

## Associative memory based on synchronized firing of spiking neurons with time-delayed interactions

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We study associative memory of a neural network of spiking neurons with time-delayed synaptic interactions incorporating the time taken by an action potential to propagate along the axon. Individual spiking neurons are described by a set of nonlinear differential equations capable of exhibiting excitability such as that of Hodgkin-Huxley and FitzHugh neurons. When a simple learning rule of the autocorrelation type based on random patterns is assumed, memory retrieval is shown to be accompanied by synchronized firing of neurons. The reduced dynamics with a few degrees of freedom of the network with a finite number of stored patterns is analytically derived in the limit of infinitely many neurons. The dependence of the appearance of retrieval states on the distribution of time delay and on the size of refractory period given implicitly in the model is obtained, showing good agreement between the result of numerical simulations and that obtained from the reduced dynamics. The behavior of the network with an extensive number of patterns is also investigated and an approximate analysis is presented to discuss the storage capacity. [S1063-651X(98)09009-6]

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### I. INTRODUCTION

Since Hopfield's work [1] extensive studies have been conducted on neural networks of associative memory by means of statistical mechanical theory of spin glasses [2–10] and some alternatives of it [11–15]. Model neurons have been mostly taken to be of Ising spin type or of analog neuron type. They represent states of neuronal activity of firing and resting for Ising spin neurons, and a graded response or the mean firing rate for analog neurons. Memory retrieval based on such neurons is expressed as a dynamical flow to one of fixed point type attractors generated corresponding to the stored patterns in a network that has a Lyapunov function as a result of assuming symmetric couplings between neurons.

Some attempts have been made to make the models more biologically plausible by modifying the learning rule for synaptic couplings. Among them are the model of the correlated attractors [16–19] to explain Miyashita and Chang's experiment [20] on performing monkeys in which temporal order between patterns of stimuli has been shown to be converted to spatial correlations between attractors, and also are the model with asymmetric connections for memorizing presynaptic or postsynaptic activity of neurons [21–23], or for sequence processing [19,24]. Introduction of asymmetry to the synaptic couplings brings about rich dynamical behaviors of attractor networks including limit cycle and chaotic oscillations [19,24–29].

Since the discovery of oscillatory responses of neurons to stimuli in the physiological experiments on a cat's visual cortex [30,31], oscillatory behaviors of neural activity have received the growing interest of researchers, and theoretical investigations of associative memory models on oscillator networks have been performed [32–34].

Synchronized oscillations in membrane potential or synchronized firing of neurons observed in physiological experiments [30,31] suggest the importance of not only the mean

firing rate but also the spatiotemporal pattern of neuronal firing based on single firing events in the information processing of neural networks [35,36]. Synchronized oscillations have been attracting much attention, because the problem of binding the separately processed information in cortical neural networks may happen to be solved by such cooperative activity of neurons. In this regard, the spike timing in general seems to carry richer and more important information than the mean firing rate.

In addition there is some criticism against the assumption of mean firing rate for information coding on the grounds that it would not achieve the computational speed of biological nervous systems [37]. The concept of temporal coding has been proposed to make good use of firing times as analog variables to represent neuronal information.

Taking the spike timing or firing times of neurons into account to construct neural networks, one will be led to necessarily choose spiking neurons as model neurons [38].

A spiking neuron that is characterized by the threshold and refractory period originates from the model described by the Hodgkin-Huxley equations [39] representing the dynamics of ionic current gated by voltage-dependent channels. Since the equations require four variables to describe the behavior of a single neuron, reducing the number of variables to simplify the model has been attempted by FitzHugh [40], Nagumo and Arimoto [41], and Rinzel [42] while keeping the essential features of the firing of a neuron given by the Hodgkin-Huxley equations. The FitzHugh neuron is represented by a pair of ordinary differential equations as in the Rinzel neuron, which incorporates the representation of clearly identified biophysical quantities. They have the advantage of being easily studied by phase plane analysis, which makes it convenient to observe the bifurcations of several types of solutions occurring as the parameters are changed. A spiking neuron is often represented by a much simplified dynamics of the so-called leaky integrate-and-fire neuron [43–45], which consists of a linear differential equation representing relaxational motions of membrane potential

and a threshold gadget that only yields a symbolic pulse representing a neuronal firing when the membrane potential exceeds a threshold. In this case, the refractory period is either neglected or added to by considering an artificial prescription.

Associative memory models based on spiking neurons have been studied by several authors [46–48]. Most studies, however, eventually employ mean firing rates to code neuronal information.

Gerstner *et al.* [46] studied a network of a stochastic version of integrate-and-fire type spiking neurons with discrete time dynamics incorporating synaptic couplings with distributed time delays. Conducting numerical simulations they showed that retrieval of spatiotemporal patterns is possible and there the mean firing rate coding does not make sense.

To our knowledge very few associative memory models based on such nonlinear dynamics as that representing the FitzHugh neuron have been proposed for discussing the storage capacity.

The aims of the present paper are (1) to construct an associative memory neural network of spiking neurons that incorporates the refractory period of a neuron and the time delay in signal transmission between neurons in a biologically realistic way without deliberately introducing an oversimplified or abstract representation of the basic properties of neurons, and then (2) to investigate conditions in terms of the sizes of the refractory period and time delays and also of the number of stored patterns to ensure memory retrieval accompanying synchronized firing.

To this end, we choose the FitzHugh neuron as a model neuron and assume time-delayed synaptic couplings [49] with distributed time delays allowed. The analysis of the network based on the FitzHugh neuron may be straightforwardly extended to cases with more realistic model neurons such as the Rinzel or the Hodgkin-Huxley neuron without difficulty. We further introduce a synapse function [50] to represent the conversion from the firing event of a presynaptic neuron to the current injected to a postsynaptic neuron.

With the assumptions above, we suppose the neurons of the network to work in the following manner. An action potential that is generated with the weighted sum of injected current large enough to exceed a threshold exerts an excitatory or inhibitory influence after some time delay on a postsynaptic neuron in the form of injecting current whose temporal variation is given by the synapse function.

The main point of this work is to see to what extent the seemingly complicated model becomes amenable to a satisfactory level of analysis.

The present paper is organized as follows. In Sec. II we present the details of the general framework of the model construction based on spiking neurons that are represented by a set of nonlinear differential equations together with time-delayed synaptic couplings. An autocorrelation type learning rule based on random patterns is assumed to define the synaptic couplings with asymmetry included. In the case of storing a finite number of patterns we show that the sublattice method [26,51,52,26,29] mostly works in such a way that neurons in the same sublattice undergo synchronized firing, and that the reduced dynamics for sublattice variables are derived even in the presence of distributed time delays. Section III is devoted to the description of the results of the

network of the FitzHugh neurons obtained from both numerical integrations of the reduced dynamics and numerical simulations carried out with  $N=200$ . Good agreement between the two results of the existence of retrieval states exhibiting synchronized firing implies the validity of the analysis in Sec. II. In Sec. IV we deal with the case of extensive loading. We present the result of numerical simulations to show the phase diagram representing the storage capacity that is quite difficult to evaluate exactly due to the presence of crosstalk noise. To explain the qualitative behavior of the storage capacity we conduct an approximate analysis of it by reducing the problem to that of a certain analog network. Finally, in Sec. V we give a brief summary and discussion.

## II. NETWORK MODEL

### A. Network of spiking neurons with time-delayed interactions

Model neurons such as the Hodgkin-Huxley one and the FitzHugh one are, in general, modeled by a nonlinear dynamics that is described by a set of differential equations of the form

$$\dot{V} = f(V, W_1, \dots, W_q), \quad (1)$$

$$\dot{W}_j = g_j(V, W_1, \dots, W_q), \quad j = 1, \dots, q, \quad (2)$$

where  $V$  expresses membrane potential and  $W_j$  ( $j=1, \dots, q$ ) are auxiliary variables necessary for a system to exhibit a spiking oscillatory behavior. In the case of the FitzHugh neuron an example of the dynamics is expressed as

$$\dot{V} = -\left(\frac{V^3}{3} - V + W\right), \quad (3)$$

$$\dot{W} = \frac{1}{10}(V + 1.3), \quad (4)$$

which can easily be shown to exhibit excitability using phase plane analysis.

