Synchronization of pulse-coupled excitable neurons

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Collective behavior of pulse-coupled oscillatory neurons has been investigated widely. In many cases, however, real neurons are intrinsically not oscillatory but excitable. The networks of excitable neurons can have their own characteristic dynamics, and they are of interest also from the viewpoint of functional assemblies. In the present paper, the collective behavior of pulse-coupled excitable neurons has been investigated using phase description. It is shown that full synchronization is achieved in networks of excitable leaky integrate-and-fire neurons and discrete-time Nagumo–Sato neurons. The cooperative roles of external spike inputs, decay of internal states, and feedback spikes are explained. Enhancement of synchronization by refractoriness and noise is also reported.

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I. INTRODUCTION

Investigations in various fields have observed the synchrony of coupled elements such as synchronous firing of neurons [1–4] and the synchronous flashing of tropical fireflies [5]. Particularly, synchronous firing of cortical neurons has been widely studied both by physiological experiments and by model analysis. Eckhorn *et al.* [1] and Gray *et al.* [2] investigated the synchronous firing of neurons in cat primary visual cortex, and found that neurons that have the same preferred stimulus are likely to synchronize. It is pointed out that synchronization can serve as a mechanism for representing coherent features such as objects and motions. The synchronized neurons driven by a common preferred stimulus form a dynamical functional assembly. Vaadia *et al.* [3] showed that the correlations between firing neurons in the frontal cortex are modulated by behavioral tasks, and Rodriguez *et al.* [4] suggested that synchronized gamma oscillations (30–80 Hz) in neuronal discharge play an important role in human perception, contributing to feature binding. The neurons that belong to a certain assembly can desynchronize to join different assemblies when another stimulus comes. Synchronization is also important with regard to the information coding; the coding of information with synchronous firing can be robust against noises and disorder in a small number of neurons. Many theoretical and numerical investigations of synchronization have been motivated by these biological evidences for synchronization, and also by various physical and chemical oscillation phenomena.

The investigations of the synchronization began with the analysis of oscillators coupled by gap junctions or mean field [6–10]. Pulse-coupled neural networks, however, have attracted more attention these days since neurons usually interact by sending and receiving spikes. Peskin [11] derived the synchronization condition for two pulse-coupled model neurons. Mirollo and Strogatz [12], and Kuramoto [13] applied phase reduction technique [14], to extend the results in Ref. [11]. They showed that, for almost all initial conditions, full synchronization is achieved in pulse-coupled networks of leaky integrate-and-fire (LIF) neurons. Although their models are too simple to represent the behavior of biological neurons, these approaches were the important starting points of studying pulse-coupled neural networks. Then these results have been extended to various neuron models: neurons with a constant positive delay [15–17], or a delay given by α-function [15,16,18–22], linear neurons [23–25], neurons linked by inhibitory coupling [15,20,22,26–28], neurons linked by nonuniform coupling [15,19,21,25,29], heterogeneous neurons [18,23–25,30], and neurons linked by generalized coupling with delay [31]. The spike response model [7] has also been studied to investigate the collective behavior of neural networks. 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 [17,22,27,32,33], stable asynchronous behavior [18,20,34], bursting [20], and traveling waves [16,19–21] have also been found in other situations.

In some works, a single neuron was assumed to be an inherent oscillator even without feedback spikes from other neurons [12,13,16–27,29,30,34]. The inherent oscillations are induced by external bias. Biological neurons are, however, more naturally quiescent with the resting potential and excitable for suprathreshold stimuli rather than spontaneously oscillatory.

The dynamics of some networks of excitable neurons is considered to resemble that of oscillatory ones driven by external biases and feedback inputs [20], based on approximation of the spike inputs to excitable neurons by the corresponding continuous inputs to oscillatory neurons. Nevertheless, it is worth studying pulse-driven neurons in particular. Networks of excitable neurons can be regarded as a model of a certain functional assembly of cortical neurons that are receiving feedback spikes from other neurons. Consequently, the properties of the inputs can be different from those of the continuous counterparts that are often identified with external stimuli. Furthermore, excitable systems can have peculiar dynamics different from oscillatory systems. It is also possible that modulated interspike intervals of spike timings represent the signal information in spatiotemporal spike coding schemes to be engaged in information processing in neural

systems [31,35]. Excitable systems are also related to asynchronous computation in which the elements exchange interactive spikes asynchronously to carry out information processing.

In the work reported in this paper, we study networks of excitable but not intrinsically oscillatory neurons. The excitable neurons that fire with the help of external spikes in addition to feedback interactions are considered. These neurons are different from those in Refs. [20,36] whose firing is mainly based on feedback interactions.

We investigate the collective dynamics of these networks by using phase reduction methods [8,14,32,33,37], and unify the descriptions of oscillatory and excitable systems. We deal here with two neuronal models. In Sec. III we show that coupled excitable LIF neurons [17,36,38,39] synchronize based on the similar mechanism to that of oscillatory ones. The effects of noise and refractoriness are also examined. We then investigate networks of Nagumo–Sato (NS) neurons [40] in Sec. IV. The NS neuron are discrete in time and can be regarded as both oscillatory and excitable. Our purpose in considering this model is to present a method to unify discrete-time systems and continuous-time systems with the help of phase description. We show a mechanism that leads to full synchronization in coupled NS models. Noise-induced synchronization is also observed.

