

# COLLECTIVE BEHAVIOR OF PULSE-COUPLED FITZHUGH-NAGUMO NEURONS

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## ABSTRACT

*Synchronization and clustering of pulse-coupled oscillatory neurons has been investigated. Though the leaky integrate-and-fire neurons have widely been used in the analysis, they have some implausible properties which allow neurons to synchronize through unrealistic mechanisms. In the present report, we examine the collective behavior of pulse-coupled FitzHugh-Nagumo neurons using the phase reduction method. We show that the neurons tend to synchronize to form a fully synchronous state or a small number of clusters. We also analyze the stable behavior of two pulse-coupled neurons analytically.*

## 1. INTRODUCTION

Experimental results have shown the existence of oscillatory synchronizations in honeybees [18], cat primary visual cortex [4], cat superior colliculus [1], frontal cortex of monkey [21] and motor cortex of monkeys [16]. These synchronous oscillations occur when a group of neurons with the same preferred stimulus are activated by that stimulus. These experimental results combined with analysis by the mutual information and the correlation coefficients indicate that the synchronization serves as a mechanism for representing coherent features such as odors [18] and motions [16], with the synchronized neurons forming a temporal functional assembly [4, 8]. Furthermore, the cooperative signal coding by synchronous oscillation can be more robust against noises and disorder in a small number of neurons [18].

Many theoretical and numerical investigations of synchronization in neural networks as well as clustered states and asynchronous states have been motivated by these biological evidence, and also by synchronous behavior appearing in physical and chemical oscillations. Especially, pulse-coupled neural networks are of more concern these days since neurons not only interact

through gap junctions but also by exchanging pulses. These feedback pulses play a central role in signal processing in neural systems. By using the phase reduction method [9], Mirollo and Strogatz [14] showed that, for almost all initial conditions, full synchronization is achieved in pulse-coupled networks of leaky integrate-and-fire (LIF) neurons. During the last decade, their results have been extended to various neuron models: those with a constant positive delay [2, 20], or a delay given by  $\alpha$ -function [2, 3, 22], linear neurons [17], neurons linked by inhibitory coupling [2, 3, 5, 6, 22], neurons linked by nonuniform coupling [2, 17], heterogeneous neurons [17], and neurons linked by generalized coupling with delay [8]. The dynamical behavior of a neural network depends very much on these factors as well as on external inputs and the initial conditions. Clustered states [10, 11, 20, 22], stable asynchronous behavior, bursting and traveling waves [3] have also been found in various neural networks. This multistability is related to the superposition problem [20].

Though abundant results have been presented regarding the LIF neurons, the LIF neuron models can not capture some important characteristics of biological neurons. For example, once the LIF neuron fires, the membrane potential is reset to the resting potential instantaneously. The resetting potential is always the same regardless of any other factors as well.

Related to these unnatural suppositions in the LIF neuron model, two orbits starting from two close points on the  $N$ -dimensional torus which is the phase space of  $N$  neurons may take quite different time courses to synchronization [13, 14]. In other words, full synchronization of the LIF neuron is caused by orbital ergodicity and chaoticity combined with absolute absorption. It is different from the ubiquitous synchronization mechanisms based on generic local or global stability of dynamical systems. In the coupled LIF neurons, the stability of the synchronous state is based on total absorption. It means that when a pulse is

arrived to many neurons, the neurons which has fired are reset to the same resting potential regardless of the membrane potential (which must be beyond the firing threshold) before resetting. Though ergodicity-based scenarios are mathematically perfect, their application to the synchronization of actual network of neurons is questionable because total absorption is biologically implausible. If absorption is not absolute, small differences caused by noise might increase because of the repulsive dynamics. Furthermore, the proofs are largely combinatorial and say nothing about the synchronization time. Synchronization may require a longer time than is biologically feasible. The LIF neuron belongs to the different class from that for Hodgkin-Huxley neurons and FitzHugh-Nagumo neurons in terms of the possibility of synchronization [11] and the possibility of oscillation frequency modulation [12]. Consequently, it is worth while examining the collective behavior of more biologically modeled neurons for which less results have been presented so far.

