Analytical condition for synchrony in a neural network with two periodic inputs

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In this study, we apply a mean-field theory to the neural network model with two periodic inputs in order to clarify the conditions of synchronies. This mean-field theory yields a self-consistent condition for the synchrony and enables us to study the effects of synaptic connections for the behavior of neural networks. Then, we obtain a condition of synaptic connections for the synchrony with the cycle time T. The neurons in neural networks receive sensory inputs and top-down inputs from outside of the network. When the network neurons receive two or more inputs, their synchronization depends on the conditions of inputs. We also analyze this case using the mean-field theory. As a result, we clarify the following points: (i) The stronger synaptic connections enhance the shorter synchrony cycle of neurons. (ii) The cycle of the synchrony becomes longer as the cycle of external inputs becomes longer. (iii) The relationships among synaptic weights, the properties of input trains, and the cycle of synchrony are expressed by one equation, and there are two areas for asynchrony. With regard to the third point, the yielded equation is so simple for calculation that it can easily provide us with feasible and infeasible conditions for synchrony.

DOI: 10.1103/PhysRevE.87.012713

PACS number(s): 87.18.Sn, 87.16.ad

I. INTRODUCTION

Neurons in neural networks interact by synaptic connections. These complex networks, even if they consist of the integrate-and-fire models or the extended models, are very complicated to deal with directly. Up to now, many studies of the neural networks have treated the inputs from another neuron as a stochastic process [1-13]. Because the stochastic process under random noises (namely Langevin forces) is well studied [14], the behavior of a neuron's membrane potential is well analyzed using the Fokker-Planck equation [15] as an Ornstein-Uhlenbeck process [16]. Essentially, however, these stochastic input models approximate the network as a single-neuron model [1-8]. Thus, it is difficult (but not impossible [9-12]) to introduce synaptic connections appropriately into the distribution functions of random inputs.

Recently, Chen and Jasnow [17] introduced the mean-field theory to study synaptic plasticity. In this theory, we need to introduce the "effective input" as a mean value of inputs to a population of several neurons, namely cluster neurons, from outside of the cluster neurons. In particular, Chen and Jasnow [17] focused this virtue of the mean-field theory on the behavior of neural networks driven by Poisson noises with fixed mean frequency for all neurons. In addition, they clarified the relation between the mean firing frequency (or the mean firing rate) and the mean synaptic weight using the self-consistent condition obtained from the mean-field theory [17]. Because the mean-field theory can reduce many synaptic connections to one connection, it enables us to analyze the effects of many synaptic connections in neural networks with ease. When there are a lot of neurons with connections and the input trains are stationary, it is reasonable to apply the mean-field theory to this system [9]. However, the mean-field theory is not applicable when the variance of the values is so large and/or the population size of the variables (synaptic

connections per neuron, for example) are so small that the mean value cannot be regarded as representative. In addition, when we focus on synchronized firings, its stability cannot be discussed from the viewpoint of this mean-field theory because we do not take into account the transient to the steady state. This is one of the limitations of the method.

Biologically, accompanied by visual perception or motor control, coherent oscillations have been reported in the cortices [18–25]. The oscillations are thought to play an important role in the information processing in the cortices [26,27]. For example, precise synchronization among cortical areas suggests visuomotor integration [28]. On the other hand, both feedforward and feedback anatomical projections exist in corticocortical connections [29]. The pyramidal neurons of the superficial layer project to the middle layer of the higher functional region, whereas those of the deep layer project back to the superficial and deep layers [30]. Thus cortical areas are reciprocally connected by feedforward (bottom-up) and feedback (top-down) pathways. The bottom-up signals usually originate from sensory information. Consequently, some cortical regions receive both bottom-up (sensory) and top-down signals [31].

According to the modeling study using a population of neurons that receives bottom-up and top-down periodic inputs with different periods [32], the synchrony of firing often collapses. In other words, the loss of synchronized firings requires remarkably different cycles of inputs. When the differences of the cycle times are small, the loss of synchrony does not occur. When the neurons receive independently fixed periodic inputs, what determines critically if the firings synchronize or not? It is expected that the strength of the synaptic connections has a big effect on synchrony because numerical studies showed that synaptic plasticity evokes synchrony [33,34]. Taken together, generally, synchrony depends on the synaptic connections as well as the periods of inputs.