II. PULSE-COUPLED OSCILLATORY LEAKY INTEGRATE-AND-FIRE NEURONS

Mirollo and Strogatz [12], and Kuramoto [13] showed that pulse-coupled identical oscillatory LIF neurons eventually synchronize under almost any initial condition. Although we are interested in excitable systems in this paper, we briefly review their results because we will be defining the phase variable of an excitable LIF neuron in comparison with that of an oscillatory LIF neuron. The dynamics of an oscillatory LIF neuron can be represented by

$$\frac{dx}{dt} = I_0 - \gamma x, \tag{1}$$

where x is the internal state corresponding to the membrane potential, γ is the leak rate, and I_0 is the external bias with $I_0 > \gamma$. The external input is implicitly assumed to be continuous. When x exceeds the given threshold, the neuron fires and x is reset to the resting potential. Without losing generality, the threshold and the resting potential can be set equal to 1 and 0, respectively. The period T of the firing is given by

$$T = \frac{1}{\gamma} \ln \frac{I_0}{I_0 - \gamma}.$$

Mirollo and Strogatz [12] examined a network of pulse-coupled N neurons in which a firing neuron sends a spike of amplitude ϵ to all the other neurons. They assumed instantaneous interactions, common external input I_0 to all the neurons, and uniform all-to-all couplings. To clarify the dynamics of individual neurons, they introduced the phase variable $\phi \in [0,1]$. ϕ corresponds to x in a one-to-one manner, and the transformation is given by

$$\phi = g(x) = \gamma^{-1} \ln \frac{C}{C - x}, \tag{2}$$

where $C = (1 - e^{-\gamma})^{-1}$. It follows that $g(0) = 0$, $g(1) = 1$, and

$$\frac{d\phi}{dt} = \frac{1}{T}. \tag{3}$$

The phase of a neuron receiving a spike from another neuron jumps from ϕ to $\tau(\phi)$, and the phase return map $\tau(\phi)$ is expressed as

$$\tau(\phi) = g[g^{-1}(\phi) + \epsilon] = \phi - \frac{1}{\gamma} \ln\{1 - \epsilon e^{\gamma\phi}(1 - e^{-\gamma})\}. \tag{4}$$

We outline the typical behavior of N neurons along [12]. First, the convexity of $g^{-1}(\phi)$ ($g^{-1\prime} > 0$ and $g^{-1\prime\prime} < 0$) is essential, and it leads to

$$\frac{d\tau}{d\phi} = \frac{1}{1 - \frac{\epsilon}{C} e^{\gamma\phi}} > 1. \tag{5}$$

We denote the phase variable of the ith neuron by ϕ_i. The aggregated dynamics is equivalent to the dynamics of $\Phi = (\phi_1, \phi_2, \ldots, \phi_N)$ on a N-dimensional torus. Φ has neutral stability almost everywhere because of Eq. (3). Φ evolves with local instability when a stimulating spike is emitted from a neuron; $N-1$ ϕ_i's correspond to the recipients of the spike, and they have local expansiveness owing to Eq. (5). Consequently, the trajectory of Φ is essentially repulsive. Φ travels ergodically on the torus until it comes into an attractive basin of absorption [12], where multiple ϕ_i's are coalesced into an identical value. After absorption, the virtual dimension of Φ is decreased since once the two phase values become equal, they remain equal forever. N neurons finally synchronize by repeating this procedure.

Since synchronous firing with more neurons drives the system to synchrony more strongly. As a result, full synchronization is achieved in an accelerated manner. This phenomenon is called avalanche.

We note that, owing to Eq. (5), two trajectories starting from two close points on the N-dimensional torus may take quite different courses to synchronization. Full synchronization is ensured by orbital ergodicity combined with absolute absorption. This is in contrast with ubiquitous synchronization scenarios in which local stability assures synchronization. The synchronization conditions have been widely discussed and extended to various neural networks (see Sec. I).

III. PULSE-COUPLED EXCITABLE LEAKY INTEGRATE-AND-FIRE NEURONS

As mentioned in Sec. I, the collective behavior of oscillatory LIF neurons has been widely investigated. On the other hand, LIF neurons with excitable dynamics, which receive pulselike external inputs, seem more plausible in the cortex. In contrast to the neuron model whose dynamics is represented by Eq. (1), the model of such a neuron must be intrinsically nonoscillatory. The state of such a LIF neuron decays exponentially with time to the resting level when no spike input (either external or feedback) is received or when subthreshold inputs are received. When occasional incident spikes arrive at a suprathreshold rate, each spike pushes up the state value successively to the threshold, and makes the neuron fire. We call this kind of neuron excitable. Excitable LIF neurons can often model biological neurons more plausibly than oscillatory ones. For example, neurons in a functional assembly receive spikes from neurons outside the assembly as well as feedback spikes from constituent neurons within the assembly. In the network models of excitable LIF neurons, those spikes from outside the assembly can be considered to be coming from a source of external spikes. We show that neurons in a network synchronize in most cases when external spikes are periodic, in a manner similar to the oscillatory case. We also extend the proof to the case of aperiodic external spikes to elucidate the possibilities of other scenarios of collective behavior.

We use the following excitable LIF neuron model [17,36,38,39]. In this model, an external input is a spike with an amplitude $\overline{\epsilon}$ rather than a constant or smoothly varying bias. The response of the excitable LIF neuron to external spikes is represented as follows:

$$x(t)=[x(t_k)+\overline{\epsilon}]e^{-\overline{\gamma}(t-t_k)}, \quad (t_k \leqslant t < t_{k+1}), \tag{6}$$

where $x(t)\in[0,h]$ is the internal state at time t, $h>0$ is the threshold, $\overline{\gamma}>0$ is the decay rate, and t_k is the instant when the neuron received the kth external spike. When the neuron receives a spike at t, the state jumps instantaneously from $x(t)$ to $x(t)+\overline{\epsilon}$. When $x(t)+\overline{\epsilon}$ reaches the fixed threshold h, the neuron fires and the state is reset to 0.