In this report, we investigate the collective dynamics of pulse-coupled FitzHugh-Nagumo (FHN) neurons [7, 15] by using phase reduction method [9, 10, 11]. In Sec. 2, we show that the neurons starting from the arbitrary states tend to converge to clustered states including the fully synchronous state. We also analyze the final states of two pulse-coupled FHN neurons using the numerically obtained phase return maps in Sec. 3. The routes to synchronization and clustered states for the pulse-coupled FHN neurons will shown to be quite different from those for the pulse-coupled LIF neurons. The simulation results in Sec. 4 will show that the synchronization is achieved in many cases whereas clustered states can generally appear.

### 1.1. FitzHugh-Nagumo Neurons

The FHN neuron model [7, 15] can describe such properties of real neurons as firing with thresholds, relative refractoriness and cooperation of fast and slow variables. The dynamics of the FHN neuron is described by the following formula:

$$\begin{aligned} \alpha \frac{dv}{dt} &= -v(v - 0.5)(v - 1) - w + I, \\ \frac{dw}{dt} &= v - w - 0.15, \end{aligned}$$

where  $\alpha \ll 1$ ,  $I$  is the external input,  $v$  is the fast variable, and  $w$  is the slow one. The FHN neuron is oscillatory when  $I > I_0$  where  $I_0$  is the Hopf bifurcation point. Our theoretical analysis concentrate on this oscillatory case. As the simulation results in Sec. 4 shows, however, the mechanisms for the oscillatory

cases can also explain the tendency to synchronous behavior of the excitable FHN neurons where  $I < I_0$ .

We examine collective dynamics of  $N$  coupled FHN neurons. If the couplings are based on gap junctions, neurons eventually synchronize when the coupling strengths are large enough [19]. In this work, we investigate pulse-coupled FHN neurons by using the phase reduction method. Let us suppose that the neuron is oscillatory. We give the same phase value to the two points  $(v, w) \in \mathbf{R}^2$  which approach each other in the limit as  $t \rightarrow \infty$ . Consequently, the whole dynamics of the FHN neuron can be reduced to the phase dynamics on a one-dimensional limit cycle. The phase variable  $\phi(v, w) \in [0, 1]$  can be defined on the limit cycle so that  $\dot{\phi}$  has a constant velocity.  $\phi = 0$  and  $\phi = 1$  designate the identical point. Furthermore, it is assumed that  $\dot{\phi} = 1 (= 0)$  when the neuron fires. As a result, the two-dimensional dynamics of the FHN neuron is reduced to dynamics on a ring [10, 11]. This description is valid as far as  $\alpha \ll 1$ . In this case,  $v$  changes sufficiently fast compared with  $w$ , and the point  $(v, w)$  quickly approach the limit cycle when disturbed by finite amount.

We couple  $N$  FHN neurons by pulse couplings. When a neuron fires, it emits a pulse with amplitude  $\epsilon$  to all the other neurons with synaptic delay  $\tau$ . We set the firing threshold equal to  $v_{th} = 0.7$ , and use  $\alpha = 0.005$  and  $I = 0.18$  unless otherwise stated.

We consider an instantaneous pulse input of amplitude  $\epsilon > 0$  to  $v$ . This pulse has been emitted by another neuron. Its effect depends on the value of  $\phi$  when the neuron receives the pulse [3, 10, 11]. We denote by  $f(\phi)$  the phase value after the pulse input. The phase return maps  $f(\phi)$  obtained numerically for various values of  $\epsilon$  are shown in Fig. 1. Firstly a pulse advances or delays  $\phi$  depending on the value of  $\phi$  when the neuron receives the pulse; the FHN neuron has a type II phase-resetting curve (defined by  $f(\phi) - \phi$ ) [11]. We also observe that  $f'(\phi) < 1$  in wide ranges independent of  $\epsilon$ . It suggests that the phase difference between two neurons can often shrink when common pulse inputs are received. These properties are quite different from those of the LIF neuron in which an excitatory pulse always advances  $\phi$ ; the LIF neuron has a type I phase-resetting curve [11]. Furthermore,  $f'(\phi) > 1$  or  $f'(\phi) = 0$  for the LIF neuron. The neurons with any  $\phi$  satisfying  $f'(\phi) = 0$  fire due to an external pulse [13, 14]. When more than one neurons fire at the same time, they are reset to the same resting potential, and they behave identically afterwards. The synchronization of the LIF neurons highly depends on this absolute absorption. As a result, we expect different synchronization mechanisms for the FHN neurons.