Thus the purpose of our study is to understand the effects of input trains such as amplitude and period, and synaptic connections on the synchrony of neural networks, using the mean-field theory. For convenience of applying this

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framework, we regard the state in which two neurons fire with the same period as synchronous in this paper. Thus, although this synchrony does not require simultaneous firings, so-called synchrony never occurs if this synchrony does not occur. Before we try to achieve this aim, we discuss two more fundamental cases, that is, connected neurons without input trains and a single neuron receiving periodic inputs.

In Sec. II, we apply the mean-field theory for the simplest neural network without external inputs. We assume that this network can be represented by a cluster consisting of only two integrate-and-fire model neurons. This analysis clarifies that the stronger synaptic connections enhance the shorter cycle synchrony cycle of cluster neurons. In Sec. III, we consider the cycle of synchrony when one periodic external input is provided to a neuron. The result shows that the cycle of the synchrony becomes longer as the cycle of external inputs becomes longer. In Sec. IV, we describe that the network receiving two different cycle inputs (which are supposed to be bottom-up inputs and top-down inputs) shows the loss of synchronies in certain conditions.

II. MEAN-FIELD THEORY WITH EFFECTIVE INPUTS

In this section, using our formulation, we discuss a periodic synchronized firing of neurons located in the same cortical region. At first, to simplify many neurons connected complicatedly, we assume that two particular neurons *i* and *j* with a synaptic connection from *j* to *i* represent "cluster neurons." The membrane potentials are denoted as $V_i(t)$ and $V_j(t)$, respectively. The neuron *j* receives inputs from other neurons located outside the cluster. The effective value (mean value) of the inputs is assumed to be an "effective input" I_{eff} . This approximation is illustrated in Fig. 1. After the firings of neuron *j* through the synaptic weight w_{ij} . Thus, we can obtain the effective equations of the membrane potentials $V_i(t)$ and $V_j(t)$ as follows:

 $\tau \frac{d}{dt} V_j(t) = -V_j(t) + I_{\text{eff}}$

and

$$\tau \frac{d}{dt} V_i(t) = -V_i(t) + \sum_{j=1}^c \tau w_{ij} \sum_k \delta(t - t_j^k), \qquad (2)$$

where the parameters τ , c, and t_j^k denote the time constant, the number of connections, and the *k*th firing time of neuron j, respectively. Here, we assumed that I_{eff} is constant because the number of inputs from outside of the cluster is so large that the time average corresponds to the population average.

From Eq. (1), the membrane potential $V_i(t)$ is obtained as

$$V_i(t) = I_{\text{eff}}(1 - e^{-t/\tau}).$$
 (3)

Then we obtain the firing time $t_j^k = kT_j$ using the effective input I_{eff} as

$$T_j = -\tau \log \frac{I_{\rm eff} - \theta}{I_{\rm eff}} \tag{4}$$

with the threshold θ . Here, for convenience of calculations, we use a simple condition that the resting potential and the reset potential after firing take the same value of 0. In our



FIG. 1. (Color online) We show the essential figure to clarify the meaning of effective inputs. In our study, inputs from outside of the cluster neurons *i* and *j* [whose membrane potentials are denoted as $V_i(t)$ and $V_j(t)$] are assumed to be the effective inputs I_{eff} . We focus on the neurons *i* and *j* with I_{eff} . The self-consistency Eq. (7) requires the correspondence between output signals of the neuron *i* (namely I_{out}) and input signals to the neuron *j* (namely I_{eff}). Consequently, the self-consistency requires the global transition symmetry of the neural network. This approximation is part of the mean-field theory.

study, using the integrate-and-fire model, we assume that the membrane potentials reset their potential $V_i(t)$ and $V_j(t)$ for the reset potential $V_0 = 0$ after firing immediately.