We assume here that N excitable LIF neurons are coupled by spikes and each neuron receives feedback spikes from other neurons. We also assume that this interaction is instantaneous, and we denote the amplitude of a stimulating spike by ϵ. All the neurons receive the same external spikes and the neuronal connections are all-to-all and uniform. The state of the ith neuron $(1\leqslant i\leqslant N)$ at time t is denoted by $x_i(t)$.

We investigate what kind of collective behavior appears in response to the external inputs with the probability density $\rho(t)$ of interspike intervals. $\rho(t)$ satisfies $\int_0^\infty \rho(t)=1$, and $\rho(t)=0$, $(t\leqslant 0)$. First of all, there is a necessary condition that an excitable LIF neuron fires spontaneously, receiving external spikes; external spikes must come at a higher rate than a critical value $1/t_0$ with a finite probability. The neurons might keep firing due to feedback spikes even if the external firing rate is slightly less than $1/t_0$. However, $1/t_0$ is a good lower bound unless ϵN is large enough. This is because we could not expect the contribution of feedback spikes if external spikes arrived at a significantly lower rate to make every neuron quiescent. The sufficient condition for sustained firing is

$$\inf \operatorname{supp} \rho(t) < t_0, \tag{7}$$

where supp denotes the support of a function, and t_0 is defined so that it satisfies

$$h e^{-\overline{\gamma} t_0}+\overline{\epsilon}=h. \tag{8}$$

If Eq. (7) is not satisfied, then $x_i(t)$ finally decays to zero unless ϵN is large enough. Under this condition, a sufficient condition for full synchronization is given by the following theorem. The proof of this theorem is given in the Appendix.

Theorem: If Eq. (7) is satisfied and $\sup \operatorname{supp} \rho(t) > t_0$, then N excitable LIF neurons synchronously fire with a finite probability. Furthermore, synchronization can occur even without pulse coupling among neurons.

We should say that this route to full synchronization is biologically exceptional; k_1 external spikes with long enough interspike intervals contract the distances among the neuronal states $x_i(t)$'s without making the neurons fire, and then k_2 external spikes with a suprathreshold rate must arrive in order to let them fire simultaneously. This synchronization scheme is also unrealistic because the first k_1 steps of synchronizing process can be easily disturbed by external spikes with smaller interspike intervals. Moreover, synchronization without mutual interactions is biologically implausible [1]. We are instead interested in more realistic routes to synchronization driven by pulse interactions. To develop the analysis, we extend the phase reduction of oscillatory systems [8,12–14,32,33] to excitable systems. As is shown later, phase description is useful for treating the effects of decay and of the jump of the state in a unified manner. It is also useful in deriving synchronization conditions for pulse-coupled excitable neurons that correspond to those for oscillatory LIF neurons [12,13].

We first treat the case in which external spikes are periodic with period T_0; $\rho(t)=\delta(t-T_0)$. An excitable LIF neuron [Eq. (6)] approaches an oscillatory LIF neuron [Eq. (1)] in the limit as $\overline{\epsilon}\to 0$ and $T_0\to 0$ with $\overline{\epsilon}$ and T_0 satisfying the conditions below. To benefit from the theoretical results in Ref. [12], we define the phase $\phi\in[0,1]$ for an excitable LIF neuron so that these phases are consistent with those for an oscillatory LIF neuron defined by Eq. (2) in this limit.

Accordingly, we explore the relations among γ, I_0, $\overline{\gamma}$, $\overline{\epsilon}$, and T_0 in the limit as $\overline{\epsilon}\to 0$ and $T_0\to 0$. We note that $\overline{\epsilon}$ and T_0 are not independent when the other variables are fixed. We denote by x^* the asymptotic value of x when the threshold h were absent. For an oscillatory LIF neuron, Eq. (1) yields

$$x^*=I_0/\gamma. \tag{9}$$

For an excitable LIF neuron, we can determine x^* from

$$(x^*+\overline{\epsilon})e^{-\overline{\gamma}T_0}=x^*. \tag{10}$$

Given Eqs. (9) and (10), we know that a necessary condition for consistent phase description of excitable LIF neurons is

$$x^* = \frac{I_0}{\gamma} = \frac{\overline{\epsilon}}{e^{\gamma T_0} - 1}. \tag{11}$$

Another condition is on the increasing rate of x in the limit as $\overline{\epsilon} \to 0$ and $T_0 \to 0$. Using Eq. (1), we have

$$\lim_{T_0 \to 0} \frac{(x+\overline{\epsilon}) e^{-\overline{\gamma} T_0 - x}}{T_0} = \frac{dx}{dt} = I_0 - \gamma x. \tag{12}$$

The substitution of Eq. (11) into Eq. (12) yields

$$I_0 - \gamma x = \lim_{\epsilon \to 0} \frac{(x+\overline{\epsilon})\left(1 - \dfrac{\overline{\epsilon}\gamma}{\overline{\epsilon}\gamma + I_0}\right) - x}{\dfrac{1}{\overline{\gamma}} \ln\left(1 + \dfrac{\overline{\epsilon}\gamma}{I_0}\right)} = \frac{\overline{\gamma}}{\gamma}(I_0 - \gamma x).$$