The interactions between  $N$  neurons comprising a network should be expressed by the form of current injection such that an injection of excitatory electric current makes a neuron fire. The dynamics of a network of many neurons under the influence of these electric currents is written by the equations

$$\dot{V}_i = f(V_i, W_{i1}, \dots, W_{iq}) + I_{\text{syn},i}(t) + I_{\text{ext},i}(t), \quad (5)$$

$$\begin{aligned} \dot{W}_{ij} &= g_j(V_i, W_{i1}, \dots, W_{iq}), \\ i &= 1, \dots, N, \quad j = 1, \dots, q, \end{aligned} \quad (6)$$

where  $I_{\text{ext},i}(t)$  denotes an injection of external electric current, that can be controlled, say, to set initial conditions, as is often done in biological experiments of inserting electrodes, and  $I_{\text{syn},i}(t)$  denotes an injection of the synaptic currents contributed from other neurons coupled via synaptic interactions.

If the amplitude of the electric current  $I_i(t) = I_{\text{syn},i}(t) + I_{\text{ext},i}(t)$  is large enough to fire a neuron, an action potential is generated to propagate along the axon. After some elapsed time the action potential reaches a postsynaptic neuron and gives rise to an injection of synaptic electric current. To describe the situation mathematically, we define the firing time

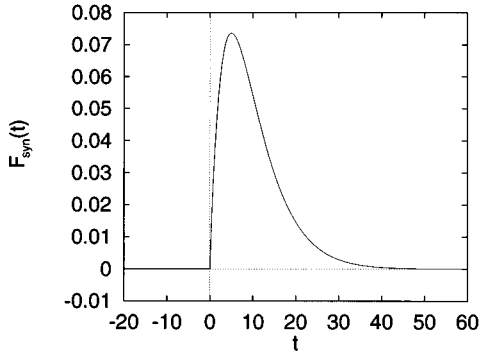


FIG. 1. Shape of the synapse function (8) with  $t_s=5$ .

of a neuron as the time when the membrane potential of a neuron exceeds a certain value  $V_0$  required for the firing of a neuron. We note that such  $V_0$  cannot be uniquely determined. In our case it will suffice to set  $V_0=0$  for convenience. We denote the firing time by  $t_i(k)$ , where  $k$  represents  $k$ th firing of neuron  $i$  counted from the initial time  $t=0$ .

Introducing time delay  $d_{ij}$  ( $i=1, \dots, N$ ,  $j=1, \dots, N$ ), which expresses time taken by an action potential of neuron  $j$  to reach postsynaptic neuron  $i$ , we write the synaptic injection  $I_{\text{syn},i}(t)$  as

$$I_{\text{syn},i}(t) = I_{\text{amp}} \sum_j^N J_{ij} \sum_k F_{\text{syn}}[t - t_j(k) - d_{ij}], \quad (7)$$

where  $J_{ij}$  expresses the strength of synaptic couplings between neurons  $j$  and  $i$ ,  $I_{\text{amp}}$  is a parameter adjusting amplitudes for every  $I_{\text{syn},i}(t)$ , and a synapse function  $F_{\text{syn}}(t)$  describes a temporal change of the injected synaptic electric current after an arrival of an action potential. In the present study, we use the synapse function written in the form [50]

$$F_{\text{syn}}(t) = \begin{cases} 0, & t < 0 \\ \frac{t}{t_s^2} \exp\left(-\frac{t}{t_s}\right), & 0 \leq t, \end{cases} \quad (8)$$

where  $t_s$  is a parameter controlling the shape of the synapse function. Figure 1 shows the shape of the function with  $t_s=5$ . Note that the time integration of the synaptic electric current per one arrival of an action potential is normalized to be constant for any  $t_s$ .

The behavior of a system of spiking neurons with interactions of the form (7), which is usually called pulse-coupled type, has recently been studied in the case of integrate-and-fire neurons [53–56]. There, conditions for synchronization of oscillations are investigated in terms of the parameter  $t_s$  of the synapse function (8) [54,56]. In our present study spiking neurons are utilized as elements exhibiting excitability as well as refractoriness and hence we deal with the case where the interactions (7) and an initial injection of pulsed external current for preparing initial firing of neurons are necessary ingredients for a coupled system of spiking neurons to exhibit oscillatory behavior. In other words, without any external current injection, i.e.,  $I_{\text{ext},i}(0)=0$ , each neuron remains to be at the fixed point of the single  $V$ – $W$  dynamics. In that case time delays  $d_{ij}$  and the refractory period become rel-

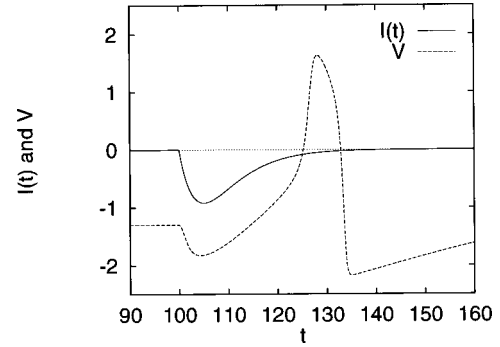


FIG. 2. Effect of the inhibitory electric current on the firing behavior of the FitzHugh neuron. The FitzHugh neuron subjected to an injection of inhibitory electric current can fire with some delay. The same behavior is observed in the case of Hodgkin-Huxley neurons.

evant quantities for determining the dynamical behavior of the system. Such a situation can easily be understood for a system of two coupled FitzHugh neurons. In the Appendix A we present a sketch of the dynamical behavior of that system to see the role played by the time delay and the refractory period that is implicitly (though not uniquely) given in the FitzHugh dynamics.

### B. Synaptic couplings $J_{ij}$ for associative memory

Considering random patterns for associative memory, we assume that  $P$  patterns are represented by independent random variables  $\xi_i^\mu$  ( $i=1, \dots, N$ ,  $\mu=1, \dots, P$ ) taking a quenched value 0 or 1 according to the probability distribution:

$$P(\xi_i^\mu) = (1-a) \delta(\xi_i^\mu) + a \delta(\xi_i^\mu - 1), \quad (9)$$

where  $a$  is the average of the  $\xi_i^\mu$ .

Considering a learning rule to store the memory patterns, we note that our model neuron exhibits a peculiar behavior regarding the generation of a spike as the Hodgkin-Huxley neuron does: *even an injection of inhibitory electric current may bring about a firing of the FitzHugh neuron as shown in Fig. 2*. So use of the standard symmetric synaptic couplings  $J_{ij} = (1/N) \sum_\mu (\xi_i^\mu - a)(\xi_j^\mu - a)$ , which is mostly assumed in associative memory, turn out to be inappropriate for large value of  $I_{\text{amp}}$  from the viewpoint of making the network biologically plausible. In view of this we assume synaptic couplings  $J_{ij}$  to be

$$J_{ij} = \frac{1}{N} \sum_\mu^P \xi_i^\mu (\xi_j^\mu - a), \quad (10)$$

which are asymmetric:  $J_{ij} \neq J_{ji}$ .

As can be shown in what follows, the above couplings ensure memory retrieval based on synchronized firing of neurons.

### C. The reduced dynamics describing synchronized firings in the case of the low loading limit

Although the model network defined in the previous subsection looks a little complicated, synchronized firings ex-

pected to occur in the low loading limit  $\alpha = P/N = 0$  can be analyzed rigorously in the limit of  $N \rightarrow \infty$ . At first consider the case when all of the time delay  $d_{ij}$  take a single constant value. In this case we can easily see that dividing  $N$  neurons into  $2^P$  sublattices, one knows everything on the network, because the dynamics of the system is reduced to the dynamics of  $2^P$  neurons representing the sublattices, instead of  $N$  dynamics. When initial conditions and  $I_{\text{ext},i}(t)$  for neurons in the same sublattices are same, this scheme is rigorously correct.

The sublattice method also works even in the case where time delay  $d_{ij}$  are not constant but they distribute according to a certain probability distribution  $P_d(d_{ij})$  with  $d_{ij}$  taken as random variables, as is shown below. Although such a treatment of  $d_{ij}$  should be incorrect when considering network topology, we proceed with the above simplification.