The time dependence of $V_i(t)$ is derived from Eq. (2) under the firing of the *j*-neuron satisfying Eq. (4) as follows:

$$V_{i}(t) = \frac{1}{\tau} e^{-t/\tau} \int_{0}^{t} e^{s/\tau} \sum_{j=1}^{c} \tau w_{ij} \sum_{k} \delta(s - t_{j}^{k}) ds$$
$$= W \frac{1 - e^{-t/\tau}}{1 - e^{-T_{j}/\tau}},$$
(5)

(1)

where the parameter $W = \sum_{j} w_{ij}$ means the total synaptic weight. Then, we obtain the cycle-time T_i of the *i*-neuron's firings as

$$T_i = -\tau \log \left[1 - \frac{\theta}{W} (1 - e^{-T_j/\tau}) \right].$$
(6)

Now, we consider the self-consistency $I_{\text{eff}} = I_{\text{out}}$ (the mean output of the neuron *i* is denoted as I_{out} in Fig. 1),

$$I_{\text{eff}} = \frac{1}{T_0} \int_0^{T_0} ds \sum_{j=1}^c \tau w_{ij} \sum_k \delta(s - t_i^k)$$
$$\simeq \frac{\tau}{T_0} \sum_{j=1}^c w_{ij} \sum_{k=1}^{T_0/T_i} \int_0^{T_0} ds \,\delta(s - kT_i) = \frac{\tau}{T_i} W. \quad (7)$$

This consistency assumes that the firings of neurons are periodic and synchronized. Thus the value of I_{eff} should indicate the mean value of the periodic inputs. The formula of I_{eff} in Eq. (7) looks plausible because it corresponds to the assumed mean value of inputs with periodicity in the mean-field theory of previous studies [10–12]. We assumed the hypothetical cycle time T_i of the effective inputs. Then, if the periodic firings can occur, we can find the appropriate cycle time T_i . But if there does not exist the cycle time T_i , the periodic firings cannot occur. This condition for the T_i is expressed in the self-consistency Eq. (7).

From Eqs.(4), (6), and (7), we obtain the self-consistent equation as

$$\frac{\tau}{T}(1 - e^{-T/\tau}) = \left(\frac{\theta}{W}\right)^2,\tag{8}$$

where we have redefined $T = T_i$. The cycle time T of spontaneous firing of the cluster neurons is given as a solution of Eq. (8). The function $f(T/\tau)$ is defined as the left-hand side of Eq. (8), namely $f(T/\tau) = (\tau/T)(1 - e^{-T/\tau})$. The function $f(T/\tau)$ can be expanded as

$$f(T/\tau) = \frac{\tau}{T} (1 - e^{-T/\tau})$$
$$= \frac{\tau}{T} \left\{ 1 - \left[1 - \left(\frac{T}{\tau} \right) + \frac{1}{2} \left(\frac{T}{\tau} \right)^2 - \cdots \right] \right\}$$
$$= 1 - \frac{1}{2} \left(\frac{T}{\tau} \right) + \cdots,$$
(9)

with respect to T/τ . Then, the function $f(T/\tau)$ has the asymptotic value 1 in the case of $T \to 0$ (namely the frequency $\nu = 1/T \to \infty$). Consequently, in the case of $\theta > W$, there does not exist the spontaneous firing. On the other hand, in the case of $\theta < W$, there does exist the spontaneous firing. This result is supported by the following physical phenomena, that is, the firing frequency of neurons is enhanced by effective inputs (from neighbor neurons) exceeding the threshold. Meanwhile the spontaneous firing does not occur under the weak effective inputs.

III. A SINGLE NEURON FIRING WITH A PERIODIC INPUT TRAIN

In this section, we consider the case of a single neuron receiving a periodic input train. This simple example may be useful to discuss the specific cases of the neural networks including the connections and input trains. The membrane potential $V_i(t)$ of neuron *i* is characterized as follows:

$$\tau \frac{d}{dt} V_i(t) = -V_i(t) + I(t), \qquad (10)$$

where the input train I(t) is denoted by

$$I(t) = \tau I_0 \sum_{k: \text{ all past firings}} \delta(t - t_k), \quad t_k = \lambda + k T^{\text{in}}.$$
(11)

Here the parameter T^{in} means the cycle time of periodic input trains and λ means a firing phase (time lag). λ is the initial phase in a cycle so that the next firing time shifts linearly with λ .