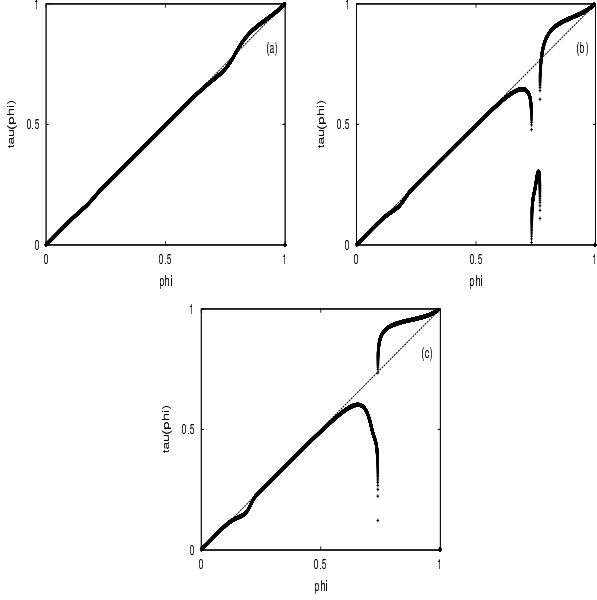


Figure 1: Phase return maps  $f(\phi)$  of the FHN neuron.  $\alpha = 0.005$  and  $I = 0.18$ . (a):  $\epsilon = 0.02$ , (b):  $\epsilon = 0.06$ , and (c):  $\epsilon = 0.12$ .

## 2. FROM SPRAY STATES TO CLUSTERED STATES

In this section, we examine how the phase difference between two neurons changes by receiving common pulses. We denote by  $\phi_i(t) \in [0, 1]$  ( $1 \leq i \leq N$ ) the phase variable of the  $i$ -th neuron at time  $t$ . We consider the dynamics of  $\Delta\phi = \phi_i(t) - \phi_j(t)$  ( $i \neq j$ ) in the pulse-coupled networks. By definition of the phase variables,  $\phi_i(t)$  and  $\phi_j(t)$  drift independently at a constant speed when no pulse inputs are received by the two neurons. When the two neurons receive a common pulse with amplitude  $\epsilon$  at time  $t$ , the phase difference changes from  $\Delta\phi$  to

$$\begin{aligned} f(\phi_i(t)) - f(\phi_j(t)) &= f(\phi_i(t)) - f(\phi_i(t) - \Delta\phi) \\ &= a(\phi_i(t))\Delta\phi. \end{aligned} \quad (1)$$

If  $\Delta\phi$  is not so large,  $a(\phi_i(t))$  can be approximated by  $f'(\phi_i(t))$ .

Let us suppose  $n$  common pulses are received at  $t = t_1, \dots, t_n$ . Then the final phase difference is given by

$$\left( \prod_{k=1}^{k=n} a(\phi_i(t_k)) \right) \Delta\phi = \exp \left( \sum_{k=1}^{k=n} \log a(\phi_i(t_k)) \right) \Delta\phi. \quad (2)$$

We next assume that  $\phi_i(t_k)$  is uniformly distributed in  $[0, 1]$ . This hypothesis is plausible when there are many clusters, or when common external inputs with random interspike intervals are applied to the two neurons in the form of pulses. Equation (2) implies that the distribution of  $\log a(\phi)$  gives us the insight into the time course of the phase difference. If  $f(\phi)$  were a one-to-one mapping, we would have

$$E[a(\phi)] \cong E[f'] = \int_0^1 f' d\phi = 1,$$

where  $E$  denotes the expectation with respect to  $\phi$  with the uniform distribution in  $[0, 1]$ . As is shown in Fig. 1, however,  $f(\phi)$  of the FHN neuron is many-to-one. This leads to

$$E[a(\phi)] > 1. \quad (3)$$

Equation (3) suggests that the expectation of the LHS of Eq. (2) diverges in the limit as  $n \rightarrow \infty$ . The divergence is because  $a(\phi)$  takes huge values with small probability. Nevertheless, Eq. (3) does not necessarily mean that the phase difference does not converge to zero in most cases. For example, phase differences larger than 1 does not make sense since the phase variables are defined on the torus. Furthermore, the phase difference converges to zero in the probabilistic sense, that is,

$$\lim_{n \rightarrow \infty} \text{Prob} \left[ \exp \left( \sum_{k=1}^{k=n} \log a(\phi_i(t_k)) \right) \Delta\phi < \epsilon' \right] = 1, \quad (4)$$

for any  $\epsilon' > 0$  if

$$E[\log a(\phi)] < 0. \quad (5)$$

We have numerically calculated the probability distribution of  $\log a(\phi)$  when  $\epsilon = 0.12$  using the phase return map shown in Fig. 1. The result is shown in Fig. 2, and  $E[\log a(\phi)] = -0.28$ . In combination with Eq. (4), we expect that the phase difference dies out after many pulse inputs are received.

