronal networks with a star-like structure consisting of Morris–Lecar (ML) neurons with class I and class II excitabilities. This is to mimic the action of a hub in a complex network of neurons. This coupled system is a basic motif in complex networks. Many studies confirm that oscillatory dynamics of neural activity and its

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**Fig. 1.** A network with a hub structure. Circled numbers correspond to the index  $i$  in Eq. (3).

synchronization play a crucial role in information processing in the brain [7]. The oscillation mechanisms of neurons are classified into two types by their bifurcations [23]: class I (saddle-node bifurcation) and class II (Hopf bifurcation). The oscillation of the former and the latter has almost zero frequency and a finite frequency at the bifurcation point, respectively. Recently, neurons with these characteristics have been experimentally found in the somatosensory cortex [24]. Thus, the effect of these differences on neural activities has been studied using model equations [25,26]. For mutual synchronization of two neurons, it is clarified by using the phase resetting curve (PRC) that class II neurons easily achieve synchronization [27–29]. Also for a large number of neurons with random connections, class II neurons present a good level of synchronization regardless of their connection topology [30]. For forced synchronization, class II neurons have the advantage of acquiring synchronization [31,32]. However, Tsuji and coworkers showed that class I neurons have wider parameter regions of synchronous firings than those of class II neurons by a detailed bifurcation analysis [33].

In this paper, we will connect class I and class II neurons bidirectionally by chemical synapses with a time delay and consider homogeneous (coupling inside the same class) and heterogeneous (coupling between different classes) systems for both excitatory and inhibitory coupling. In homogeneous systems, excitatory synapses have the advantage leading to synchronous firings but the inhibitory ones promote cluster synchronization; i.e. neurons are divided into two or three groups. In heterogeneous systems, the same class neurons are synchronized through excitatory synapses of the hub neuron.

## 2. The model system

In this study, we focus on synchronous firings, i.e. the timing of firings is the same. In most cases it equals to complete synchronization, but in some case neurons produce synchronous firings regardless of their distinct waveforms, i.e. phase synchronization. For analysis of synchronization of periodic firings, we use the bifurcation theory to identify its observable parameter regions. For non-periodic states, we use a brute-force method.

The ML neuron model [34] proposed as a model for describing a variety of oscillatory voltage patterns of Barnacle muscle fibers is described by

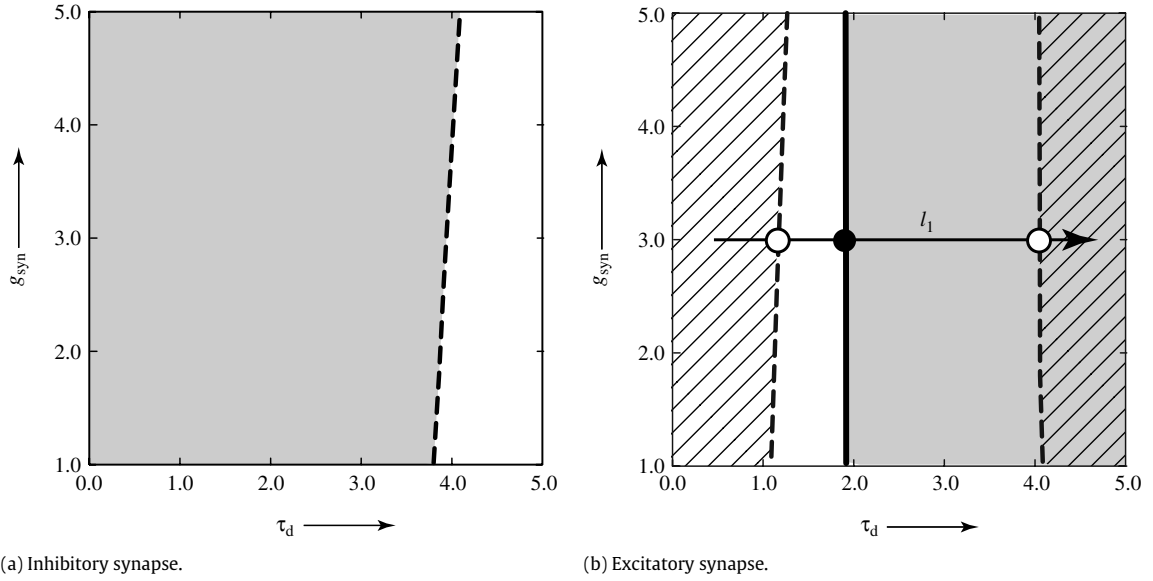
$$\begin{aligned} C \frac{dV}{dt} &= -g_l(V - V_l) - g_{ca}M_\infty(V - V_{ca}) - g_kN(V - V_k) + I_{ext} \\ \frac{dN}{dt} &= \frac{N_\infty - N}{\tau_N} \end{aligned} \quad (1)$$

where  $V$  is the membrane potential,  $N \in [0, 1]$  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  $V$ ,  $M_\infty$ ,  $N_\infty$  and  $\tau_N$  are given by

$$\begin{aligned} M_\infty &= 0.5[1 + \tanh(V - V_a)/V_b], \\ N_\infty &= 0.5[1 + \tanh(V - V_c)/V_d], \\ \tau_N &= 1.0/[\phi \cosh(V - V_c)/(2V_d)], \end{aligned} \quad (2)$$

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  $\phi$  is the temperature-like time scale factor.