From Eqs. (10) and (11), the time dependence $V_i(t)$ is obtained as

$$V_i(t) = I_0 e^{\lambda/\tau} \frac{e^{-t/\tau} - e^{-\lambda/\tau}}{1 - e^{T^{\text{in}}/\tau}} \quad (t < T_i),$$
(12)

where T_i denotes the firing cycle of the *i*-neuron. Then the condition for the firing $V_i(t) = \theta$ (θ means the threshold) gives the firing cycle $T = T_i$ as

$$T = \lambda - \tau \log \left[1 + \frac{\theta}{I_0} (1 - e^{T^{\text{in}}/\tau}) \right].$$
(13)

The derivative dT/dT^{in} is derived as

$$\frac{dT}{dT^{\rm in}} = \frac{\theta e^{T^{\rm in}/\tau}}{I_0 + \theta(1 - e^{T^{\rm in}/\tau})} = \frac{1}{e^{(T_{\rm c} - T^{\rm in})/\tau} - 1} \simeq \frac{\tau}{T_{\rm c} - T^{\rm in}}$$
(14)

for the condition $T_c \simeq T^{in}$, where T_c is defined as $T_c = \tau \log(1 + I_0/\theta)$. Here the function T of T^{in} is defined in the region $0 < T^{in} < T_c$ in Eq. (13), so that Eq. (14) shows that the firing cycle T diverges exponentially with increase of T^{in} . From the above discussion, the firing cycle depends on the cycle time of input trains as a monotonically increasing function.

IV. LOSS OF SYNCHRONY WITH TWO EXTERNAL INPUTS

In the previous discussions in Secs. II and III, the stronger synaptic connections yield the synchrony with the shorter cycle, while the longer cycle input train yields the longer cycle synchrony. Thus, one can predict catastrophes of synchrony if periodic spikes with a longer (or shorter) period are input to the neurons with stronger (or weaker) synaptic weights. This is the reason why the relationship between the synaptic connections and the cycle of inputs under the condition of synchrony in the neural networks is not so simple. In this section, we examine the neural network receiving two external periodic inputs. To clarify this condition and related phenomena analytically, we apply the mean-field theory to the cluster neurons i and j in the network with two external inputs, namely $J_1(t)$ and $J_2(t)$. These two external inputs $J_1(t)$ and $J_2(t)$ have the independent cycle T_1^{in} and T_2^{in} , respectively, and the time dependence of these inputs is expressed as

$$J_l(t) = \tau J_0 \sum_k \delta\left(t - \left(\lambda + kT_l^{\text{in}}\right)\right) \quad (l = 1, 2).$$
(15)

Here J_0 means the strength of inputs. In this study, we assume that the two external inputs have common strength. These input trains are constructed by independent Poisson processes, whose mean interstimulus interval is λ . For the convenience of analysis, these input trains are averaged over the period from $t = kT_1^{\text{in}}$ (or kT_2^{in}) to $t = (k+1)T_1^{\text{in}}$ [or $(k+1)T_2^{\text{in}}$]. This averaging procedure does not lose the periodicity of input trains.

These inputs are received by the cluster neurons i and j as a total external input,

$$J(t) = pJ_1(t) + (1-p)J_2(t).$$
 (16)

The parameter *p* denotes the rate of the input $J_1(t)$, which implies the balance ratio (relative strength) of the two inputs. For example, in the case of p = 0.5, both inputs $J_1(t)$ and $J_2(t)$ have the same intensity of the input current. When p > 0.5, $J_1(t)$ has a stronger intensity than $J_2(t)$. From the above discussion, we obtain the effective equations of motion about the cluster neurons as follows:

$$\tau \frac{d}{dt} V_j(t) = -V_j(t) + I_{\text{eff}} + J(t)$$
(17)

and

$$\tau \frac{d}{dt} V_i(t) = -V_i(t) + \sum_j \tau w_{ij} \sum_{\substack{t_j^k < t}} \delta\left(t - t_j^k\right) + J(t).$$
(18)