Consequently, we have $\overline{\gamma} = \gamma$, and we identify $\overline{\gamma}$ and γ in the following. To guarantee the constant positive phase velocity which oscillatory LIF neurons have [Eq. (3)], $\phi = g(x)$ must satisfy

$$g(x) + \Delta\phi = g[(x+\overline{\epsilon}) e^{-\overline{\gamma} T_0}], \tag{13}$$

where $\Delta\phi$ is the infinitesimal phase shift for T_0 independent of ϕ. Substitution of Eq. (11) into Eq. (13) yields

$$\frac{dg}{dx}\left(1 - \frac{\gamma x}{I_0}\right) = \frac{\Delta\phi}{\overline{\epsilon}}, \tag{14}$$

in the limit as $T_0 \to 0$ ($\overline{\epsilon} \to 0$ and $\Delta\phi \to 0$). Integrating Eq. (14), we have

$$g(x) = -\frac{\Delta\phi I_0}{\overline{\epsilon}\gamma} \ln(I_0 - \gamma x) + \text{const.}$$

Applying the boundary conditions

$$g(0) = 0 \quad \text{and} \quad g(h) = 1, \tag{15}$$

we obtain

$$g(x) = \ln \frac{\overline{\epsilon}}{\overline{\epsilon} - (e^{\gamma T_0} - 1)x} \Big/ \ln \frac{\overline{\epsilon}}{\overline{\epsilon} - (e^{\gamma T_0} - 1)h}, \tag{16}$$

which is essentially the same as Eq. (2).

We next proceed to the nonlimiting case in which $\overline{\epsilon}$ and T_0 are finite. Motivated by Eq. (16), we postulate that $g(x)$ be written in the form

$$g(x) = B \ln \frac{A}{A - x} + D \quad (0 \leqslant x \leqslant h), \tag{17}$$

where $A > h$, $B > 0$, and D are parameters to be determined. Also in this case, we require a constant phase velocity when x is observed at the periodic times of external spikes. We substitute Eq. (17) into Eq. (13) to obtain

$$B \ln \frac{A}{A-x} + D + \Delta\phi = B \ln \frac{A}{A - \dfrac{(x+\overline{\epsilon})I_0}{I_0 + \overline{\epsilon}\gamma}} + D. \tag{18}$$

Consequently,

$$A = x^* = \frac{\overline{\epsilon}}{e^{\gamma T_0} - 1},$$

and

$$\exp\left(\frac{\Delta\phi}{B}\right) = 1 + \frac{\overline{\epsilon}\gamma}{I_0},$$

where x^* is defined in Eq. (11). By the boundary conditions specified in Eq. (15), we have

$$D = 0, \quad B = \left(\ln \frac{\overline{\epsilon}}{\overline{\epsilon} - (e^{\gamma T_0} - 1)h}\right)^{-1}.$$

As a result, $g(x)$ of an excitable LIF neuron has the same expression as that of an oscillatory LIF neuron represented in Eq. (16). Accordingly we can benefit from the results obtained for the networks of oscillatory neurons [12,13]; we expect that N neurons synchronize in finite time based on the convexity of g^{-1}. The difference between pulse-coupled oscillatory and excitable LIF neurons is in their detailed phase dynamics; ϕ of an excitable LIF neuron drifts to the negative direction with the following velocity,

$$\frac{d\phi}{dt} = -\frac{(e^{\gamma T_0} - 1)\gamma x}{\overline{\epsilon} - (e^{\gamma T_0} - 1)x} \left(\ln \frac{\overline{\epsilon}}{\overline{\epsilon} - (e^{\gamma T_0} - 1)h}\right)^{-1} < 0, \tag{19}$$

when input spikes are absent and $x < x^*$. An input spike makes ϕ jump to the positive direction. As a result, the phase ϕ is changing with a constant positive velocity on the average. According to Eq. (19), the negative phase shift during two external spikes is larger for bigger ϕ since ϕ is a monotonously increasing function of x. On the other hand, the effect of an external spike on the phase shift is qualitatively similar to that of a feedback spike. Considering Eq. (4), we can see that the positive phase shift caused by an external spike is larger for bigger ϕ. As a result, the positive phase shifts caused by external spikes compensate the negative phase shifts between the external spikes. As a whole, we encounter the dynamics of ϕ with a constant phase velocity when we observe the population of excitable neurons at $t = kT_0$, $(k = 1,2,\ldots)$.

The effect of discreteness in input time is nontrivial, but not grave. If $x_i(t) = h$ whenever the ith neuron is about to fire as a result of receiving an external or feedback spike, the convexity of g holds in the strict sense. In this case, the result in Ref. [12] is applicable and full synchronization always occurs. In general, however, $x_i(t)$ exceeds h when the neuron is going to fire. We assume that $x_i(t)$ exceeds h by Δh when the ith neuron fires. Then a small fluctuation in $x_i(t)$ is negligible because it is absorbed by margin Δh when firing. As a result, attractive basins of clustered states, which have