Figure 1 also shows that the ranges in which  $f'(\phi) < 1$  are almost independent of  $\epsilon$  though the value of  $f'(\phi)$  itself depends on  $\epsilon$ . That this region stably exists is evidence of the convergence of the phase difference. Therefore over a wide range of  $\epsilon$ , the coupled FHN neurons typically fall into the synchronous state or the clustered states with a few clusters, depending on initial conditions and parameter values. The pulse-coupled LIF neurons also have the tendency toward clustered states [5, ?].

We note that the mechanism described above holds only when two neurons can be considered to receive many common input spikes at random time. We have

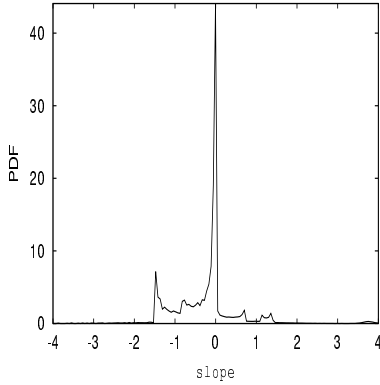


Figure 2: The distribution of  $\log(a(\phi))$ .  $\epsilon = 0.12$ .

not considered the effect of interaction between the  $i$ -th and  $j$ -th neurons, either. We suspect that the interaction enhances the stability of the synchronized state when the synaptic delay is smaller than  $\cong 0.2$ . This is suggested by Fig. 1 which shows  $f'(\phi) < 1$  ( $\phi \in [0.8, 1]$ ). When  $\Delta\phi = \phi_i(t) - \phi_j(t) > 0$  is small, the increase in  $\phi_i(t)$  with a feedback pulse input from the  $j$ -th neuron is less than that in  $\phi_j(t)$  with a pulse input from the  $i$ -th neuron.

More detailed analysis is required to know the final state of the network. So far, we postulate that the pulse-coupled many FHN neurons tend to converge to clustered states in which only a small number of clusters are present.

### 3. TWO PULSE-COUPLED NEURONS

In principle, it is necessary to analytically examine the time course of  $\Delta\phi$  in order to know which clustered states are finally realized. In this report, we only examine the two pulse-coupled neurons since analytical study of many pulse-coupled neurons is formidable. We explore existence and stability of the synchronous state and the phase-locked states. The networks both with synaptic delay and without delay are analyzed.

We start from the state in which the two neurons have the phases  $\phi_1(0) = 0$  and  $\phi_2(0) = \Delta\phi$ . The first neuron just fired and was reset to the resting potential, emitting a feedback pulse with amplitude  $\epsilon$  to the other neuron. We denote by  $R(\Delta\phi)$  the new phase difference when  $\phi_1$  returns to  $\phi_1(0) = 0$  after it fires once. The function  $R(\Delta\phi)$  provides the self-consistent relation to determine the stable phase-locked states. Similar functions have been used to analyze the phase-locked solutions for pulse-coupled LIF neurons [5, 6, 14]. It is to

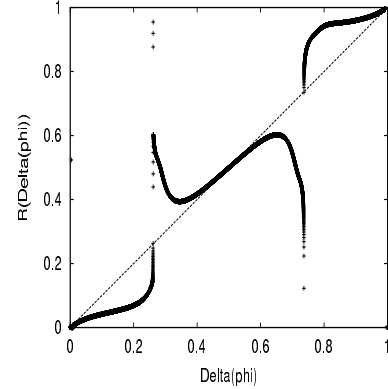


Figure 3: The return map  $R$  of the phase difference for the two pulse-coupled FHN neurons without delay.  $\epsilon = 0.12$ .

be noted that Fig. 1 indicates  $f(\phi) \leq 1$  for all  $\phi$ , which is an important condition in establishing  $R(\Delta\phi)$ .