We assumed that I_{eff} is constant because a large number of synaptic inputs to each neuron will cancel out the periodicity of input signals except the external inputs. From Eq. (17), the membrane potential $V_i(t)$ is obtained as

$$V_j(t) = I_{\text{eff}}(1 - e^{-t/\tau}) + \frac{1}{\tau} e^{-t/\tau} \int_0^t J(s) e^{s/\tau} ds$$
(19)

with using the effective input I_{eff} . The integration shown in the second term of Eq. (19) is performed as follows:

$$\int_{0}^{t} J(s)e^{s/\tau}ds = \tau p J_{0} \sum_{t_{j}^{k} < t} \int_{0}^{t} e^{s/\tau} \delta\left(s - \left(\lambda + kT_{1}^{\text{in}}\right)\right) ds + \tau(1-p) J_{0} \sum_{t_{j}^{k'} < t} \int_{0}^{t} e^{s/\tau} \delta\left(s - \left(\lambda + k'T_{2}^{\text{in}}\right)\right) ds$$

$$= \tau p J_{0} \sum_{k=0}^{(t-\lambda)/\tau} e^{(\lambda + kT_{1}^{\text{in}})/\tau} + \tau(1-p) J_{0} \sum_{k=0}^{(t-\lambda)/\tau} e^{(\lambda + k'T_{2}^{\text{in}})/\tau} = \tau p J_{0} e^{\lambda/\tau} \frac{1 - e^{(t-\lambda)/\tau}}{1 - e^{T_{1}^{\text{in}}/\tau}} + \tau(1-p) J_{0} e^{\lambda/\tau} \frac{1 - e^{(t-\lambda)/\tau}}{1 - e^{T_{2}^{\text{in}}/\tau}}.$$
(20)

Then the condition to determine the firing cycle T_j of the neuron j is obtained as

$$\theta = I_{\text{eff}}(1 - e^{T_j/\tau}) - J_0 \left[pg(T_1^{\text{in}}) + (1 - p)g(T_2^{\text{in}}) \right] \\ \times (1 - e^{-(T_j - \lambda)/\tau})$$
(21)

with the negative function $g(t) = 1/(1 - e^{t/\tau})$. The time dependence of $V_i(t)$ is derived from Eq. (18) as follows:

$$V_i(t) = W \frac{1 - e^{t/\tau}}{1 - e^{-T_j/\tau}} + \frac{1}{\tau} e^{-t/\tau} \int_0^t J(s) e^{s/\tau} ds.$$
(22)

The time dependence of $V_i(t)$ yields the condition to determine the firing cycle T_i of the *i*-neuron as

$$\theta = W \frac{1 - e^{-T_i/\tau}}{1 - e^{-T_j}} - J_0 \Big[pg \big(T_1^{\text{in}} \big) + (1 - p)g \big(T_2^{\text{in}} \big) \Big] \\ \times (1 - e^{-(T_i - \lambda)/\tau}).$$
(23)

From solving Eq. (21) with respect to T_j and inserting into Eq. (23), when the cycle time $T = T_i$ satisfies the self-consistent condition (7), namely $I_{\text{eff}} = \tau W/T_i$, the cluster neurons show the synchronized firings. The self-consistency is transcribed in more detail as

$$1 = \alpha (1 - e^{-x}) \frac{\alpha/x - j(T_1^{\text{in}}, T_2^{\text{in}}) e^{\lambda/\tau}}{1 + j(T_1^{\text{in}}, T_2^{\text{in}})(1 - e^{\lambda/\tau})} - j(T_1^{\text{in}}, T_2^{\text{in}})(1 - e^{\lambda/\tau - x}),$$
(24)