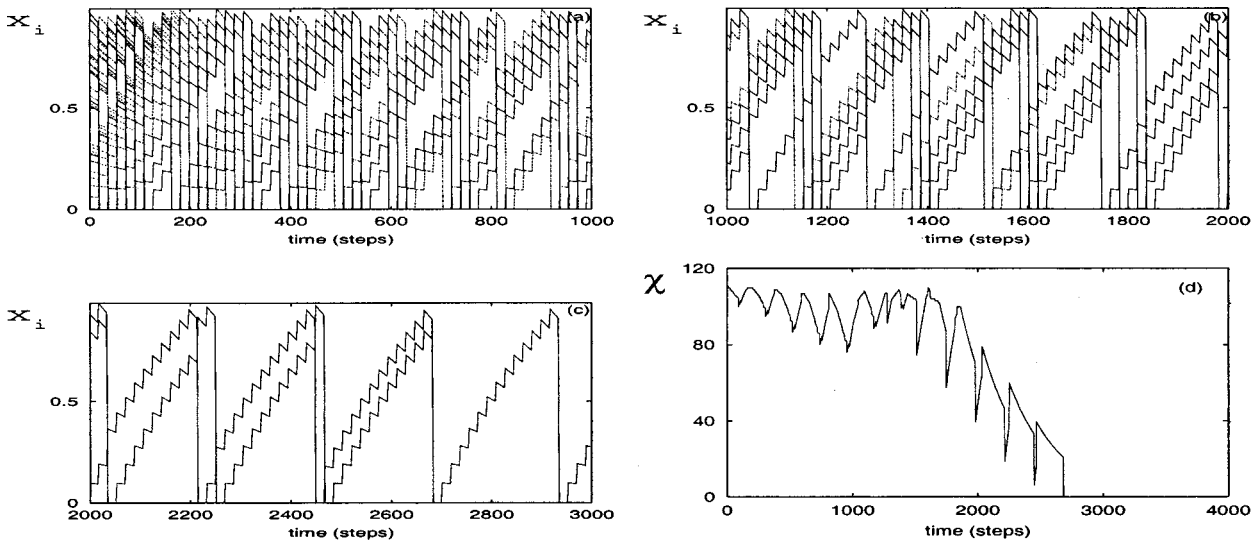

FIG. 1. (a), (b), (c) Behavior of 30 excitable LIF neurons coupled by spikes. In the following, we denote by step the time unit for integrating Eq. (6). External inputs are periodic with period $T=18$ (steps) and intensity $\overline{\epsilon}=0.1$. The coupling strength is $\epsilon=0.007$, and the decay rate is $\gamma=0.003$ (step)$^{-1}$. (d) Behavior of the synchronization parameter $\chi(t)$ of the same time series.

measure zero for oscillatory systems, have positive measures. Whether a clustered state is realized depends on initial conditions. Owing to the assumption of absolute absorption, the final state of coupled neurons is fully synchronized or clustered. Nevertheless, the basins of clustered states occupy only small regions in the phase space; for most initial conditions, N neurons fully synchronize in finite time. The synchronization of 30 excitable LIF neurons with common periodic external spikes is shown in Fig. 1(a), Fig. 1(b), and Fig. 1(c). Figure 1(d) shows the evolution of the synchronization order parameter $\chi(t)$ defined by

$$\chi(t)=\sum_{i=1}^{N}\sum_{j=i+1}^{N} d[x_i(t),x_j(t)], \tag{20}$$

where

$$d(x,x')=\min(|x-x'|,|x-x'+h|,|x-x'-h|).$$

The synchronization parameter $\chi(t)=0$ iff N neurons are fully synchronous, and $\chi(t)$ is largest when the states of N neurons distribute uniformly in [0, 1], in which case, $\chi(t)=N^2/8$. Figure 1 demonstrates that full synchronization is reached around $t=2680$ (steps), and $\chi(t)$ can characterize the degree of synchronization.

We now consider the case in which the external inputs are aperiodic. We assume that $\overline{\gamma}=\gamma$ and $\overline{\epsilon}$ are fixed. The interspike interval T_0 is determined according to the probability density $\rho(t)$. On the basis of Eq. (7), we can choose a characteristic period $T_0^*<t_0$. We define the phase ϕ by replacing T_0 with T_0^* in Eq. (16). Roughly speaking, the value of ϕ drifts toward $\phi=1$ with a constant velocity when external spikes are periodic with the period T_0^*.

If $\sup\,\mathrm{supp}\,\rho<t_0$, we should set $T_0^*=\sup\,\mathrm{supp}\,\rho$. In this situation, interspike intervals are equal to or less than T_0^*. Negative phase shifts in the absence of inputs are compensated by positive phase shifts by external spikes. When an interspike interval is T_0^*, both effects are balanced. The value of ϕ changes $\Delta\phi$ per external spike regardless of ϕ. In contrast, if the interspike interval is less than T_0^*, the effect of the external spike overrides the negative phase drift. Since the positive phase shift is larger for bigger ϕ, external spikes overcompensate the negative phase shift. The bigger ϕ is, the faster it approaches 1. As a result, the effect of an interspike interval less than T_0^* is similar to the spike effect caused by the convexity of g^{-1}. Accordingly, all the neurons eventually synchronize except those in the small attractive basins of clustered states.

Generally speaking, interspike intervals take values both larger and smaller than t_0. External spikes thus drive the network in both expansive and contractive manners. We can define the phase ϕ for an arbitrarily chosen T_0^*. In the corresponding phase space, the network is driven expansively when the interspike interval of external spikes is smaller than T_0^*. The corresponding phase jumps propel the network toward full synchronization in the same manner as those studied in Ref. [12]. On the other hand, the system is driven in a contractive manner when the interspike interval is larger than T_0^*. This situation is explained in the proof of our theorem.