When there is no synaptic delay, we have

$$R(\Delta\phi) = f(1 - f(1 - \Delta\phi)).$$

The stable fixed points of  $R$  are realizable asymptotic states. Figure 3 shows  $R$  with  $\epsilon = 0.12$  which is numerically calculated from the phase-return map in Fig. 1. The antiphase state can stably exist as well as the synchronous state, corresponding to the two stable fixed points of  $R$ . This is in contrast with the results for the two pulse-coupled LIF neurons without delay which always synchronize [13, 14]. Qualitatively similar phase-return maps are also observed for smaller  $\epsilon$  (data not shown).

We next take into account the synaptic delay  $\tau > 0$ . Based on biological evidence [12], we assume that  $\tau < T/2$  where  $T$  denotes the oscillation period when there is no pulse inputs. Three cases have to be distinguished: (1) if  $0 \leq \Delta\phi < \tau$ , the feedback pulse from the second neuron is traveling at  $t = 0$  to arrive at the first neuron at  $t = \tau - \Delta\phi$ , (2) if  $\tau \leq \Delta\phi < 1 - \tau$ , the second neuron receives the pulse from the first neuron before it fires, (3) if  $1 - \tau \leq \Delta\phi < 1$ , the second neuron fires before it receives the pulse from the first neuron. As a result, we obtain

$$R(\Delta\phi) = \begin{cases} f(\Delta\phi + \tau) - f(-\Delta\phi + \tau) - \Delta\phi, & (0 \leq \Delta\phi < \tau), \\ \tau + 1 - f(2\tau + 1 - f(\Delta\phi + \tau)), & (\tau \leq \Delta\phi < 1 - \tau), \\ 2 - \Delta\phi + f(\Delta\phi + \tau - 1) - f(-\Delta\phi + \tau + 1), & (1 - \tau \leq \Delta\phi < 1). \end{cases}$$

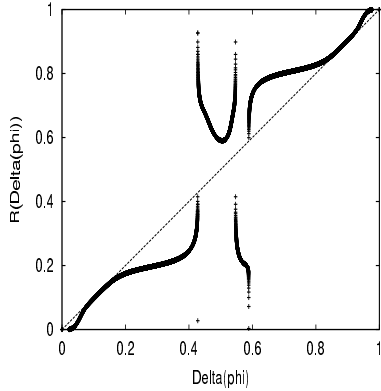


Figure 4: The return map  $R$  of the phase difference for the two pulse-coupled FHN neurons with delay.  $\epsilon = 0.12$  and  $\tau = 0.15$ .

The function  $R$  when the delay exists is shown in Fig. 4 for  $\epsilon = 0.12$  and  $\tau = 0.15$ . There are three stable fixed points of  $R$  at  $\Delta\phi = 0$ ,  $\Delta\phi = \tau$  and  $\Delta\phi = 1 - \tau$ . Both of the phase-locked states virtually have the phase difference equal to  $\tau$ . Though both the synchronous state and the phase-locked states are achievable, the phase-locked states have larger attractive basins, and therefore they are more likely to be realized. These results are consistent with those for the LIF neurons [5, 6].

As a remark, coexistence of synchrony and clustered states is also observed in coupled Hodgkin-Huxley neurons [10, 11], oscillatory LIF neurons with more general configurations [5, 6, 22] and excitable LIF neurons [20].

#### 4. SIMULATION RESULTS

In this section, we numerically examine the behavior of the pulse-coupled many FHN neurons. The couplings are supposed to be uniform and all-to-all. We first consider the case where the supra-threshold bias current is present. Figures 5(a) and 5(b) shows a route to synchronization for 30 neurons without delay. Let us recall that scenario to full synchrony for coupled FHN neurons is totally different from that for coupled LIF neurons. The former is based on contraction while the latter is based on expansion.