where $\alpha = W/\theta$, $j(T_1^{\text{in}}, T_2^{\text{in}}) = [pg(T_1^{\text{in}}) + (1 - p)g(T_2^{\text{in}})]$ J_0/θ , and $x = T/\tau$. These parameters are normalized by θ or τ . The function $j(T_1^{\text{in}}, T_2^{\text{in}})$ takes a negative value for any T_1^{in} and T_2^{in} and tends to zero as T_1^{in} or T_2^{in} tends to infinity (Fig. 2). The important parameters of input trains, namely the strength of inputs J_0 and the input balance p as well as T_1^{in} and T_2^{in} , are included in the function $j(T_1^{\text{in}}, T_2^{\text{in}})$. Then the behavior of this parameter expresses the property of input trains; therefore, we treat the parameter $j(T_1^{\text{in}}, T_2^{\text{in}})$ as a continuous real number defined in the region $(-\infty, 0)$ for characterizing the input trains. The parameter x in Eq. (24) corresponds to the cycle time of synchrony of cluster neurons. Unfortunately, one



FIG. 2. (Color online) The parameter $j(T_1^{\text{in}}, T_2^{\text{in}})$ divided by J_0/θ is shown when p = 0.8. $j(T_1^{\text{in}}, T_2^{\text{in}})$ tends to zero as T_1^{in} or T_2^{in} tends to infinity.



FIG. 3. (Color online) The firing cycle of cluster neurons: The firing cycle $x \equiv T/\tau$ is shown in the $[\alpha, j(T_1^{\text{in}}, T_2^{\text{in}})]$ space. The large $j(T_1^{\text{in}}, T_2^{\text{in}})$ corresponds to the long cycle input(s) as is shown in Fig. 2. Region 1 shows that the synchrony does not occur because strong synaptic connections (large α) conflict with the long cycle inputs [large $j(T_1^{\text{in}}, T_2^{\text{in}})]$. In region 2, the firing cycle *x* diverges exponentially with an increase of $j(T_1^{\text{in}}, T_2^{\text{in}})$. Here $\lambda/\tau = 1.3$.

cannot solve the condition Eq. (24) rigorously with respect to x. Therefore, we have solved it numerically as shown in Fig. 3.

As shown in Fig. 3, there are two typical anomalies of synchronies where the value of x cannot exist. First, in the region of larger α (stronger synaptic connections) and larger $j(T_1^{\text{in}}, T_2^{\text{in}})$ (longer cycle of external inputs), the shorter cycle synchrony enhanced by strong synaptic connections conflicts with the longer cycle of external inputs. We call this region "region 1." Second, in the region of smaller α (weaker synaptic connections) and larger $j(T_1^{\text{in}}, T_2^{\text{in}})$, the cycle time of the synchrony increases exponentially with increasing cycle time of inputs. We call this region "region 2."

The limiting cases of Eq. (24) clarify "region 1" and "region 2" in Fig. 3. In the case of $x \rightarrow 0$, Eq. (24) yields the relation

$$j(T_1^{\text{in}}, T_2^{\text{in}}) = \frac{1-\alpha}{e^{\lambda/\tau} - 1} \equiv h_0(\alpha, \lambda, \tau).$$
(25)

On the other hand, in the case of $x \to \infty$, Eq. (24) yields the relation

$$j(T_1^{\text{in}}, T_2^{\text{in}}) = -\frac{2}{2 + (\alpha - 1)e^{\lambda/\tau} + \sqrt{[4\alpha + (\alpha - 1)^2 e^{\lambda/\tau}]e^{\lambda/\tau}}}$$
$$\equiv h_{\infty}(\alpha, \lambda, \tau).$$
(26)

Then in region 1, the parameters $j(T_1^{\text{in}}, T_2^{\text{in}})$ and α satisfy the inequality

$$j(T_1^{\rm in}, T_2^{\rm in}) > h_0(\alpha, \lambda, \tau), \qquad (27)$$

while in region 2 they satisfy the inequality

$$j(T_1^{\text{in}}, T_2^{\text{in}}) > h_{\infty}(\alpha, \lambda, \tau).$$
(28)

Using Eqs. (27) and (28), we obtain the phase diagram as shown in Fig. 4. The phase boundaries are expressed by Eqs. (25) and (26). As is shown in Fig. 4, the synchrony