We note that repetitive inputs of these contractive external spikes may also result in stable clustered states that are found in more general networks [13,26,32,33]. However, the expanding effect is stronger than the contracting one since a clustered state is unstable against feedback spikes from other clusters. The time course of 30 neurons toward full synchronization is shown in Fig. 2(a). We choose $\rho(t)$ to be an exponential distribution $\rho(t)=e^{-\lambda t}/\lambda$ with $\lambda=0.04(\mathrm{step})^{-1}$ based on biological evidence of cortical neurons [31].

We also examine the effect of small white Gaussian noise to each neuron [Fig. 2(b) and Fig. 2(c)]. If σ is small enough, neurons remain synchronous without serious degradation due to noises. In Fig. 2(b), we find just a slight increase in $\chi(t)$ after the full synchronous state is almost realized [$t\geqslant 2000$

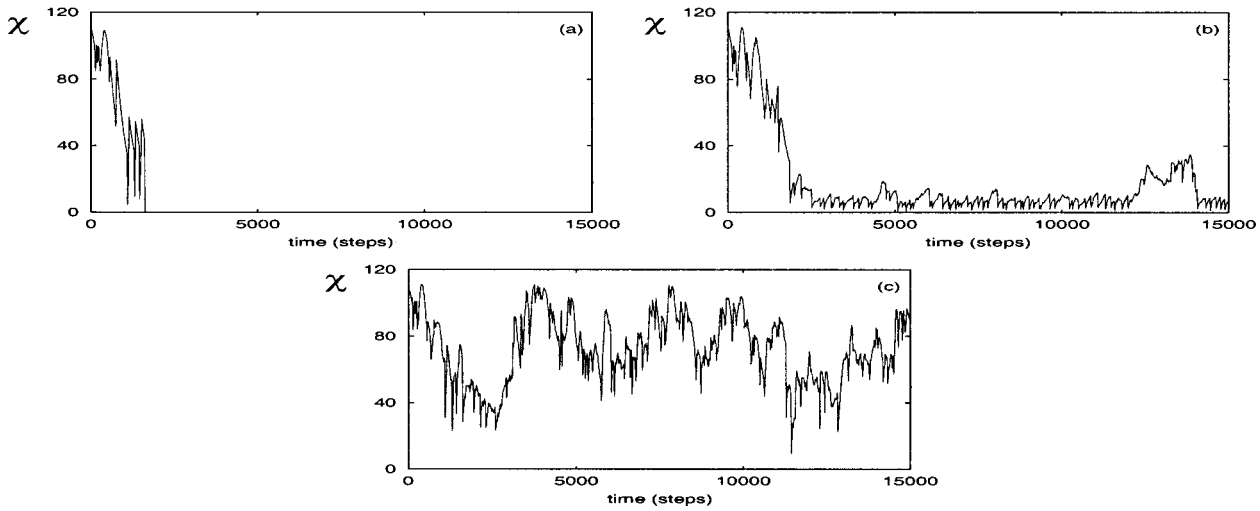

FIG. 2. Behavior of the synchronization parameter $\chi(t)$ of 30 excitable LIF neurons coupled by spikes. $\overline{\epsilon}=0.18$, $\epsilon=0.005$, and $\gamma=0.003$ $(\text{step})^{-1}$. Interspike intervals of external inputs have probability density $\rho(t)=e^{-0.04t}/0.04$ $(\text{step})^{-1}$. White noise intensity is $\sigma=0$ $(\text{step})^{-1}$ (a), $\sigma=0.003$ $(\text{step})^{-1}$ (b), and $\sigma=0.009$ $(\text{step})^{-1}$ (c).

(steps)]. Though the white noise has a tendency to break the synchrony, each external spike puts the whole network back to full synchrony. This order creation driven by external spikes is important from the viewpoint of temporal spike coding [31] that cortical information may be coded on the timing of the spikes, often in the form of synchronous firing. The firings of excitable LIF neurons can synchronize even when the states between external spikes are not equal owing to noise or other factors. On the other hand, if σ is not so small [Fig. 2(c)], neurons behave randomly where effects of noise overwhelms synchronizing effects of the external spikes.

A remarkable point is that neurons can synchronize even when they do not interact, if the noise is sufficiently weak. This type of synchronization is not possible when the external inputs are periodic, in which case the value of ϕ changes at a virtually constant velocity. Such synchronization is caused by external spikes separated by relatively short intervals, which repulsively disperse the phases of N neurons. This synchronization scenario is totally different from the contracting one stated in the previous theorem although absence of interactions is common to both cases. Common external inputs are entraining a neural population so that the neurons fire synchronously to code information robustly, regardless of interactions. Of course, synchronization with no coupling is biologically implausible [1]. Furthermore, pulse coupling accelerates synchronization even though it is mathematically unnecessary. The synchronization in biological neurons may be based on both effects of the external inputs and the mutual interactions. The time course toward synchronization when feedback couplings are absent ($\epsilon=0$) is shown in Fig. 3 for $\gamma=0.003$ $(\text{step})^{-1}$, $\overline{\epsilon}=0.18$, and $\rho(t)$