Assuming synaptic couplings to be of a more general form:

$$J_{ij} = \frac{1}{N} J(\vec{\xi}_i, \vec{\xi}_j), \quad (11)$$

where  $\vec{\xi}_i = (\xi_i^1, \xi_i^2, \dots, \xi_i^P)$ , we will derive the reduced dynamics for  $2^P$  sublattices. We denote each of  $2^P$  sublattices by an index  $n$  ( $n = 1, \dots, 2^P$ ) and the set of neurons (site) belonging to sublattice  $n$  by  $I(n)$ . We denote the number of neurons in sublattice  $n$  by  $|I(n)|$ . The common pattern vectors for sublattice  $n$  are denoted by  $\vec{\xi}(n)$ , and the ratio of the number of neurons in the sublattice to the total number of neurons by  $r(n) = |I(n)|/N$ . Assuming safely that every neuron in the same sublattice fires at the same time  $t(n, k)$  (note that this assumption is easily verified after calculating the following equation.), we have

$$\begin{aligned} I_{\text{syn},i}(t) &= \frac{I_{\text{amp}}}{N} \sum_j J(\vec{\xi}_i, \vec{\xi}_j) \sum_k F_{\text{syn}}[t - t_j(k) - d_{ij}] \\ &= \frac{I_{\text{amp}}}{N} \sum_n \sum_{j \in I(n)} J[\vec{\xi}_i, \vec{\xi}(n)] \\ &\quad \times \sum_k F_{\text{syn}}[t - t(n, k) - d_{ij}] \\ &= I_{\text{amp}} \sum_n r(n) J[\vec{\xi}_i, \vec{\xi}(n)] \sum_k \frac{1}{|I(n)|} \\ &\quad \times \sum_{j \in I(n)} F_{\text{syn}}[t - t(n, k) - d_{ij}] \\ &= I_{\text{amp}} \sum_n r(n) J[\vec{\xi}_i, \vec{\xi}(n)] \sum_k G_{\text{syn}}[t - t(n, k)], \end{aligned} \quad (12)$$

where

$$G_{\text{syn}}(t) = \int_0^\infty P_d(\tau) F_{\text{syn}}(t - \tau) d\tau. \quad (13)$$

Therefore every neuron in the sublattice  $n$  shares the common synaptic electric current and this common synaptic elec-

tric current brings about the synchronized firings of neurons in that sublattice even in the presence of distributed time delays.

For convenience, we rewrite Eq. (12) for the common synaptic electric current  $I_{\text{syn},n}(t)$  in a more concise form:

$$I_{\text{syn},n}(t) = I_{\text{amp}} \sum_m J(n, m) \sum_k G_{\text{syn}}[t - t(m, k)], \quad (14)$$

where  $J(n, m) = J[\vec{\xi}(n), \vec{\xi}(m)]r(m)$ . Then one obtains the reduced dynamics in terms of the sublattice variables  $V_n$  and  $\{W_{nj}\}$ :

$$\dot{V}_n = f(V_n, W_{n1}, \dots, W_{nq}) + I_{\text{syn},n}(t) + I_{\text{ext},n}(t), \quad (15)$$

$$\dot{W}_{nj} = g_j(V_n, W_{n1}, \dots, W_{nq}),$$

$$n = 1, \dots, 2^P, \quad j = 1, \dots, q. \quad (16)$$

Given  $I_{\text{ext},n}(t)$  together with initial conditions for  $V_n(0)$  and  $\{W_{nj}(0)\}$ , one can solve the set of Eqs. (14)–(16) numerically to obtain the behavior of the network with  $\alpha = 0$  in the limit  $N \rightarrow \infty$ .

### III. ASSOCIATIVE MEMORY IN THE NETWORK OF THE FITZHUGH NEURONS AND SYNCHRONIZED FIRINGS

Assuming the synaptic interactions in Eq. (10), we will apply the general framework of the reduced dynamics to a network composed of the FitzHugh neurons (3),(4) to observe the relationship between memory retrieval and synchronized firings of neurons. We confine ourselves only to the case of random patterns without bias to set  $a = 0.5$ .

#### A. Effects of distributed time delays, refractory period, and the averaged synapse function

To investigate the effect of the time delays and how the averaged synapse function works, we assume, for simplicity, a uniform distribution for the time delays  $d_{ij}$ :

$$P_d(d_{ij}) = \begin{cases} 0, & d_{ij} < d_1, d_2 < d_{ij} \\ 1/\Delta d, & d_1 \leq d_{ij} \leq d_2, \end{cases} \quad (17)$$

where  $\Delta d = d_2 - d_1$ .

We consider as an initial condition for the network dynamics that for all neurons ( $V_i, \{W_{ij}\}$ ) is set to be at the stable fixed point of Eqs. (5), (6) so that they remain quiescent without an external stimuli. Supposing the pattern 1 to be retrieved, we assume an injection of the external electric current to be given by

$$I_{\text{ext},i}(t) = \begin{cases} 1 & 0 \leq t \leq \Delta t \\ 0 & t < 0, \Delta t < t \end{cases} \quad (18)$$

for pattern 1 neurons (i.e., the neurons with  $\xi_i^1 = 1$ ) and otherwise  $I_{\text{ext},i}(t) = 0$ , where  $\Delta t$  is a time duration of the current injection.  $\Delta t$  should be chosen such that the above injection of current can excite the pattern 1 neurons. To study under what conditions such an external injection brings about firings of pattern 1 neurons immediately and, after that, only

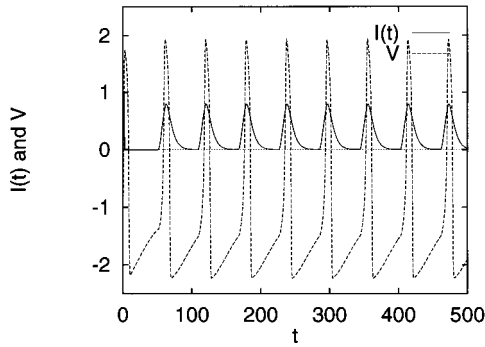


FIG. 3. Time evolution of the  $V$  variable of sublattice 2 governed by the reduced dynamics (14)–(16) with the external electric current  $I_2(t) = I_{\text{syn},2}(t) + I_{\text{ext},2}(t)$  in the case of  $d_1 = 50$ ,  $\Delta d = 10$ .

pattern 1 neurons can continue to fire synchronously, we investigate the case with a few number of stored pattern. To study the system under the condition described above it eventually suffices to consider 2 sublattices in the limit  $N \rightarrow \infty$ , because  $\sum_k F_{\text{syn}}[t - t_j(k) - d_{ij}]$  in Eq. (12) vanishes unless  $\xi_j^1 = 1$ :

$$\text{Sublattice 1: } \xi^1(1) = 0, r(1) = 0.5,$$

$$\text{Sublattice 2: } \xi^1(2) = 1, r(2) = 0.5.$$

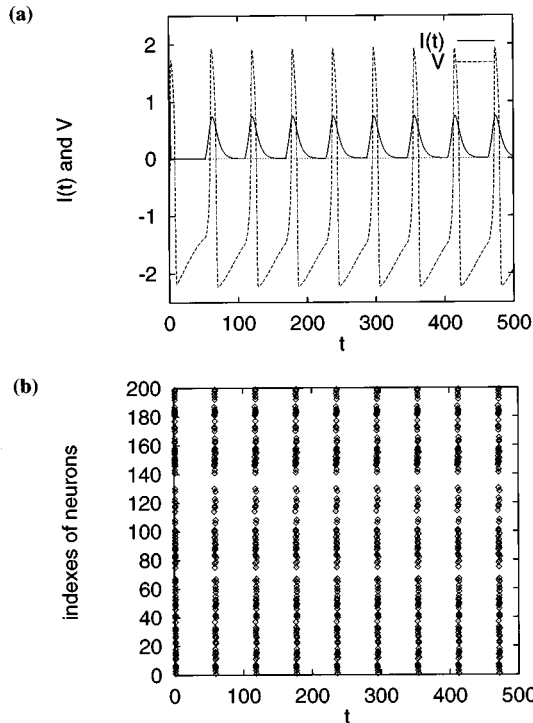


FIG. 4. The result of numerical simulations with  $N = 200$ ,  $P = 3$  under the same condition as in Fig. 3(a). The dynamical behavior of a neuron corresponding to sublattice 2 is plotted in the same way as in Fig. 3. Even in the case of memorizing an additional two patterns, that give rise to noise in the synaptic electric current for finite  $N$ , the theoretical result in Fig. 3 explains the numerical result well. (b) The traces of firing of neurons observed in the simulation. Circles represent the time when firing occurs. As discussed in text, neurons exhibit synchronized firing in the successful retrieval.

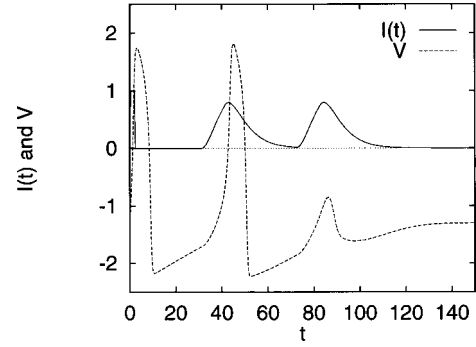


FIG. 5. The behavior of sublattice 2 exhibited by reduced dynamics (14)–(16) with  $d_1 = 30$ ,  $\Delta d = 10$ , where the network fails to retrieve the pattern because of the effect of refractoriness exhibited by the FitzHugh neuron (3),(4).