FIG. 4. (Color online) Phase diagram of synchrony: The condition obtained in Eqs. (27) and (28) is illustrated. The horizontal axis denotes the parameter α while the vertical axis denotes the parameter $j(T_1^{\text{in}}, T_2^{\text{in}})$. Here $\lambda/\tau = 1.3$. Regions 1 and 2 correspond to those in Fig. 3. In region 1 the firing cycle vanishes, while the firing cycle diverges in region 2.

occurs only in the outside of Region $1 \cup$ Region 2. This simple conditional equation can provide us with the feasibility of synchrony. From the derivation of Eqs. (25) and (26), it is clearly understood that there are two types of loss of the synchrony, that is, the firing cycle vanishes (region 1) and the firing cycle diverges (region 2). In the intersection region of regions 1 and 2, either type of synchrony loss can occur, which will be affected by the initial conditions, the boundary conditions, noises, or other factors.

V. SUMMARY AND DISCUSSION

We have shown that the synchrony of neurons depends on the conditions between the cycle times of inputs and the amount of strength of the synaptic connections, and that the synchrony collapses when they (the cycle time of inputs and the amount of synaptic connections) do not satisfy the condition. To obtain the conditions for synchronized firings, we have used the mean-field theory. The solution of the self-consistent conditions corresponds to the cycle time of synchrony. When the conditions are constructed by indeterminate equations, such parameter regions show the loss of synchronies. As a result, there are two critical cases for synchrony:

(i) When the synaptic connections are weaker enough and the cycle times of external inputs are longer enough, the frequency of synchronized firings becomes too small to observe.

(ii) The conflicts between stronger synaptic connections (which lead to the shorter cycle synchrony) and a longer cycle of external inputs result in the loss of synchronized firings of the cluster neurons.

The results mean that the synchronization in a population of neurons will never occur when the parameters are in the critical regions. From the viewpoint of information processing in the brain, this discussion suggests that a cortical region works when the synaptic structure matches the bottom-up and top-down signals. Generally, this mean-field theory is applicable to many neuron models (for example, the Hodgkin-Huxley model, as is suggested by Chen and Jasnow [17]). Because of this universality of the mean-field theory, the same results may be obtained from other neural network models.

In this study, we assume that a cluster of a number of neurons can be stochastically represented as two neurons, as shown in Fig. 1. If we assume three or more representative neurons as the cluster, are the results in this study still available? There are two factors to affect the availability. First, they may depend on the structure of synaptic connections between the neurons. When the neurons are fully connected with each other, the results will be similar because of homogeneity. However, other cases with some neurons with heterogeneous connections are too complicated to be analyzed by our method. Secondly, when the ratio of the number of neurons to the number of connections is larger, it becomes difficult for the synchrony to occur under the same condition. This is because the fluctuations of internal states of neurons become larger. Consequently, our approximation is applicable when the ratio of the number of neurons to the number of connections is not so large and the connections are homogeneous.

Finally, we would like to discuss the correspondence between the mean-field theory and the Bethe approximation

[35]. From the viewpoint of statistical mechanics, the Bethe approximation has been introduced to analyze magnetic materials. It is very difficult to analyze the magnetization because many spins interact with each other in the magnetic materials. Bethe has introduced the effective theory to approximate in order to simplify the systems. In the Bethe approximation, we choose some spins from huge spins and call them a "cluster." Then we ignore the spins on the outside of the cluster in spite of introducing the effective field interacting with the boundary spins of the cluster. The intracluster interactions can be analyzed rigorously since the cluster system is of finite size. Here the effective fields are determined by self-consistency, that is, the bulk system corresponds to the surface system. While Bethe approximations are introduced in the equilibrium systems, Chen and Jasnow or we used the mean-field theory in the neural networks as a nonequilibrium system. However, this mean-field theory will lead to appropriate results even in the time-dependent systems as far as the effective input $I_{\rm eff}$ is appropriate. As is also discussed in Sec. I, this mean-field theory can treat the synaptic connections rigorously between the cluster neurons. This is why it is useful to discuss the effects of synaptic connections. Using this mean-field theory, one may be able to clarify the other phenomena and the effects of synaptic connections in the neural networks.