The class I and II excitability can be controlled by the parameter  $V_c$ ; the critical point is about  $V_c^* = 4.6$  [35], i.e. the ML model becomes class I for  $V_c > V_c^*$  and class II for  $V_c^* > V_c > 0$ . In this study we use  $V_c = 12$  and 2 for class I and class II, respectively. We use  $I_{ext} = 73.67$  and 78.55 for class I and II neurons, respectively, to obtain almost the same oscillation frequency (about 20 Hz) for the single neurons [35]. The other parameters in Eq. (1) are fixed as follows:



**Fig. 2.** Bifurcation diagrams for the homogeneous case (class I) in Eq. (3) for  $n = 4$ . In the hatched and gray regions, we observe stable synchronous firings for all peripheral neurons. The dashed and solid curves indicate a pitchfork and tangent bifurcation, respectively.

$$\begin{aligned} C &= 20 \mu\text{F}/\text{cm}^2, \quad g_k = 8 \text{ mS}/\text{cm}^2, \\ g_l &= 2 \text{ mS}/\text{cm}^2, \quad g_{ca} = 4 \text{ mS}/\text{cm}^2, \\ \phi &= 1/15 \text{ s}^{-1}, \quad V_{ca} = 120 \text{ mV}, \\ V_k &= -80 \text{ mV}, \quad V_l = -60 \text{ mV}, \\ V_a &= -1.2 \text{ mV}, \quad V_b = 18 \text{ mV}, \\ V_d &= 17.4 \text{ mV}. \end{aligned}$$

In this paper we consider a system of synaptically coupled ML neurons. The system equation is then described by

$$\begin{aligned} C \frac{dV_i}{dt} &= -g_l(V_i - V_l) - g_{ca}M_{\infty i}(V_i - V_{ca}) - g_kN_i(V_i - V_k) + I_{ext} + I_{syn_i} \\ \frac{dN_i}{dt} &= \frac{N_{\infty i} - N_i}{\tau_{N_i}} \\ \frac{d\alpha_i}{dt} &= \frac{\beta_i}{\tau_2} \\ \frac{d\beta_i}{dt} &= -\frac{\alpha_i}{\tau_1} - \left( \frac{1}{\tau_1} + \frac{1}{\tau_2} \right) \beta_i \quad (i = 1, \dots, n), \end{aligned} \tag{3}$$

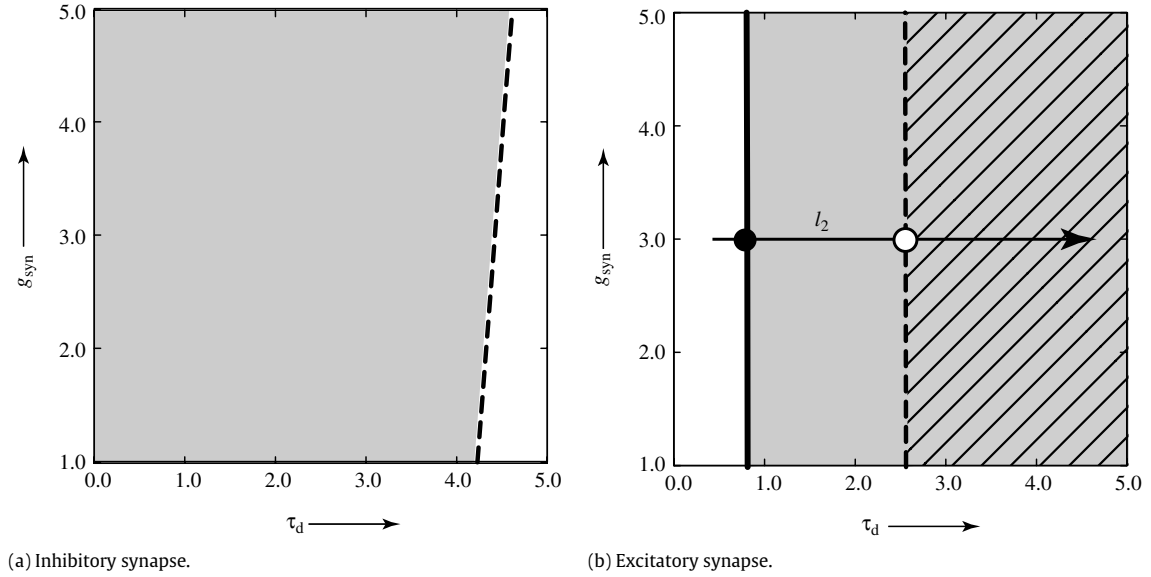
where  $\tau_1$  and  $\tau_2$  are the raise and the decay time of the synapse, respectively, and  $I_{syn_i}$  is the synaptic current given by

$$I_{syn_1} = g_{syn} \sum_{j=2}^n (V_{syn} - V_1) \alpha_j \tag{4}$$

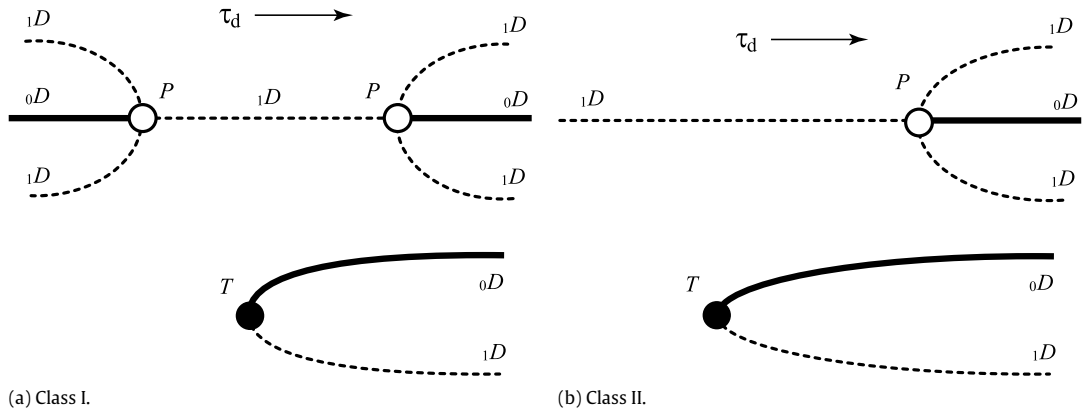
$$I_{syn_k} = g_{syn} (V_{syn} - V_k) \alpha_1 \quad (k = 2, \dots, n), \tag{5}$$