Solving numerically the reduced dynamics with the two sublattices (14)–(16) with  $t_s = 5$ ,  $I_{\text{amp}} = 50$ ,  $\Delta t = 2$ , we obtain the dynamical behavior of a neuron of sublattice 2 as shown in Fig. 3 under the condition  $d_1 = 50$ ,  $\Delta d = 10$ , where the network succeeds in retrieving the pattern. On the other hand we perform numerical simulations with  $N = 200$ ,  $P = 3$ . We depict in Fig. 4(a) the result of the neuron with  $\xi_j^1 = 1$ . The behavior of the sublattice 2 in Fig. 3 is in good agreement with the result of numerical simulations in Fig. 4(a). This indicates that the use of the averaged synapse function in Eq. (14) is proved to be valid. The expected synchronized firings are also confirmed to occur as shown by the result of numerical simulations displayed in Fig. 4(b), where all traces of firings of 200 neurons are plotted by circles.

Outside the region of appropriate parameters, the network fails in retrieval and every neuron comes back to be silent again after some time, following the trajectory in the  $V$ - $W$  plane as shown in Fig. 5, which describes one of the typical behavior of the neuron in unsuccessful retrieval. To obtain the condition for successful retrieval, we examine the behavior of the network after a long time under various conditions on the basis of the reduced dynamics to draw the phase diagram shown in Fig. 6.

In the region  $23 \lesssim \Delta d$  the network fails to retrieve the pattern. This phenomenon agrees with the intuition that the synchronized firings breaks down if the time delays are dis

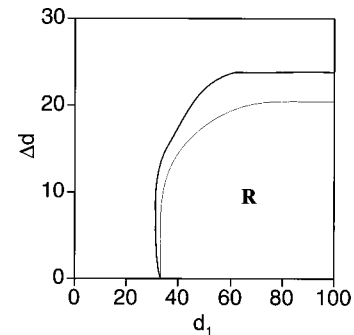


FIG. 6. Phase diagram on the  $d_1$ - $\Delta d$  plane in the case of uniformly distributed time delays (17). The thick line is determined on the basis of the reduced dynamics, and the thin line is by numerical simulations with  $N = 200$  and  $P = 3$ . **R** represents the retrieval phase, where the network succeeds in retrieving the pattern.

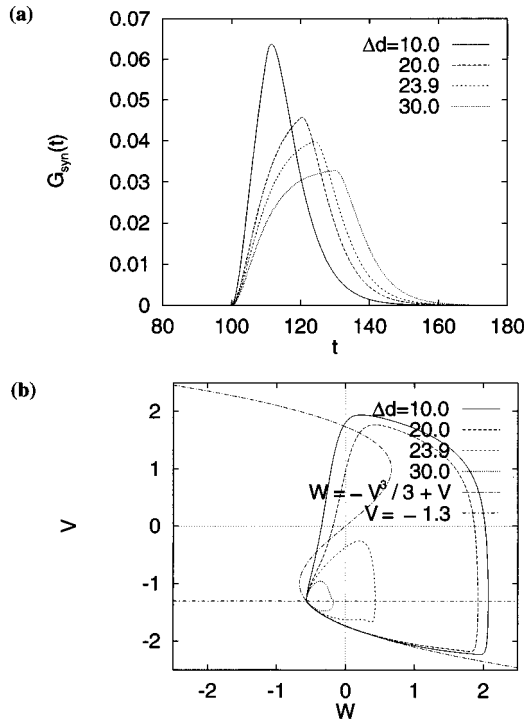


FIG. 7. Effect of  $\Delta d$  on the dynamical behavior of a single neuron. (a) Shape of the averaged synapse function  $G_{\text{syn}}(t)$  for various  $\Delta d$ , when  $d_1 = 100$ . (b) Trajectories of a neuron subjected to an injection of the electric current  $I(t) = 1(1 - 0.5)0.5G_{\text{syn}}(t)$  are plotted on the  $W$ - $V$  plane. The null clines  $W = -V^3/3 + V$  and  $V = -1.3$  are drawn as a reference.

tributed too widely. The phenomenon is attributed to the dull-shaped averaged synapse function with a large  $\Delta d$  as shown in Fig. 7(a). To investigate the relation between the shape of the synapse function and the firing of a neuron, we

show in Fig. 7(b) the behavior of a single neuron in response to an injection of electric current  $I(t) = 0.5(1 - 0.5)G_{\text{syn}}(t)$  with various  $\Delta d$ . Although the time integration of the electric current are the same for every case, difference of the shape of the synaptic function due to the different  $\Delta d$  causes a different behavior after the injection. A large  $\Delta d$  prevents a neuron from firing and that explains the nonretrieval region with large  $\Delta d$  well.

On the other hand, in the region where  $d_1 \lesssim 32$ , the network also fails to retrieve the stored patterns, because of the effect of the refractory period provided intrinsically in Eqs. (3) and (4). Like the Hodgkin-Huxley neuron, the FitzHugh neuron cannot fire within a certain time after previous firing even if there is an additional injection of electric current. In the case of Fig. 5, the time interval between the second and third synaptic injections is so close that the neuron cannot fire after the third injection.

### B. Dependence of successful retrieval on an initial overlap

As in an associative memory model based on Ising spin or analog neurons, the distance of an initial state from a target pattern must be small enough for the network to retrieve the pattern. To measure the distance of a state from the pattern  $\xi^\mu$  for the network exhibiting repetitive firings, we define an overlap as

$$m^\mu(t) = \frac{1}{N} \frac{1}{a(1-a)} \sum_i (\xi_i^\mu - a) \sum_k \exp\{-\gamma[t - t_i(k)]\} \quad (19)$$

with  $\gamma$  being appropriately chosen. We consider setting  $\gamma = 0.05$  is appropriate.

By applying  $I_{\text{ext},i}(t)$  to part of pattern 1 neuron, one can prepare an arbitrary size of an initial overlap. We consider three sublattices:

Sublattice 1:  $\xi^1(1) = 0$ , no external electric current injected,  $r(1) = 0.5$ ,

Sublattice 2:  $\xi^1(2) = 1$ , no external electric current injected,  $r(2) = 0.5(1 - R)$ ,

Sublattice 3:  $\xi^1(3) = 1$ , an external electric current injected,  $r(3) = 0.5R$ ,

where  $R$  is the ratio of the number of injected neurons to the number of all pattern 1 neurons. Note that the sublattice previously taken to classify the total neurons in terms of a set of stored patterns breaks up under the preparation of initial conditions described above. However, the reduced dynamics with the three sublattices still remains valid.

Setting all the time delay to be a constant value  $d$  ( $d_{ij} = d$   $i = 1, \dots, N$ ,  $j = 1, \dots, N$ ), we investigate the behavior of the system after a long time. We show the result in terms of  $R$ - $d$  phase diagram in Fig. 8. The network cannot retrieve the pattern in the region  $R \leq 0.3$  because the initial size of overlap is not large enough. In the region  $d \leq 35$ , time delay is so small that the system fails to retrieve the pattern because of the effect of the refractory period. In Fig. 9 we show two cases of the time evolution of the overlap observed in

numerical simulations. While  $R = 0.8$  is large enough to continue firings, the network started with  $R = 0.2$  is seen to rapidly settle down to a quiescent state.

In addition to the standard type of retrieval we can observe another type of retrieval exhibiting antiphase phase in Fig. 8, where neurons belonging to sublattice 2 (neurons free from the injection of external current), and those belonging to sublattice 3 (neurons with an external electric current injected) fire alternatively in time with smaller size of overlap than that for the standard type of retrieval. The dynamical behavior of neurons exhibiting the antiphase oscillations are depicted in Fig. 10, where (a) is for neurons of sublattice 2 and (b) is for neurons of sublattice 3. The occurrence of such oscillations is explained as follows. After neurons of sublattice 3 fire owing to the injection of an external current, the

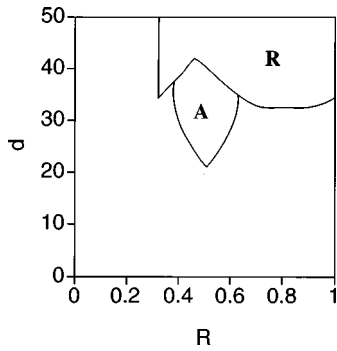


FIG. 8.  $R$ - $d$  phase diagram, where  $R$  is the ratio of the number of injected neurons to that of the neurons with  $\xi_i^1=1$  (pattern 1 is the target pattern to be retrieved) and  $d$  is a common time delay for all  $d_{ij}$  ( $d_{ij}=d$ ). **R** represents the retrieval phase, and **A** represents the antiphase phase, where the two clusters of neurons appear to and fire alternatively as shown in Fig. 10 (see text for details).

action potentials generated are transmitted to the postsynaptic neurons, and then both neurons of sublattice 2 and 3 get subjected to a common injection of synaptic electric current. While neurons of sublattice 2 fire perfectly in response to those injections, neurons of sublattice 3 cannot fire because of the effect of the refractory period; in this region the time delay  $d$  is too short to make the neuron of sublattice 3 fire. At the next updating of firings, neurons of sublattice 2 cannot fire in spite of the firing of neurons of sublattice 3. Following such a cycle of updating, pattern 1 neurons (sublattice 2 and sublattice 3) fire alternatively. In Fig. 11(a) we display the traces of alternative firing obtained in the numerical simulations with  $N=500$ , and in (b) we show the time evolutions of overlap corresponding to the firing traces (a).