We now consider subthreshold cases where  $I < I_0$ . When  $I < I_0$ , other input sources are required if the neurons are to fire. The most common phenomenon in subthreshold situations is coherence resonance [19]. Though CR is an interesting phenomenon, in this report we concentrate on such excitable systems that are made to fire by external pulse inputs; we apply com-

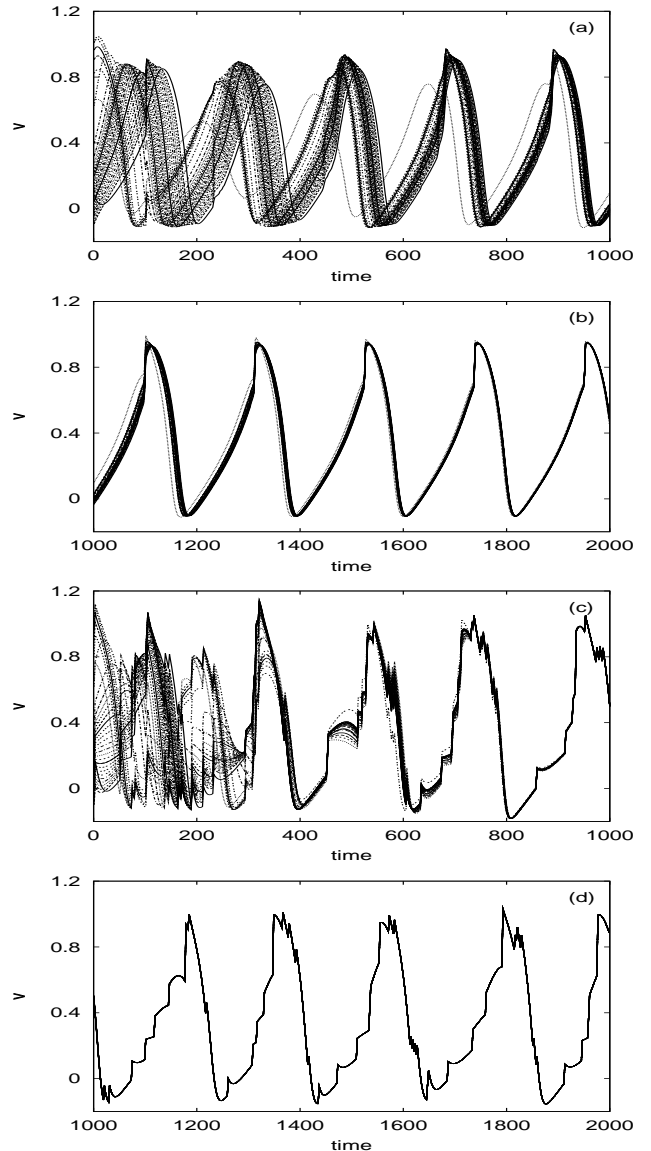


Figure 5: The time course of  $v(t)$  for 30 FHN neurons coupled by pulses without delay. The couplings are uniform and all-to-all.  $\alpha = 0.005$ , and  $\epsilon = 0.008$ . (a,b): oscillatory case ( $I = 0.18$ ). (c,d): excitable case ( $I = 0.14$ ) in which external pulses of amplitude  $\bar{\epsilon} = 0.12$  come to all the neurons. The interspike intervals of external pulse are described by the exponential distribution  $\rho(t) = e^{-0.04t}/0.04$ .

mon spike inputs from outside to make the FHN neuron excitable. Consequently, an external stimulus  $I$  can be decomposed into the continuous bias  $\hat{I} < I_0$  and the spike inputs which arrive at  $t = t_l$ , ( $l = 1, 2, \dots$ ). We can write

$$I = \hat{I} + \bar{\epsilon} \sum_l \delta(t - t_l), \quad (6)$$

where  $\bar{\epsilon}$  is the amplitude of an external pulse, and  $\delta$  is the delta function. We assume that neurons can fire with the effects of both external pulses and feedback pulses.

It is difficult to define  $\phi$  for the excitable FHN neuron analytically. Nevertheless, we benefit from the phase definitions extended to excitable LIF neurons with periodic external pulse inputs [13]. For the periodic pulse inputs, the excitable FHN neuron repetitively fires with a constant period as if it were the oscillatory FHN neuron.

Accordingly, we expect that full synchronization also occurs in many cases for pulse-coupled excitable FHN neurons. The simulation results for 30 excitable FHN neurons coupled by pulses without delay are shown in Figs. 5(c) and 5(d). External pulses of amplitude  $\bar{\epsilon} = 0.12$  were assumed to arrive uniformly to all the neurons, and the interspike intervals of the external pulses were assumed to be distributed as specified by the exponential distribution  $\rho(t) = e^{-0.04t}/0.04$  [12]. Despite individually irregular behavior of each neuron due to the exponential distribution of external interspike intervals,  $N$  neurons synchronized after only a few firings. The common external pulses helps the phase differences to shrink by the mechanism explained in Sec. 2.