- [1] G. L. Gerstein and B. Mandelbrot, Biophys. J. 4, 41 (1964).
- [2] R. B. Stein, Biophys. J. 5, 173 (1965).
- [3] R. B. Stein, Biophys. J. 7, 37 (1967).
- [4] W. H. Calvin and C. F. Stevens, J. Neurophysiol. 31, 574 (1968).
- [5] H. L. Bryant and J. P. Segundo, J. Physiol. 260, 279 (1976).
- [6] Z. F. Mainen and T. J. Sejnowski, Science 268, 1503 (1995).
- [7] D. H. Perkel, G. L. Gerstein, and G. P. Moore, Biophys. J. 7, 391 (1967).
- [8] D. H. Johnson, J. Comput. Neurosci. 3, 275 (1996).
- [9] A. N. Burkitt, Biol. Cybern. 95, 1 (2006).
- [10] D. J. Amit and M. V. Tsodyks, Network 2, 259 (1991).
- [11] D. J. Amit and N. Brunel, Cereb. Cortex 7, 237 (1997).
- [12] N. Brunel, J. Comput. Neurosci. 8, 183 (2000).
- [13] H. C. Tuckwell, Introduction to Theoretical Neurobiology (Cambridge University Press, Cambridge, 1988).
- [14] A. Einstein, Ann. Phys. (NY) 17, 549 (1905).
- [15] H. Risken, *The Fokker-Plank Equation*, 2nd ed. (Springer, New York, 1989).
- [16] G. E. Uhlenbeck and L. S. Ornstein, Phys. Rev. 36, 823 (1930).
- [17] C. C. Chen and D. Jasnow, Phys. Rev. E **81**, 011907 (2010).
- [18] M. Petrides, B. Alivisatos, A. C. Evans, and E. Meyer, Proc. Natl. Acad. Sci. USA 90, 873 (1993).
- [19] C. S. Carter, M. M. Botvinick, and J. D. Cohen, Rev. Neurosci. 10, 49 (1999).
- [20] W. J. Gehring and R. T. Knight, Nat. Neurosci. 3, 516 (2000).
- [21] R. Rodriguez, U. Kallenbach, W. Singer, and M. H. Munk, J. Neurosci. 24, 10369 (2004).

- [22] G. Buzsaki, *Rhythms of the Brain* (Oxford University Press, Oxford, 2011).
- [23] S. Ohara, T. Mima, K. Baba, A. Ikeda, T. Kunieda, R. Matsumoto, J. Yamamoto, M. Matsuhashi, T. Nagamine, K. Hirasawa, T. Hori, T. Mihara, N. Hashimoto, S. Salenius, and H. Shibasaki, J. Neurosci. 21, 9377 (2001).
- [24] C. M. Gray, P. König, A. K. Engel, and W. Singer, Nature (London) 338, 334 (1989).
- [25] D. Lee, J. Neurosci. 23, 6798 (2003).
- [26] A. K. Engel, P. Fries, and W. Singer, Nat. Rev. Neurosci. 2, 704 (2001).
- [27] P. Fries, Annu. Rev. Neurosci. 32, 209 (2009).
- [28] P. R. Roelfsema, A. K. Engel, P. König, and W. Singer, Nature (London) 385, 157 (1997).
- [29] G. M. Shepherd, *The Synaptic Organization of the Brain*, 5th ed. (Oxford University Press, Oxford, 2004).
- [30] D. J. Felleman and D. C. van Essen, Cereb. Cortex 1, 1 (1991).
- [31] J. M. Fuster, *Physiology of Executive Functions: The Perception-Action Cycle (Principles of Frontal Lobe Function)*, edited by D. T. Stuss and R. T. Knight (Oxford University Press, Oxford, 2002).
- [32] O. Araki, Lect. Notes Comput. Sci. 6443, 231 (2010).
- [33] K. Kitano and T. Fukai, Learn. Mem. 11, 267 (2004).
- [34] R. Hosaka, O. Araki, and T. Ikeguchi, Neural Comput. 20, 415 (2008).
- [35] M. Suzuki, Coherent-Anomaly Method: Mean Field, Fluctuations and Systematics (World Scientific, Singapore, 1995).