where  $g_{syn}$  is the maximum coupling conductance and  $V_{syn}$  is the reversal potential. The characteristics of neurons are the same except for the parameter  $V_{c_i}$  and the synaptic current  $I_{syn_i}$ . In our model system, the neurons are arranged in a star-like structure with neuron 1 acting as a hub (Fig. 1), i.e. neuron 1 (hub) and all other neurons are connected and all peripheral neurons are only connected with the hub. The values of  $(\tau_1, \tau_2)$  are fixed as (0.5, 2.0) and (0.5, 7.0) ms for the excitatory and the inhibitory synapse, respectively, according to experimental results [36]. The reversal potential  $V_{syn}$  is set to 0 or  $-60$  for the excitatory or the inhibitory synapse, respectively, because  $V_{syn} > V_{eq}$  for the excitatory synapse and otherwise for the inhibitory synapse, where  $V_{eq}$  indicates the resting membrane potential (about  $-59$  mV). Each vector  $(\alpha_i, \beta_i)$  jumps to the constant (0, 1) at  $t = t_i + \tau_d$  where  $t_i$  is the time when the  $i$ th neuron fires. Then  $\alpha_i$  is given by [37]

$$\alpha_i(t) = \frac{\tau_1}{\tau_2 - \tau_1} \left( -\exp\left(-\frac{t}{\tau_1}\right) + \exp\left(-\frac{t}{\tau_2}\right) \right). \tag{6}$$



**Fig. 3.** Bifurcation diagrams for the homogeneous case (class II) in Eq. (3) for  $n = 4$ . The legends are the same as Fig. 2.



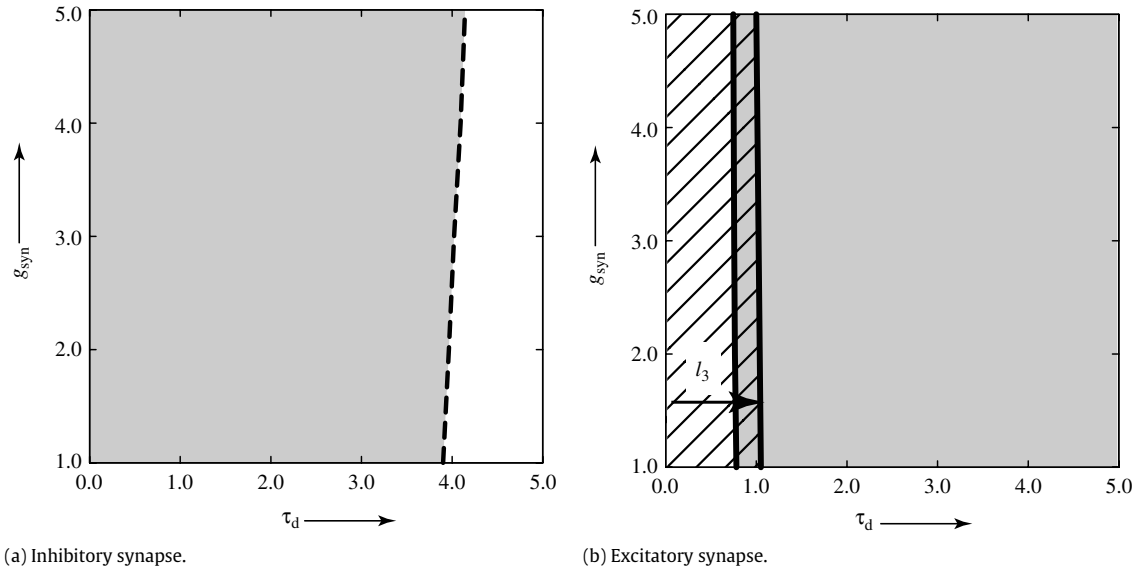
**Fig. 4.** Schematic one-parameter bifurcation diagrams for the homogeneous system coupled by the excitatory synapse. Solid and dashed curves indicate stable and unstable periodic solutions, respectively, which correspond to synchronous firings of three peripheral neurons. Subscript of  $D$  means unstable dimension of the periodic solutions.  $T$  and  $P$  means a tangent and pitchfork bifurcation point, respectively.

Namely, the firing information of the neuron transforms to the connected neurons with the time delay  $\tau_d$ . We choose  $\tau_d$  as one of the control parameters, because it can be changed by temperature [38] ( $\tau_d = 0.5$  and  $3.5$  to  $7.0$  ms at  $20$  and  $2.5$  °C, respectively).