## 5. CONCLUSIONS

In this report, we have examined the collective behavior of the pulse-coupled FHN neurons. The neurons tend to converge to the synchronized state or the clustered states with a small number of clusters. Furthermore, we have shown that two pulse-coupled neurons would synchronize or converge to the antiphase state when there is no delay, and would synchronize or converge to the phase-locked states when there is delay. Though these results are similar to those for the pulse-coupled LIF neurons, we have worked with more biological neurons with a more plausible collective dynamics based on local stabilities. We conjecture that similar results hold for the neurons which has smooth but bumpy phase return maps with  $E[\log f'] < 0$ .

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## References

- [1] M. Brecht, W. Singer and A. K. Engel, "Patterns of synchronization in the superior colliculus of anesthetized cats", *J. of Neurosci.*, Vol. 19, No. 9, pp. 3567–3579, 1999.
- [2] P. C. Bressloff, "A dynamical theory of spike train transitions in networks of integrate-and-fire oscillators", *Siam J. of Appl. Math.*, Vol. 60, No. 3, pp. 820–842, 2000.
- [3] P. C. Bressloff and S. Coombes, *Neural Computation*, Vol. 12, pp. 91–129, 2000.
- [4] R. Eckhorn, R. Bauer, W. Jordan, M. Brosch, W. Kruse, M. Munk, and H. J. Reitboeck, *Biol. Cybern.* Vol. 60, pp. 121–130, 1988.
- [5] U. Ernst, K. Pawelzik, and T. Geisel, *Phys. Rev. Lett.*, Vol. 74, No. 9, pp. 1570–1573, 1995.
- [6] U. Ernst, K. Pawelzik, and T. Geisel, *Phys. Rev. E*, Vol. 57, No. 2, pp. 2150–2162, 1998.
- [7] R. FitzHugh, *Biophysical J.*, Vol. 1, pp. 445–465, 1961.
- [8] H. Fujii, H. Ito, K. Aihara, N. Ichinose, and M. Tsukada, *Neural Networks*, Vol. 9, No. 8, 1303–1350, 1996.
- [9] L. Glass, M. C. Mackey, *From clocks to chaos – the rhythms of life*, Princeton University Press, Princeton, 1988.
- [10] D. Hansel, G. Mato, and C. Meunier, *Europhys. Lett.* Vol. 23, No. 5, pp. 367–372, 1993.
- [11] D. Hansel, G. Mato, and C. Meunier, *Neural Computation*, Vol. 7, pp. 307–337, 1995.
- [12] C. Koch, *Biophysics of computation*, Oxford University Press, New York, 1999.
- [13] N. Masuda and K. Aihara, (to be submitted).
- [14] R. E. Mirollo and S. H. Strogatz, *SIAM J. on Appl. Math.*, Vol. 50, pp. 1645–1662, 1990.
- [15] J. Nagumo, S. Arimoto, and S. Yoshizawa, *Proc. of the IRE*, Vol. 50, pp. 2061–2070, 1962.
- [16] A. Riehle, S. Grün, M. Diesmann and A. Aertsen, *Science*, Vol 278, pp. 1950–1953, 1997.
- [17] W. Senn, and R. Urbanczik, *SIAM J. on Appl. Math.*, Vol. 61, No. 4, pp. 1143–1155, 2000.
- [18] M. Stopfer, S. Bhagavan, B. H. Smith and G. Laurent, *Nature*, Vol. 390, pp. 70–74, 1997.
- [19] I. Tokuda and K. Aihara, *Proc. of 5th'00*, pp. 177–180, 2000.
- [20] M. Usher, H. G. Schuster, and E. Niebur, *Neural Computation*, Vol. 5, pp. 570–586, 1993.
- [21] E. Vaadia, I. Haalman, M. Abeles, H. Bergman, Y. Prut, H. Slovin, and A. Aertsen, *Nature*, Vol. 373, pp. 515–518, 1995.
- [22] C. van Vreeswijk, *Phys. Rev. E*, Vol. 54, No. 5, pp. 5522–5537, 1996.