#### IV. CASE WITH THE EXTENSIVE LOADING $\alpha \neq 0$

We will show that when an extensive number of patterns are loaded (i.e.,  $P = \alpha N$ ,  $\alpha \neq 0$ ), the network under consideration can retrieve the patterns if  $\alpha$  is below a critical value  $\alpha_c$  (the storage capacity). For the sake of simplicity we deal only with the case where time delay  $d_{ij}$  is not distributed. Even with this simplification, a rigorous analysis of the storage capacity is rather difficult because the injected synaptic electric current for a different neuron takes a different value owing to the so-called cross-talk noise produced by the interference among the stored patterns, and hence each neuron

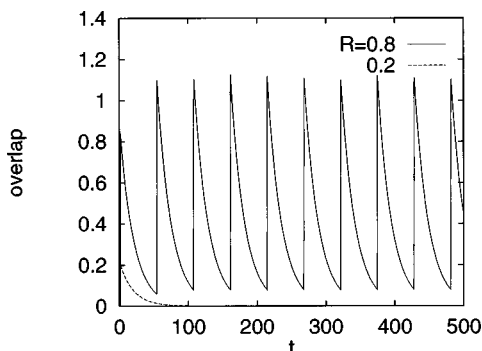


FIG. 9. Two typical time evolutions of the overlap obtained in numerical simulations with  $d=50$ ,  $N=500$ ,  $P=3$ ,  $R=0.2, 0.8$ . With small  $R$ , the network fails to continue firing.

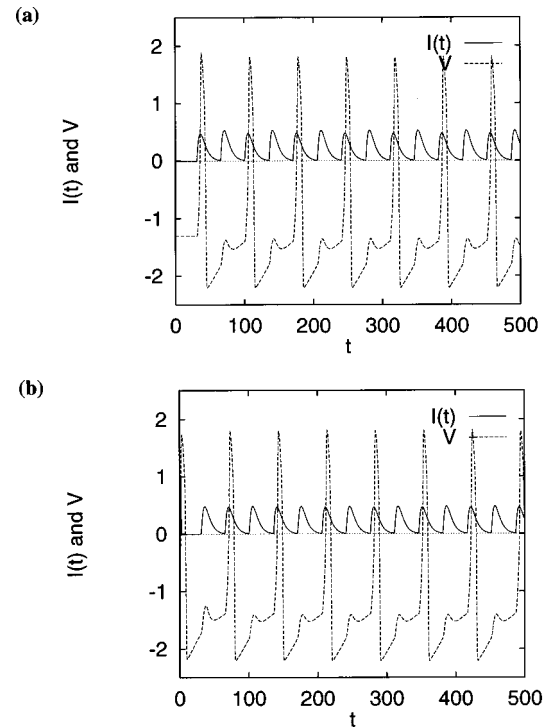


FIG. 10. The result of numerical simulations with  $R=0.5$ ,  $d=30$ ,  $P=3$ ,  $N=500$ . (a) dynamical behavior of neurons corresponding to sublattice 2. (b) The same for sublattice 3. Two neurons fire alternatively with a constant phase shift of  $\sim \pi$ .

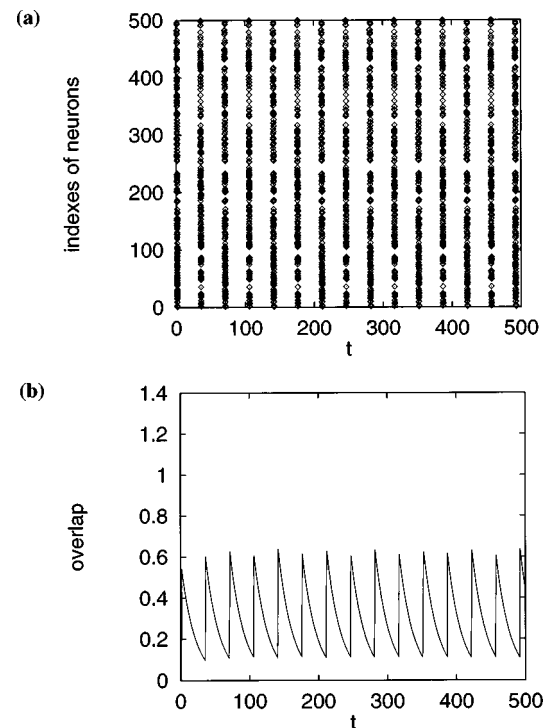


FIG. 11. (a) The traces of neuronal firing observed in the same simulation as in Fig. 10. Two clusters of neurons corresponding to sublattice 2 and sublattice 3 fire alternatively. (b) The time evolution of the overlap (19) observed with the traces of neuronal firing in (a).

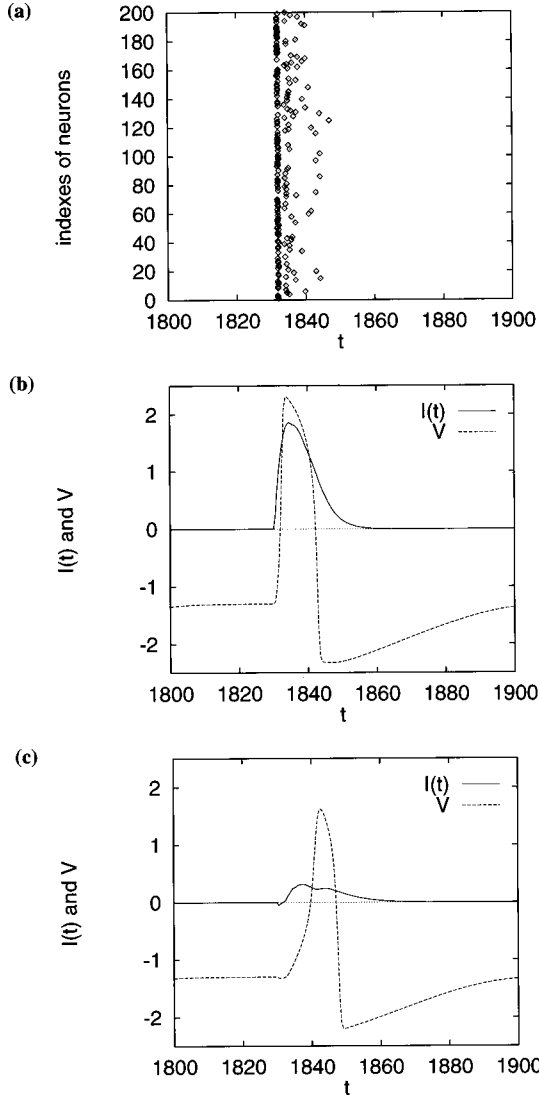


FIG. 12. The result of numerical simulations with  $t_s=5$ ,  $I_{\text{amp}}=100$ ,  $N=200$ ,  $\alpha=0.04$ . (a) The traces of firing. (b) The dynamical behavior of the firing neuron with  $\xi_i^1=1$  (pattern 1 is the target pattern to be retrieved). (c) The same with  $\xi_i^1=0$ . The neuron with  $\xi_i^1=1$  fires much faster than that with  $\xi_i^1=0$ , resulting in the simultaneous firing at  $t \approx 1830$ .

has its own firing time as displayed by the result of numerical simulations in Fig. 12.