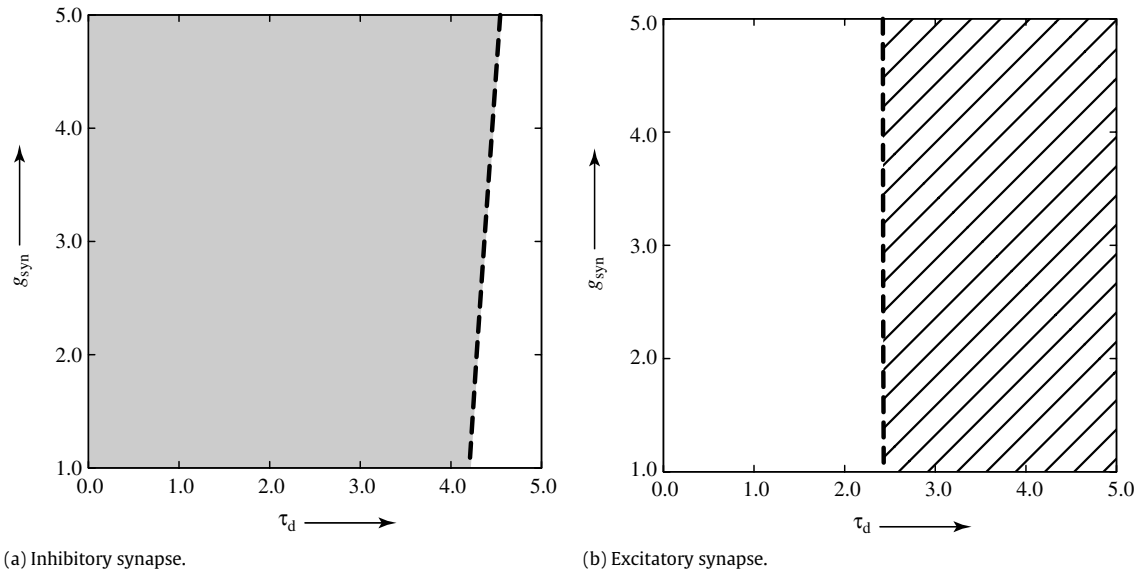
### 3. Results

Now we show the results for  $n = 4$ , which is the minimal number of neurons forming a hub structure. We calculate the bifurcation sets in the parameter plane ( $\tau_d$  (ms),  $g_{syn}$  (mS/cm<sup>2</sup>)) using methods proposed by Yoshinaga and Kawakami [39,40]. In the bifurcation diagrams, the solid and dashed curves indicate a tangent and pitchfork bifurcation, respectively. In both shaded and hatched regions, we observe three synchronous firings except the hub neuron. We use the fourth-order Runge–Kutta method with the time step  $0.01$  for solving Eq. (3). If neurons fire simultaneously in this time step, then we determine that the neurons produce synchronous firings.

Figs. 2 and 3 show the bifurcation diagrams for  $n = 4$ . For the homogeneous case, we find that the neurons connected by the inhibitory synapses can achieve synchronization for small values of the synaptic delay regardless of the neuron's class. On the other hand, in the excitatory synapse's case, neurons fire synchronously for large values of the synaptic delay. These properties are opposite compared with the case of  $n = 2$  [41]. (In the case of  $n = 2$ , the inhibitory or excitatory synapse needs a large or small delay for achieving synchronization.) Moreover, in the excitatory case, coexistence of synchronous firings is observed for a large value of the delay and the bifurcation structure becomes more complicated (Figs. 2(b) and 3(b)).



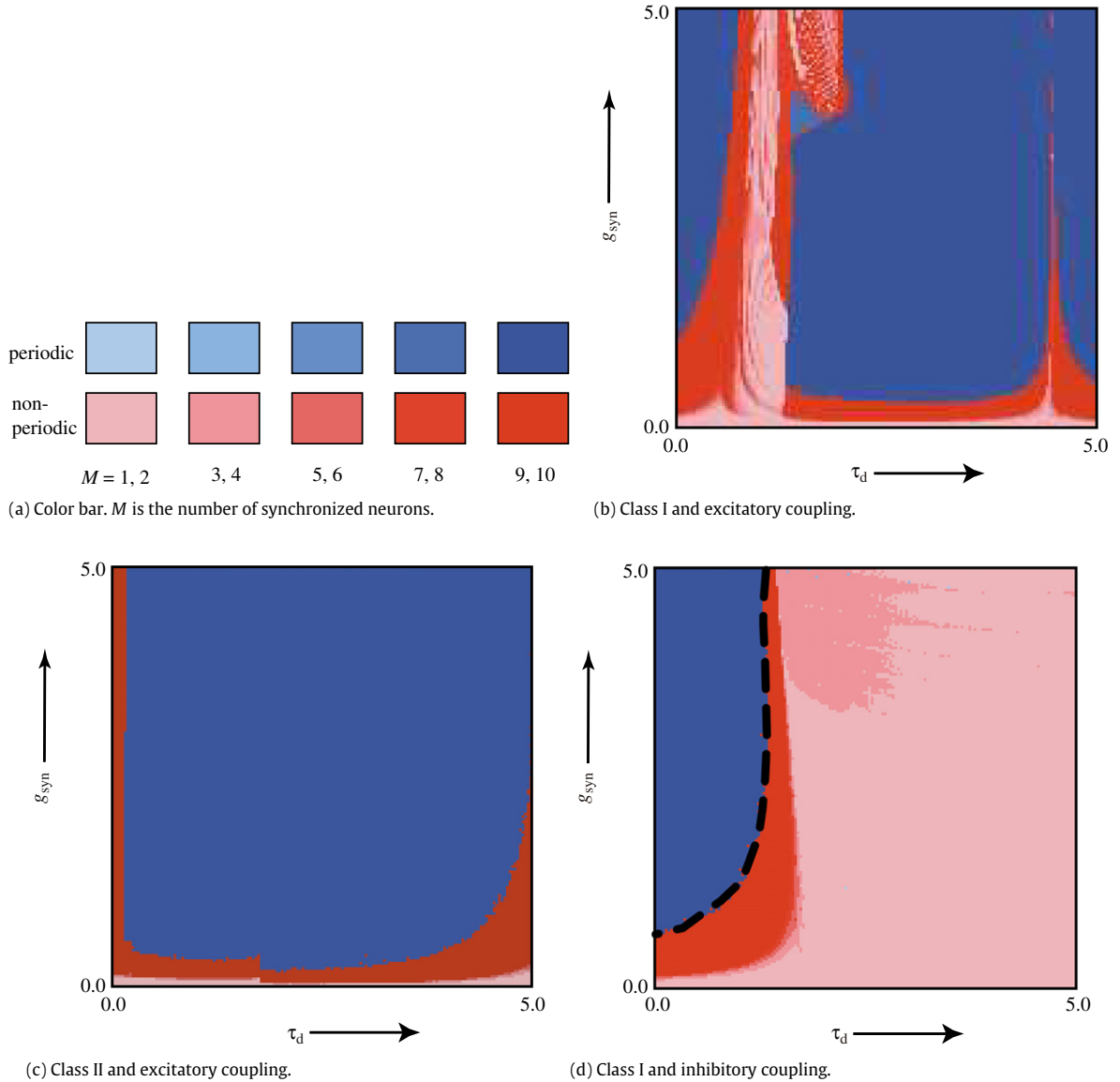
**Fig. 5.** Bifurcation diagrams for the heterogeneous case; hub (class II) and the others (class I).