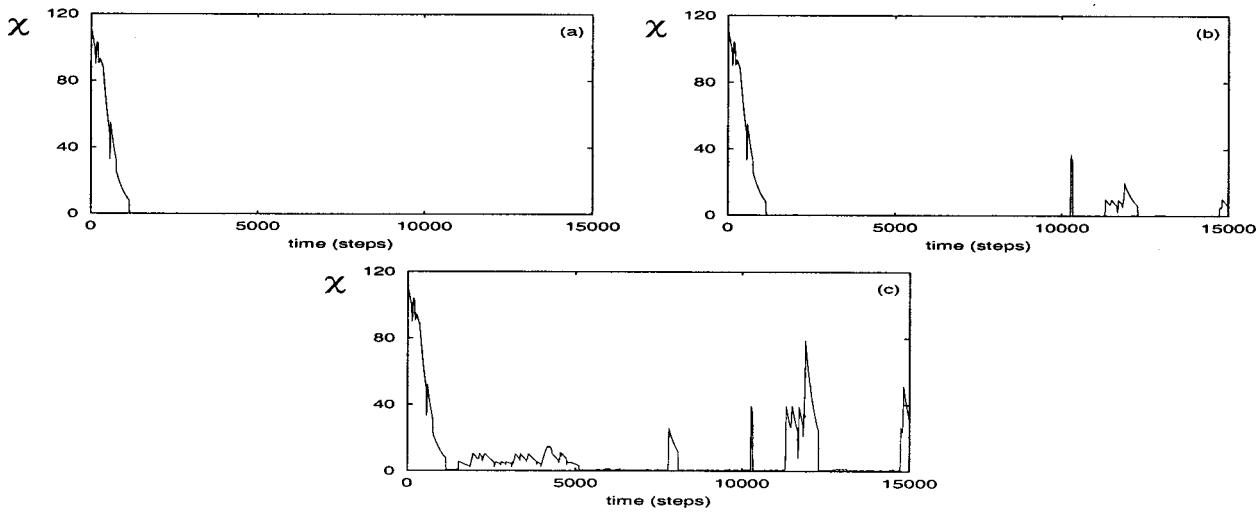

FIG. 3. Behavior of the synchronization parameter $\chi(t)$ of 30 excitable LIF neurons without coupling. $\overline{\epsilon}=0.18$, $\epsilon=0$, and $\gamma=0.003$ $(\text{step})^{-1}$. Interspike intervals of external inputs have probability density $\rho(t)=e^{-0.04t}/0.04$ $(\text{step})^{-1}$. White noise intensity is $\sigma=0$ $(\text{step})^{-1}$ (a), $\sigma=0.0001$ $(\text{step})^{-1}$ (b), and $\sigma=0.0003$ $(\text{step})^{-1}$ (c).

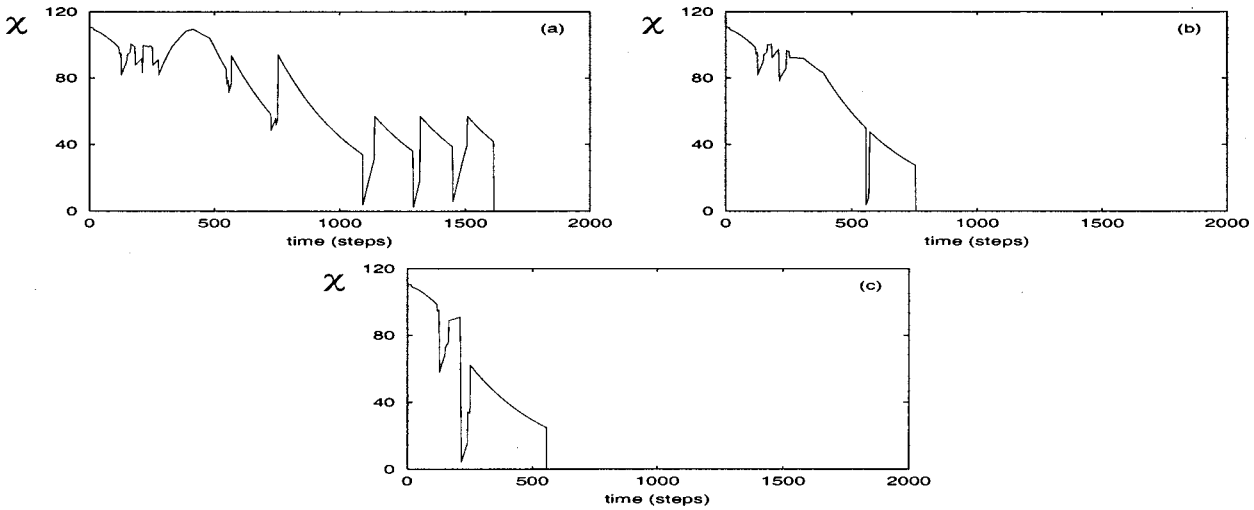

FIG. 4. Behavior of the synchronization parameter $\chi(t)$ of 30 pulse coupled excitable LIF neurons with absolute refractoriness. $\overline{\epsilon}=0.18$, $\gamma=0.003$ (step^{-1}), and $\epsilon=0.005$. Interspike intervals of external inputs have probability density $\rho(t)=e^{-0.041}/0.04$ (step^{-1}). The absolutely refractory period Δt of the neuron is set equal to 0 (step)$^{-1}$ (a), 6 (step)$^{-1}$ (b), and 10 (step)$^{-1}$ (c).

being the same exponential distribution as in Fig. 2. We also investigated noise effects in Fig. 3(b) and Fig. 3(c). Full synchronization is achieved even in the absence of pulse coupling [Fig. 3(a)]. However, this synchronization is not stable against noises; Fig. 3(b) and Fig. 3(c) shows that synchronization collapses intermittently. Cooperation of external spikes and pulse couplings plays an important role in realizing and keeping synchronous behavior.