Assuming that every firing neuron emits a spike simultaneously, we can, however, conduct an approximate analysis of the stationary states of the network. It then turns out that firing of neurons occurs periodically after a long time. The injection of the synaptic electric current for neuron  $i$  is written in the form

$$I_{\text{syn},i}(t) = I_{\text{amp}} \sum_j^N J_{ij} x_j \sum_k F_{\text{syn}}(t - kT), \quad (20)$$

where  $T$  denotes the period of the firing, and  $x_i$  an index representing activity of a neuron such that  $x_i=1$  if neuron  $i$  fires and  $x_i=0$  otherwise. In view of the nature of the neuron of the present model, we can assume  $x_i$  to obey the following equation:

$$x_i = \Theta \left( I_{\text{amp}} \sum_j J_{ij} x_j - \theta(t_s) \right), \quad (21)$$

where the  $\Theta(h)$  is the Heaviside function

$$\Theta(h) = \begin{cases} 0 & h \leq 0 \\ 1 & 0 < h \end{cases} \quad (22)$$

and  $\theta(t_s)$  is a threshold for firing determined by the synaptic function with  $t_s$ . When the time delay  $d$  is sufficiently large, the firing period  $T$  becomes large as well, and the evaluation of  $\theta(t_s)$  can be reduced to a problem of a single body non-linear dynamics in Eqs. (5) and (6). Since, in this case, every neuron is fixed into the fixed point just before the firing, it will suffice to investigate the behavior of a single neuron after an injection of electric current of the form

$$I_{\text{syn}}(t) = h F_{\text{syn}}(t). \quad (23)$$

We show the result of evaluating the  $\theta(t_s)$  in Fig. 13.

Introducing  $\tilde{\xi}_i^\mu = 2\xi_i^\mu - 1$  and their average  $\tilde{a} = 2a - 1$  for  $J_{ij}$  in Eq. (10), Eq. (21) is rewritten as

$$x_i = \Theta \left( \frac{1}{N} \sum_\mu \sum_{j \neq i} (\tilde{\xi}_i^\mu + 1) (\tilde{\xi}_j^\mu - \tilde{a}) x_j - \frac{4\theta(t_s)}{I_{\text{amp}}} \right). \quad (24)$$

Note that we set  $J_{ii}=0$ . Now the problem is formulated as finding the fixed point of Eq. (24), which corresponds to the Hopfield type network with asymmetric couplings in Eq. (10). A method of the SCSNA (self-consistent signal-to-noise analysis) in our previous study [11,12,21,22] is available for such a problem. In applying the SCSNA to Eq. (24) the local fields of neurons  $h_i$  are basic physical quantities. In the present case the local field  $h_i$  reads

$$\begin{aligned} h_i &= \frac{1}{N} \sum_\mu \sum_{j \neq i} (\tilde{\xi}_i^\mu + 1) (\tilde{\xi}_j^\mu - \tilde{a}) x_j \\ &= (\tilde{\xi}_i^\mu + 1) m^1 + (\tilde{a} + 1) S + \frac{1}{N} \sum_{\mu \geq 2} \sum_{j \neq i} (\tilde{\xi}_i^\mu - \tilde{a}) (\tilde{\xi}_j^\mu - \tilde{a}) x_j, \end{aligned} \quad (25)$$

where

$$S = \sum_{\mu \geq 2} m^\mu \quad (26)$$

with

$$m^\mu = \frac{1}{N} \sum_i (\xi_i^\mu - \tilde{a}) x_i. \quad (27)$$

The  $S$  appears as a result of considering asymmetric couplings in Eq. (10), and is a pattern-dependent quantity of  $O(1)$  [21,22]. Given a set of patterns,  $S$  contributes only a static field independent of each neuron to the local field and hence makes the network behavior sample dependent.

The SCSNA equations read



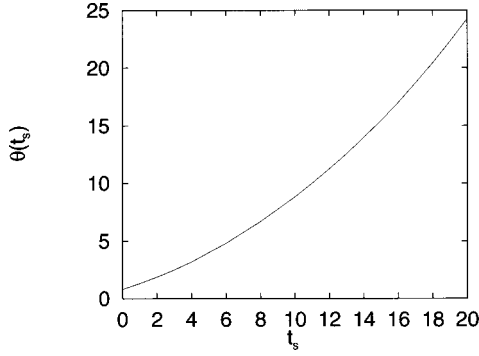


FIG. 13. The threshold for firing of a neuron plotted against  $t_s$  [refer to Eq. (21)].

$$Y = \Theta \left( (\tilde{\xi} + 1)m + (\tilde{a} + 1)S - \frac{4\theta(t_s)}{I_{\text{amp}}} + \sqrt{\alpha r}z + \Gamma Y \right), \quad (28)$$

$$m = \langle \langle (\tilde{\xi} - \tilde{a})Y \rangle \rangle, \quad (29)$$

$$U\sqrt{\alpha r} = \langle \langle zY \rangle \rangle, \quad (30)$$

$$q = \langle \langle Y^2 \rangle \rangle, \quad (31)$$

$$\Gamma = \alpha \frac{(1 - \tilde{a}^2)^2 U}{1 - (1 - \tilde{a}^2)U}, \quad (32)$$

$$r = \frac{(1 - \tilde{a}^2)^2 q}{\{1 - (1 - \tilde{a}^2)U\}^2}, \quad (33)$$

$$\langle \langle f(\tilde{\xi}, z) \rangle \rangle = \left\langle \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} \exp\left(-\frac{z^2}{2}\right) f(\tilde{\xi}, z) dz \right\rangle_{\tilde{\xi}}. \quad (34)$$

Although the statistical behavior of  $S$  is difficult to treat rigorously, its probability distribution over various samples of patterns may well be approximated to be Gaussian [21,22]. This means that setting  $S=0$  in Eq. (28) gives a rough estimate of the behavior of the network [21,22]. In Fig. 14(a) we give the phase diagram obtained by Eqs. (28)–(33) with  $S=0$  and, in Fig. 14(b) we show the phase diagram obtained by a numerical simulation with  $N=200$ . Note that another numerical simulation with random patterns generated by a different seed for random numbers will give a slightly different result even with a larger  $N$  because of the sample-dependent feature of the network. We see, however, that the theoretical phase diagram Fig. 14(a) qualitatively explains the numerical result in Fig. 14(b) except for the region with large  $40 \lesssim I_{\text{amp}}$ , where the deviation of the numerical result from the theoretical one is seen to become appreciable. The cause of the deviation can be attributed to the breakdown of the assumption for the simultaneous firings of neurons with  $x_i=1$ . Indeed the firing time of the firing neuron distributes to an appreciable extent as shown by the results of the numerical simulations in Fig. 12(a). The broad distribution is caused by the fact that the firing neurons with  $\xi_i^1=1$  receives much larger synaptic electric current than that

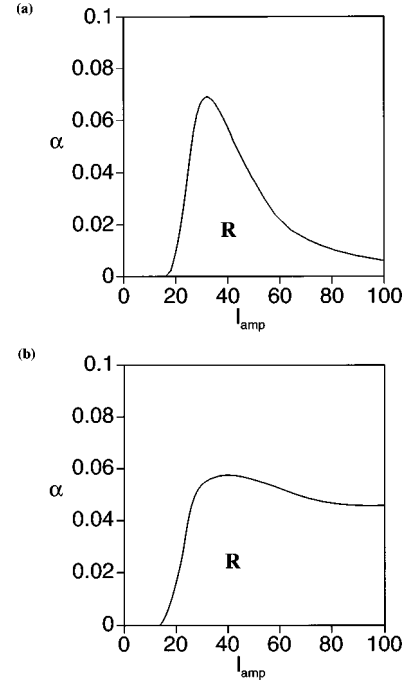


FIG. 14. (a) The phase diagram showing the storage capacity as a function of  $I_{\text{amp}}$ , which is obtained by Eqs. (28)–(33) with  $t_s=5$ ,  $\tilde{a}=0$ ,  $S=0$ . (b) The corresponding result of numerical simulations with  $N=200$ . Note that another simulation with a different random seed will give another result even with  $N=\infty$  because of the sample-dependent feature of the network (see text for details).

with  $\xi_i^1=0$  and fires faster as shown in Fig. 12(b) and 12(c). These fast firings are observed as the simultaneous firings at  $t \approx 1830$  in Fig. 12(a).

## V. DISCUSSION

Assuming a simple learning rule we have studied an associative memory neural network of spiking neurons interacting each other via synaptic couplings with time lags due to the propagation of an action potential. Whether a neuron fires or not is determined with a set of differential equations. The time-dependent behavior of synaptic electric current is described by a synapse function. We have observed that the network can work as an associative memory based on synchronized firing of neurons not only for the low loading limit  $\alpha=0$  but also for the extensive loading  $\alpha \neq 0$ . The time delay has been found to play a crucial role for the occurrence of synchronized repetitive firings of neurons, which lead to memory retrieval.