**Fig. 6.** Bifurcation diagrams for the heterogeneous case; hub (class I) and the others (class II).

Fig. 4(a) and (b) show the schematic one-parameter bifurcation diagrams along the line  $l_1$  and  $l_2$  in Figs. 2(b) and 3(b), respectively. Open and closed circles represent a pitchfork and tangent bifurcation, respectively. From these figures, we can see that all pitchfork bifurcations are subcritical, two pitchfork bifurcations in Fig. 2(b) are bifurcations of the same periodic solution and the tangent and the pitchfork bifurcations are for different periodic solutions. Note that the regions of existence of stable periodic solutions corresponding to synchronous firings of three peripheral neurons overlap in the parameter plane.

Figs. 5 and 6 represent the bifurcation diagrams for the heterogeneous case. Here, only the hub has a different class from the others. For the inhibitory synapse, the region observed three synchronized firings is almost the same as that of the homogeneous case. For the excitatory synapse, when the hub has the class II excitability, the regions observed synchronous firings are spread and in the whole parameter region we observe synchronization of all peripheral neurons. Moreover, increasing the value of the parameter  $\tau_d$  along the line  $l_3$  in Fig. 5(b), before the tangent bifurcation, all four neurons produce almost synchronous firings even when the hub has a dynamics different from the others. We never find the existence of such a synchronous state in the homogeneous case. This means that the class II hub neurons promote synchronous firings of connected class I neurons. For the excitatory synapse, when the hub has the class I excitability, the gray area and the tangent



**Fig. 7.** Synchronization diagrams for the homogeneous case. The dashed curves indicate a pitchfork bifurcation.

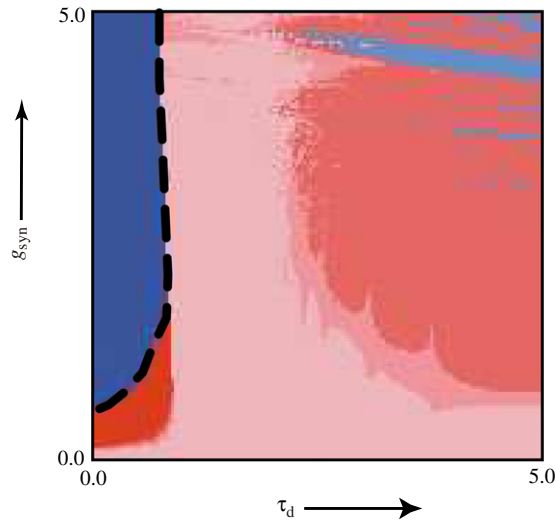
bifurcation in Fig. 3(b) disappear and the region of synchronization becomes narrow. In the white region in Fig. 6(b), we observe two synchronous firings.

Next, we analyze larger configurations with  $n = 11$ . Fig. 7(b)–(e) show the synchronization diagrams for  $n = 11$ . For studying non-periodic synchronous firings, we use a brute-force method (here, “non-periodic” is used when we cannot find periodicity of solutions by 1500 firings of neuron 1). The meaning of the colors is shown in Fig. 7(a).

We first show the results of the homogeneous case. For excitatory coupling ((b) and (c)) regardless of the class, we observe stable complete synchronization of all peripheral neurons in the parameter region of  $g_{syn} > 0.5$ . However, from an initial state near the resting membrane potential, some non-periodic states appear for class I neurons for a small time delay. If we change the class for the hub neuron, this non-periodic state disappears [41].

We give the results of the inhibitory connection in Fig. 7(d) and (e). For periodic synchronization, class I neurons have a wide parameter region (dark blue) of synchronous periodic firings. Comparing with the case of  $n = 4$ , the region of synchronous periodic firings is narrow, however further interesting phenomena explained below are observed in this case.

Class II neurons have a wide parameter region of cluster synchronization. In the region colored by light blue (Fig. 7(e)), cluster periodic synchronization is observed (Fig. 8(a)). 10 peripheral neurons are divided into two in-phase synchronized groups. Each group consists of five neurons. We call this clustering 0:5-5, where the numbers before and after a colon indicate in-phase synchronized neurons with class I and II excitability, respectively, and a hyphen is used for dividing sub-clusters



(e) Class II and inhibitory coupling.

Fig. 7. (continued)

in the same class. Neurons in the same or different sub-cluster group are synchronized in in-phase or anti-phase, respectively. By a subcritical pitchfork bifurcation, this solution becomes unstable, however 0:5-5 clustering and anti-phase synchronization of both groups are kept.

For non-periodic synchronization, in the case of class I, we observe 3-3-4:0 cluster synchronization as shown in Fig. 9. There are in-phase synchronized three groups and each group consists of three, three and four neurons. From this figure we can see that three groups are synchronized in almost three-phase. In coupled class II neurons we observe a quasi-periodic 0:5-5 clustered state as shown in Fig. 8(b).

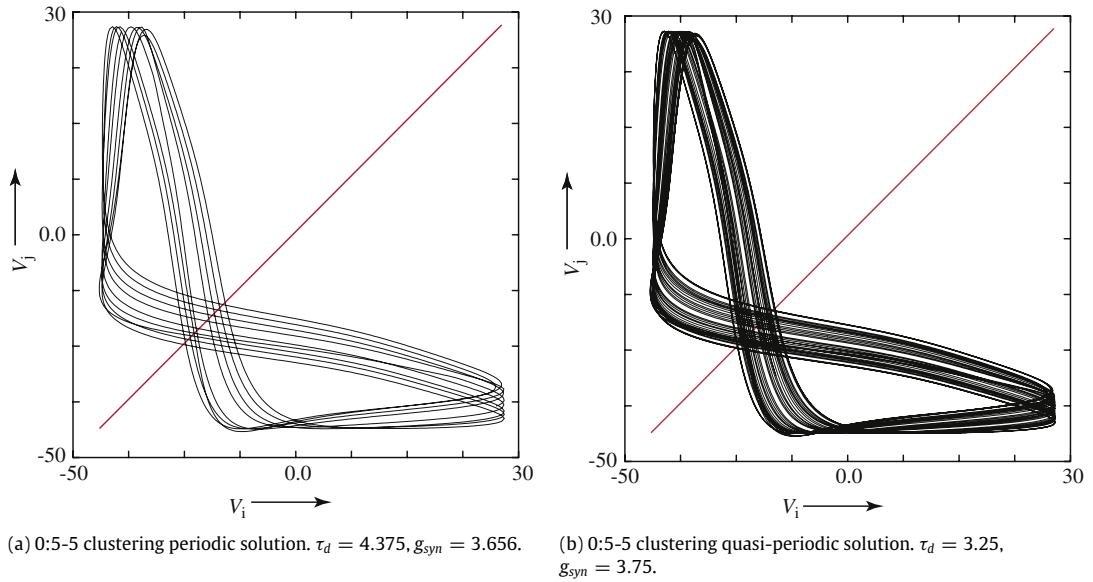
Next, we consider a system consisting of the same number of peripheral class I and class II neurons but change the class of the hub neuron. Fig. 10(a) and (b) show the bifurcation diagrams for the excitatory coupling when the hub has the class I and class II excitability, respectively. In this whole parameter region neurons with the same class form a cluster with synchronous firings. We denote this state as 5:5. In the hatched and shaded region, 5:4-1 and 5:3-2 synchronized state is observed, respectively. Neurons in the same group are synchronized in in-phase. In Fig. 10(b) (the hub has the class II excitability) when  $g_{syn} < 1.0$  we observe synchronous firings of all 11 neurons, qualitatively the same as in the case of  $n = 4$ .

Fig. 11 (a) and (b) are the one-parameter bifurcation diagrams along the lines  $l_1$  and  $l_2$  in Fig. 10(a), respectively. The closed circles indicate pitchfork bifurcations which break the symmetry; i.e. the in-phase property is broken at this bifurcation point. In Fig. 11(a) the in-phase membrane potentials of three neurons bifurcate into two in-phase potentials and another. Similarly, in Fig. 11(b) four neurons bifurcate to two and two. When the hub has the class I excitability, bifurcations of cluster-synchronized states are observed and other clustering is generated. However, clustering always occurs for class II neurons. A detailed analysis of this is one of the problems to be studied in future.

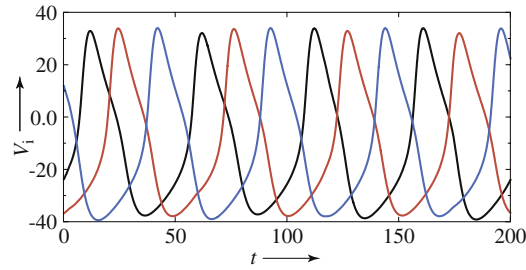
We show now our results for inhibitory coupling in Fig. 12. When the hub has the class I excitability (Fig. 12(a)), we observe synchronous periodic firings. On the other hand, in the case of the class II hub neuron (Fig. 12(b)), synchronous periodic firings cannot be observed and the region of synchronous non-periodic firings is very narrow. Thus, the class I hub neuron has the advantage of achieving synchronization.