The assumption that time delay  $d_{ij}$  are independent random variables obeying a certain probability distribution enables one to analytically investigate the time-dependent behavior of the network with the low loading rate by means of the sublattice method. Good agreement between the results obtained from the reduced dynamics and numerical simulations with  $N=200$  or  $500$  implies the validity of the analysis.

Based on the reduced dynamics we have analyzed the stationary state of the network with uniformly distributed time delay to obtain the retrieval phase. The result has been summarized into the phase diagram showing the dependence of the appearance of the retrieval states on the parameters

characterizing the distribution of  $d_{ij}$ . Much broad distribution of time delays makes the averaged synapse function too dull to sustain synchronized firing of neurons as shown in Fig. 7. On the other hand, the network with too short a time delay also fails in retrieval because of the effect of the refractory period implicitly defined in the model neuron.

In the case of the extensive loading the firing times of neurons have been found to distribute as a result of the appearance of the cross-talk noise. Since the appearance of such a distribution makes it difficult to rigorously analyze the statistical behavior of the network, we have to neglect the effect of the distributed firing time to conduct an approximate analysis of the storage capacity by means of the SC-SNA. Although the pattern-dependent random variable  $S$  due to the asymmetric synaptic couplings considered brings about the sample-dependent behavior of the network, the solution of the SCSNA equations (28)–(33) with  $S=0$  has been found to give a rough sketch of the behavior of the network in the case of small  $I_{amp}$ . However, in the case of large  $I_{amp}$ , where the threshold of the transfer function gets effectively smaller, the influence of the distributed firing time becomes appreciable to cause the observed difference between the results of simulations and approximate analysis.

Our analysis given in the present study is quite simple in spite of the seemingly complicated model. It may be applied to a wide class of models with the same structure as the present system. For example, the network retrieving spatiotemporal patterns may also be investigated as long as the learning rule is written as in Eq. (11). Furthermore, as is noted earlier, we may easily replace the FitzHugh neurons taken in the present study by the Hodgkin-Huxley neurons. Working with networks based on the Hodgkin-Huxley neurons will enable one to incorporate experimental data obtained for biological neurons to get insight into the mechanisms for information processing of real nervous systems.

In real nervous systems, synaptic couplings may have correlations with time delay  $d_{ij}$ , and such synaptic couplings may be expected to process spatiotemporal patterns more efficiently. In that case, assuming for instance,  $J_{ij} = (1/N)J(\vec{\xi}_i, \vec{\xi}_j, d_{ij})$ , we can proceed in almost the same manner as described here to analyze the system under appropriate conditions.

Finally we discuss the implications of the result of the present study from the viewpoint of biological plausibility. The occurrence of synchronized firing ensuring memory retrieval in our network is a result of a combined work of the refractory period of neurons and time delays in signal transmissions. The period of synchronized repetitive firing is determined to be nearly equal to the mean time delay.

We have observed that memory retrieval can be achieved in a very small number of firing pulses, that is, mostly one or two pulses. This implies that the network exhibits efficient computational speed amounting to that required by real nervous systems to perform such information processing as a visual pattern matching.

In fact, there is an experimental indication that human brains perform visual pattern processing in 100 msec through 10 synaptic stages [57]. Then one can expect that the time taken by a neuron to process signals is roughly estimated to be  $T_p = 10$  msec.

Assuming the propagation velocity of action potentials  $v$

$= 9$  m/s and the average length of axons of excitatory neurons  $r = 0.08$  m for cortical neurons in the human brain [58], one can obtain a rough estimate of axonal delay as  $d = 10$  ms. On the other hand, since the firing frequencies of cortical neurons are reported to range from 60 to 200 Hz, assuming 100 Hz gives a spike interval  $T = 10$  ms, which is comparable in order of magnitude with the axonal time delay  $d$ . Such a quite roughly estimated relation  $T \approx d \approx T_p$  seems to be in favor of the result of our study.

A major drawback of our model, however, will be that the appearance of the retrieval phase is limited only for a small value of the relative width of the distribution of time delays  $2\Delta d / (2d_1 + \Delta d)$ .

It should also be noted that the network of spiking neurons for associative memory based on synchronized firing can be approximately viewed as a kind of the standard Little-Hopfield model with discrete time synchronized updating dynamics, as has been shown by the approximate treatment of obtaining the storage capacity. In this sense our model seems to serve as a bridge between the two prototype coding schemes of a neuron. Investigating the problem of how and which of the two schemes of the rate codings and single firing events are chosen for use to optimize the computational capability for a particular task and the problem of possible interrelations between them, if any, are one of the future targets in the direction of our study.

#### ACKNOWLEDGMENT

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#### APPENDIX: BEHAVIOR OF THE PULSE-COUPLED SYSTEM OF TWO FITZHUGH NEURONS WITH THE TIME-DELAYED INTERACTION

We study the behavior of the two FitzHugh neuron system under the pulse-coupled type interaction with time delay. Since in the present paper we consider a system of spiking neurons as an input-driven oscillator system, we assume that without any external input the two FitzHugh neuron system exhibits no oscillations and each neuron remains at its fixed point. The model equation reads

$$V_i = - \left( \frac{V_i^3}{3} - V_i + W_i \right) + I_{syn,i}(t) + I_{ext,i}(t), \quad (A1)$$

$$W_i = \frac{1}{10} (V_i + 1.3), \quad i = 1, 2, \quad (A2)$$

where  $I_{syn,i}(t)$  describes the time-delayed interaction due to an injection of synaptic electric current [in Eq. (7) set  $N = 2$ ,  $J_{12} = J_{21} = 1$ ,  $J_{11} = J_{22} = 0$ ] and  $I_{ext,i}(t)$  denotes an injection of external electric current.

We confine ourselves to investigating qualitative dynamical behaviors with a special type of initial condition and preparation of an initial external current injection that are used in the study of our associative memory model. They are, for instance, given by

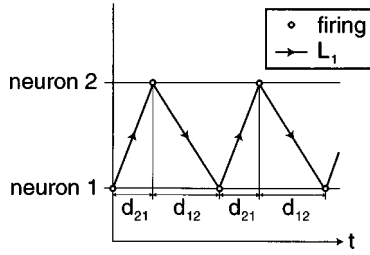


FIG. 15. Schematic diagram representing a series of firing times  $L_1$  of neurons that starts from the initial firing of neuron 1 due to an injection of external current.

$$I_{\text{ext},i}(t) = c \zeta_i \delta(t), \quad \zeta_i = 0 \text{ or } 1, \quad (\text{A3})$$

$$V_i(0_-) = V_{\text{eq}}, \quad (\text{A4})$$

$$W_i(0_-) = W_{\text{eq}}, \quad i = 1, 2, \quad (\text{A5})$$

where  $c$  is a constant and  $(V_{\text{eq}}, W_{\text{eq}})$  denotes the stable fixed point of the FitzHugh neuron dynamics [Eqs. (3) and (4)].

We have substantially two cases according to the number of neurons subjected to the initial injection of pulsed external current for firing.

First, let us assume that only one neuron, say neuron 1, receives an initial input current to fire at time  $t=0$ . After time delay  $d_{21}$  a synaptic electric current (SEC) is induced at the postsynaptic neuron 2 due to the propagated action potential via the interaction between the two neurons. Under the assumption that the magnitude of the SEC is large enough to evoke a spiked firing of the FitzHugh dynamics, there occurs firing of neuron 2 almost at time  $d_{21}$ , if any time delay involved in the transformation from the SEC to the generation of an action potential is negligibly small. The firing of neuron 2 in turn brings about that of neuron 1 after another time delay  $d_{12}$ . Repeating this process, neurons 1 and 2 can continue to fire alternatively, if  $d_{12} + d_{21}$  is larger than the refractory period implicitly given in the FitzHugh dynamics. Then the system exhibits periodic oscillations with period  $d_{12} + d_{21}$ . Figure 15 shows a schematic diagram for a series of firing times of the neurons, which we denote by  $L_1$ , following the initial injection of input current to neuron 1 at time  $t=0$ .