#### 4. Summary

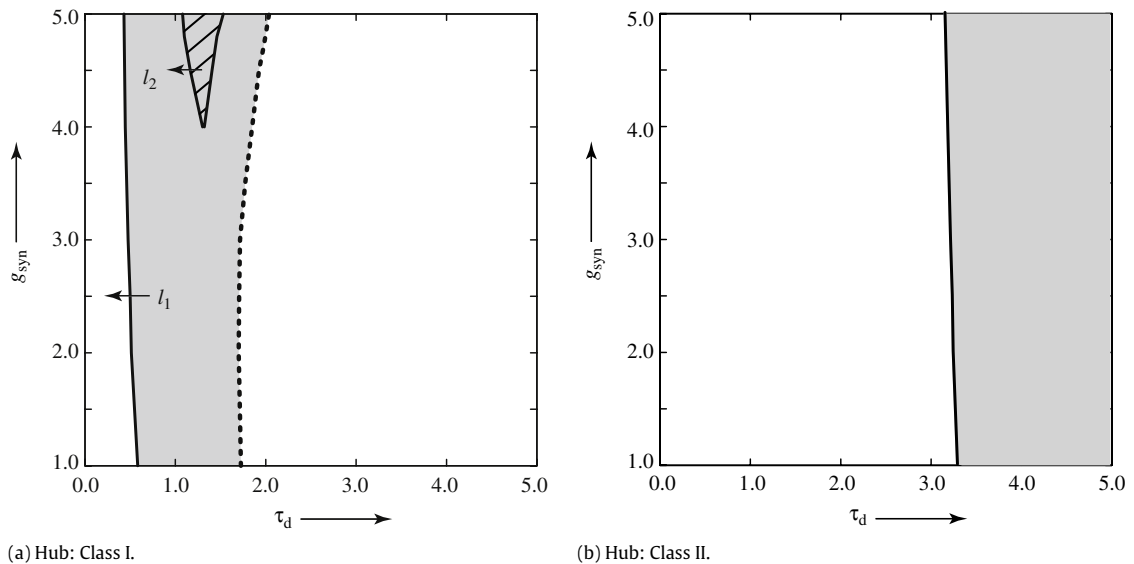
We have investigated synchronous firings in hub-based neuronal networks. This coupled system is a basic motif in complex networks. The network is composed of ML neurons with the class I and class II excitabilities. We have considered homogeneous (coupling the same class neurons) and heterogeneous (coupling different class neurons) systems for both excitatory and inhibitory coupling. We have studied the effect of these two classes and two types of coupling on synchronous firings in the parameter plane of the maximum synaptic conductance and the delay of the synaptic current. In homogeneous systems, the excitatory synapses have the advantage leading to synchronous firings but the inhibitory ones promote cluster synchronization; i.e. neurons are divided into two or three groups. In heterogeneous systems with inhibitory coupling, the class I hub neuron has a wider parameter region of synchronous firings than the class II hub. Moreover, the class I hub neuron with the excitatory synapse gives rise to bifurcations of synchronized states and multi-stability (coexistence of three different states) is observed. This result is consistent with Ref. [33], which shows a system of coupled class I neurons has many synchronized states.



**Fig. 8.** Phase portrait. Red and black curves indicate trajectories mapped on the plane of any two voltages  $V_i$  and  $V_j$  ( $i \neq j$ ) in the same and different group, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

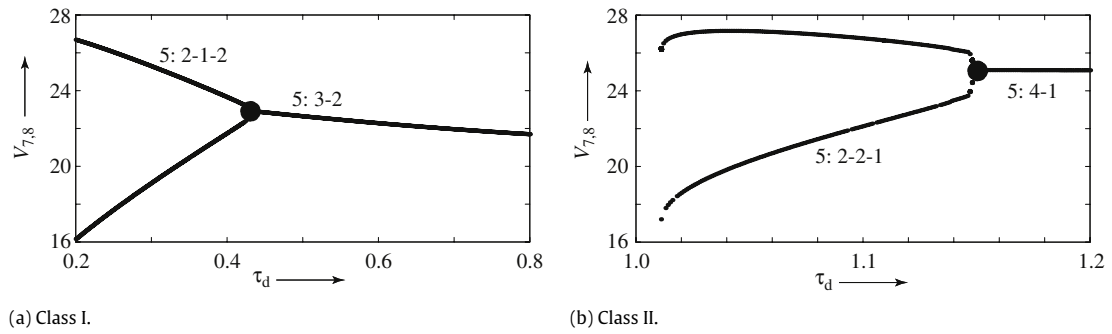


**Fig. 9.** Waveforms of neurons in three groups.  $\tau_d = 2.0$ ,  $g_{syn} = 4.5$ .

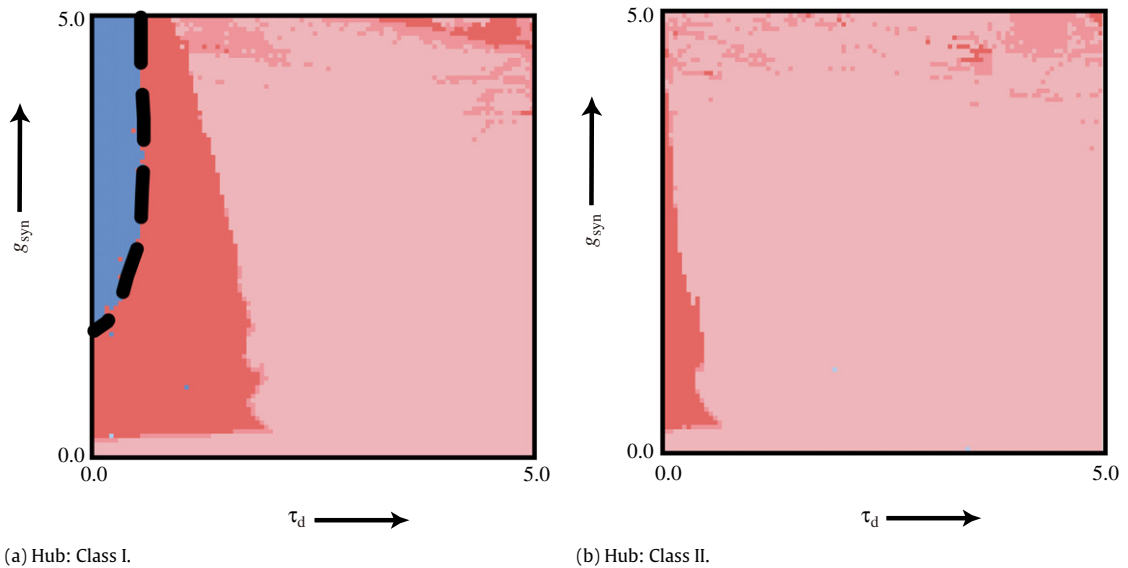


**Fig. 10.** Bifurcation diagrams for the heterogeneous case (excitatory coupling). The dotted curve indicates a Neimark–Sacker bifurcation.





**Fig. 11.** Schematic one-parameter bifurcation diagrams for the heterogeneous system coupled by the excitatory synapse. Closed points indicate a pitchfork bifurcation.



**Fig. 12.** Synchronization diagrams for the heterogeneous case (inhibitory coupling). The meaning of colors is the same as Fig. 7. The dashed curves indicate a pitchfork bifurcation.

Here, we have studied rather subnetworks with a star-like configuration and we consider that this is a basic step for understanding structure formation in large networks. It is an open problem to study synchronization in neurons coupled by both excitatory and inhibitory synapses.

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## References

- [1] O. Sporns, D.R. Chialvo, M. Kaiser, C.C. Hilgetag, Trends Cogn. Sci. 8 (2004) 419.
- [2] D.S. Bassett, A.M. Lindenberg, S. Achard, T. Duke, E. Bullmore, Proc. Natl. Acad. Sci. U.S.A. 103 (2006) 19518.
- [3] L. Zemanová, C. Zhou, J. Kurths, Physica D 224 (2006) 202.
- [4] K.V. Srinivas, R. Jain, S. Saurav, S.K. Sikdar, Eur. J. Neurosci. 25 (2007) 3276.
- [5] C.J. Stam, Neurosci. Lett. 355 (2004) 25.
- [6] C.J. Stam, J.C. Reijneveld, Nonlinear Biomed. Phys. 1 (2007) 3.
- [7] A. Pikovsky, M. Rosenblum, J. Kurths, Synchronization: A Universal Concept in Nonlinear Sciences, Cambridge University Press, 2001.
- [8] Y.L. Li, Z.Y. Chen, J. Ma, Y.H. Chen, Acta Neuropsychiatr. 20 (2008) 25.
- [9] M. Barahona, L.M. Pecora, Phys. Rev. Lett. 89 (2002) 054191.
- [10] T. Nishikawa, A.E. Motter, Physica D 224 (2006) 77.
- [11] T. Nishikawa, A.E. Motter, Y.C. Lai, F.C. Hoppensteadt, Phys. Rev. Lett. 91 (2003) 014101.
- [12] I. Belykh, E. de Lange, M. Hasler, Phys. Rev. Lett. 94 (2005) 188101.
- [13] A.L. Barabási, R. Albert, Science 286 (1999) 509.
- [14] R. Albert, A.L. Barabási, Rev. Modern Phys. 74 (2002) 47.
- [15] F. Sorrentino, M. di Bernardo, G.H. Cuéllar, S. Boccaletti, Physica D 224 (2006) 123.

- [16] A. Arenas, A. Díaz-Guilera, C.J. Pérez-Vicente, *Physica D* 224 (2006) 27.
- [17] C. Zhou, J. Kurths, *Chaos* 16 (2006) 015104.
- [18] D. Huang, G. Pipa, *EPL* 77 (2007) 50010.
- [19] N. Masuda, N. Konno, *Social Networks* 28 (2006) 297.
- [20] P.N. McGraw, M. Menzinger, *Phys. Rev. E* 68 (2003) 047102.
- [21] A. Arenas, A. Díaz, J. Kurths, Y. Moreno, C. Zhou, *Phys. Rev.* 469 (2008) 93.
- [22] R. Milo, S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, U. Alon, *Science* 298 (2002) 824.
- [23] A.L. Hodgkin, *J. Physiol.* 107 (1948) 165.
- [24] T. Tateno, A. Harsch, H.P.C. Robinson, *J. Neurophysiol.* 92 (2004) 2283.
- [25] M. St-Hilaire, A. Longtin, *J. Comput. Neurosci.* 16 (2004) 299.
- [26] R. Hosaka, T. Ikeguchi, IEICE Technical Report NLP2005-139, 2006, pp. 11–16.
- [27] B. Ermentrout, *Neural Comput.* 8 (1996) 979.
- [28] J. Rinzel, B. Ermentrout, Analysis of neural excitability and oscillations, in: C. Koch, I. Segev (Eds.), *Methods in Neuronal Modeling*, The MIT Press, 1998.
- [29] B. Ermentrout, M. Pascal, B. Gutkin, *Neural Comput.* 13 (2001) 1285.
- [30] L.F. Lago-Fernández, F.J. Corbacho, R. Huerta, *Neural Netw.* 14 (2001) 687.
- [31] E. Ioka, H. Kitajima, *J. Signal Process.* 11 (2007) 111.
- [32] H. Kitajima, J. Kurths, *Int. J. Bifur. Chaos* 7 (2007) 3523.
- [33] S. Tsuji, T. Ueta, H. Kawakami, K. Aihara, in: *Proceedings of Nonlinear Circuit and Signal Processing*, Honolulu, 2004, pp. 495–498.
- [34] C. Morris, H. Lecar, *Biophys. J.* 35 (1981) 193.
- [35] K. Tsumoto, H. Kitajima, T. Yoshinaga, K. Aihara, H. Kawakami, *Neurocomputing* 69 (2006) 293.
- [36] T. Tateno, H.P.C. Robinson, *J. Neurophysiol.* 95 (2006) 2650.
- [37] B. Pfeuty, G. Mato, D. Golomb, D. Hansel, *Neural Comput.* 17 (2005) 633.
- [38] G. Katz, R. Miledi, *J. Physiol.* 181 (1965) 656.
- [39] T. Yoshinaga, Y. Sano, H. Kawakami, *Int. J. Bifur. Chaos* 9 (1999) 1451.
- [40] H. Kawakami, *IEEE Trans. Circuits Syst.* 31 (1984) 246.
- [41] H. Kitajima, in: *Proceedings of Nonlinear Dynamics of Electronic Systems*, Tokushima, 2007, pp. 186–189.