Next, let both of the neurons be forced to fire simultaneously by an initially injected current. One might expect, by following the same reasoning as above, that there appears a superposition of the two firing time series  $L_1$  and  $L_2$  that are generated following the initial injection to neurons 1 and 2,

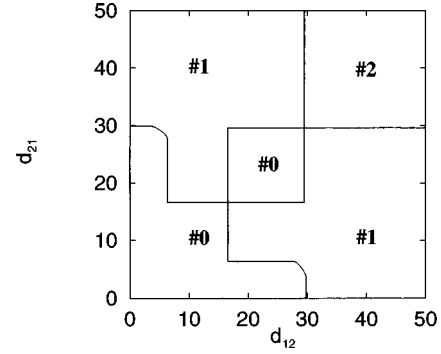


FIG. 16. Schematic phase diagram on the  $d_{12}$ - $d_{21}$  plane displaying each regime of the three types of firing behavior 1 (#0), 2 (#1), 3 (#2) (see text) in the case where both neurons are subjected to initial firings. The phase diagram is drawn based on the result of numerical integrations of Eqs. (A1) and (A2) for  $t_s=5$ ,  $I_{\text{amp}}=20$ .

respectively. This holds true only under a restricted condition that both  $d_{12}$  and  $d_{21}$  be sufficiently large, because of the refractoriness of the FitzHugh dynamics. To see the role played by the refractoriness we will suffice to consider the case where  $d_{21}$  is small enough to satisfy the condition that the effective refractory period of the FitzHugh dynamics be larger than  $d_{21}$ . Then, neuron 2 is prevented from firing too soon, that is, after the time delay  $d_{21}$  from the initial firing due to the injected current. Then the series  $L_1$  turns out to die afterward. Only  $L_2$  can survive in this case.

To summarize the behavior of the two neurons eventually observed for a long time, one has three types of behavior: (1) Neither  $L_1$  nor  $L_2$  is allowed to exist and both neurons get quiescent; (2) only one series of  $L_1$  and  $L_2$  can survive. (3) both  $L_1$  and  $L_2$  can exist. In the case of 2 and 3, the system exhibits synchronized periodic oscillations, though not always of in-phase type. We show in Fig. 16 a typical schematic phase diagram on the  $d_{12}$ - $d_{21}$  plane displaying the appearance of the three types of behavior that are obtained from the result of numerical integrations of the coupled FitzHugh dynamics, Eqs. (A1), (A2), in the case of two neurons with an initial current injection. As far as the stationary property attained for a long time is concerned, the schematic phase diagram depicts a qualitative dynamical behavior of the two-neuron-coupled system. We note, however, that there can occur the case where the time taken during the process of transformation from the SEC to an action potential at a postsynaptic neuron cannot be neglected and exerts an influence on a transient behavior of the system.

[1] J. J. Hopfield, Proc. Natl. Acad. Sci. USA **79**, 2554 (1982).  
 [2] D. J. Amit, H. Gutfreund, and H. Sompolinsky, Appl. Phys. **173**, 30 (1987).  
 [3] M. Shiino and T. Fukai, J. Phys. A **23**, L1009 (1990).  
 [4] R. Kuhn, S. Bos, and J. L. van Hemmen, Phys. Rev. A **43**, 2084 (1991).  
 [5] J. Phys. A **22** (1989).  
 [6] E. Gardner, J. Phys. A **21**, 257 (1988).  
 [7] R. Kuhn and S. Bos, J. Phys. A **26**, 831 (1993).

[8] A. C. C. Coolen and D. Sherrington, Phys. Rev. E **49**, 1921 (1994).  
 [9] T. Fukai and M. Shiino, Phys. Rev. A **42**, 7459 (1990).  
 [10] F. R. Waugh and C. M. Marcus, Phys. Rev. Lett. **64**, 1986 (1990).  
 [11] M. Shiino and T. Fukai, J. Phys. A **25**, L375 (1992).  
 [12] M. Shiino and T. Fukai, Phys. Rev. E **48**, 867 (1993).  
 [13] S. Amari, Neural Networks **2**, 451 (1989).  
 [14] S. Amari and K. Maginu, Neural Networks **1**, 63 (1988).

- [15] M. Okada, *Neural Networks* **9**, 1429 (1996).
- [16] L. F. Cugliandolo and M. V. Tsodks, *J. Phys. A* **27**, 741 (1994).
- [17] M. Griniasty, M. V. Tsodks, and D. J. Amit, *Neural Comput.* **5**, 1 (1993).
- [18] L. F. Cugliandolo, *Neural Comput.* **6**, 220 (1994).
- [19] M. Shiino (unpublished).
- [20] Y. Miyashita and H. S. Chang, *Nature (London)* **331**, 68 (1988).
- [21] M. Yoshioka and M. Shiino, *Phys. Rev. E* **55**, 7401 (1997).
- [22] M. Yoshioka and M. Shiino, *J. Phys. Soc. Jpn.* **66**, 1294 (1997).
- [23] P. Peretto, *J. Phys. (France)* **49**, 711 (1988).
- [24] A. C. C. Coolen and D. Sherrington, *J. Phys. A* **25**, 5493 (1992).
- [25] A. C. C. Coolen and Th. W. Ruijgrok, *Phys. Rev. A* **38**, 4253 (1988).
- [26] M. Shiino, H. Nishimori, and M. Ono, *J. Phys. Soc. Jpn.* **58**, 763 (1989).
- [27] H. Nishimori, T. Nakamura, and M. Shiino, *Phys. Rev. A* **41**, 3346 (1990).
- [28] U. Reidel, R. Kuhn, and J. L. van Hemmen, *Phys. Rev. A* **38**, 1105 (1988).
- [29] T. Fukai and M. Shiino, *Phys. Rev. Lett.* **64**, 1465 (1990).
- [30] R. Eckhorn, R. Bauer, W. Jordan, M. Brosch, W. Kruse, M. Munk, and R. J. Reitboeck, *Biol. Cybern.* **60**, 121 (1988).
- [31] C. M. Gray and W. Singer, *Proc. Natl. Acad. Sci. USA* **86**, 1698 (1989).
- [32] T. Aoyagi and K. Kitano, *Phys. Rev. E* **55**, 7424 (1997).
- [33] A. Arenas and C. J. Perez Vicente, *Europhys. Lett.* **26**, 79 (1994).
- [34] T. Fukai and M. Shiino, *Neural. Comput.* **7**, 529 (1995).
- [35] T. T. Sejnowski, *Nature (London)* **376**, 21 (1995).
- [36] M. Abeles, H. Bergman, E. Margalit, and E. Vaadia, *J. Neurophysiol.* **70**, 1629 (1993).
- [37] S. Thorpe and J. Gautiais, *Advances in Neural Information Processing Systems 10* (Morgan Kaufmann, San Mateo, 1997).
- [38] W. Mass, *Neural. Comput.* **8**, 1 (1996).
- [39] A. L. Hodgkin and A. F. Huxley, *J. Physiol. (London)* **117**, 500 (1952).
- [40] R. FitzHugh, *Biophys. J.* **1**, 445 (1961).
- [41] J. S. Nagumo and Yoshizawa S. Arimoto, *Proc. IRE* **50**, 2061 (1962).
- [42] J. Rinzel (unpublished).
- [43] A. Treves, *Network* **4**, 259 (1993).
- [44] L. Lapique, *J. Physiol. Gen.* **9**, 620 (1907).
- [45] *From Clocks to Chaos: The Rhythm of Life* (Princeton University Press, Princeton, 1988).
- [46] W. Gerstner, R. Ritz, and J. L. van Hemmen, *Biol. Cybern.* **69**, 503 (1993).
- [47] A. V. M. Herz, Z. Li, and J. L. van Hemmen, *Phys. Rev. Lett.* **66**, 1370 (1991).
- [48] A. Treves, E. T. Rolls, and M. W. Simmen, *Physica D* **107**, 392 (1997).
- [49] K. H. Lee, K. Chung, J. M. Chung, and R. E. Coggeshall, *Comp. Neurol.* **243**, 335 (1986).
- [50] J. J. B. Jack, D. Noble, and R. W. Jsiens, *Electric Current Flow in Excitable Cells* (Clarendon Press, Oxford, 1975).
- [51] J. L. van Hemmen and R. Kuhn, *Phys. Rev. Lett.* **57**, 913 (1986).
- [52] M. Shiino, *J. Stat. Phys.* **59**, 1051 (1990).
- [53] D. Hansel, G. Mato, and C. Meunier, *Neural Comput.* **7**, 307 (1995).
- [54] C. van Vreeswijk, L. F. Abbott, and G. B. Ermentrout, *J. Comp. Neurosci.* **1**, 313 (1994).
- [55] W. Gerstner, *Phys. Rev. E* **51**, 738 (1995).
- [56] P. C. Bressloff, S. Coombes, and B. De Souza, *Phys. Rev. Lett.* **79**, 2791 (1997).
- [57] S. J. Thorpe and M. Imbert, *Connectionism in Perspective* (Elsevier, Amsterdam, 1989).
- [58] W. Rall, *J. Neurophysiol.* **30**, 1138 (1967).