Our result is consistent with the known results for the excitable neurons without external spike inputs [36]: full synchronization in most cases and cluster states in some cases. In Ref. [36], the increase in internal states were driven only by mutual interactions at a sufficiently high rate. They derived the condition of sustained firing and synchronization for $\gamma=0$ analytically and for $\gamma>0$ numerically. Although our model does not include delay, we have treated general cases with $\gamma>0$.

We can also generalize uniform coupling constants to nonuniform ones [12,24,29]. We denote the generalized coupling strength by $\epsilon_{i,j}$, which has the dependence on a presynaptic (jth) neuron and a postsynaptic (ith) neuron. Full synchronization is guaranteed also when $\epsilon_{i,j}$ depends only on i [12,24], or only on j [24]. We note that a network with random positive $\epsilon_{i,j}$ can also be led to synchronization (data not shown) [29]. Excitatory interactions result in the full synchronization driven by external spikes, and this phenomenon is regardless of precise coupling structures.

Synchronization is more easily reached when absolute refractoriness is introduced [17]. We assume that a neuron receives neither external nor feedback spike effects for Δt after its latest firing. For simplicity let us conjecture a simple network comprising only two neurons. We assume that the states of two neurons come close enough to each other so that the second neuron fires within Δt after the first neuron fires. In this case the first neuron does not receive a spike effect from the second one; the first one waits for the second one, without a phase jump. The simulation results exploring the effect of absolute refractoriness are shown in Fig. 4. The absolutely refractory period Δt is set equal to 0 (step)$^{-1}$ (a), 6 (step)$^{-1}$ (b) and 10 (step)$^{-1}$ (c). Figure 4 shows that synchronization is accelerated when the absolute refractoriness is introduced.

In this section we have shown by applying the phase descriptions that excitable LIF neurons with pulse coupling can synchronize by the same mechanism as oscillatory LIF neurons. We have also observed phenomena such as entrainment driven by external spikes and acceleration of synchronization by refractoriness. They are based on the pulselike nature of external inputs.

IV. PULSE-COUPLED NAGUMO-SATO NEURONS

The LIF neuron models are continuous in time, but there are also many discrete-time neuron models. Discrete-time neuron models can be naturally derived from continuous neuron models [17,36]. They have been widely used because they are easier to analyze and numerically calculate, and can exhibit important properties of biological neurons. The analytical calculation benefits from abundant results, for example, of combinatorial mathematics, Turing machines, and cellular automata. Discrete-time neuron models are also useful in applications such as associative memories; they also suit to implementation on electronic devices.

Discrete-time neurons have often been analyzed by using combinatorial methods [17,36] that are not based on phase reductions. Considering the results in the last section, it seems advisable to combine the discrete-time and continuous-time neuron models. In this section, we unify discrete-time models and continuous-time models using the phase description; we extend the phase description to the discrete-time neuron models.

We use the NS neuron model [40] as an example of discrete-time neurons. This model is derived on the basis of the Caianiello's neuronic equation [41], which is equivalent to time-discretization of the neuron model used by Caianiello and De Luca [42]. The dynamics of the NS neuron is de-

scribed by one-dimensional mapping with the internal state denoted by $x(t)$ ($t \in \mathbf{N}$) as follows:

$$x(t+1)=\begin{cases} \dfrac{x(t)}{b}+a-1 & [x(t)\geqslant 0], \\ \dfrac{x(t)}{b}+a & [x(t)<0], \end{cases} \tag{21}$$

where $b>1$ and $0<a<1$. $x(t)$ is monotonically increasing in $[-\infty, 0)$ and $[0, \infty]$. If an iteration starts from $x(t)<0$, then x increases until x satisfies $x(t')>0$ after $t'-t$ steps. $x=0$ is understood as the threshold for firing. Consequently, the neuron fires and $x(t')$ is reset to a smaller value in the next step. $x(t'+1)$ falls in the left branch ($x<0$) unless $x(t')$ is too large or the neuron receives too much feedback input from other neurons (interactions between neurons will be defined later). The effect of the external input is reflected in a monotonically increasing property of Eq. (21) in $[-\infty, 0)$. We can regard the NS neuron as both an oscillatory neuron and an excitable neuron. It is considered oscillatory if we suppose we are periodically observing a leaky neuron receiving a suprathreshold bias. On the other hand, it is considered excitable if we suppose that it is a leaky neuron receiving a subthreshold bias, and we are observing it at every instant it receives an external spike.

The minimum possible value of $x(t)$ is $a-1$ except in transient states caused by negative large initial conditions. Since $x(t)>0$ is reset to a negative value in one step if $x(t)$ is not too large, we are mainly interested in $x(t) \in [a-1,0]$. In this range, the phase $\phi=g(x)$ should be monotonously increasing, and as the boundary conditions, we suppose

$$g(a-1)=0 \quad \text{and} \quad g(0)=1.$$

We allow $\phi>1$ corresponding to $x>0$. The phase ϕ for an excitable LIF neuron has been defined so that it changes at a constant velocity on the average under periodic external spikes. Recalling Eq. (18), we define $\phi=g(x)$ for the NS neuron so that it satisfies

$$g(x)+\Delta\phi=g\left(\frac{x}{b}+a\right) \quad (x<0), \tag{22}$$

with a fixed $\Delta\phi$. $\Delta\phi$ denotes the positive phase shift per iteration, independent of ϕ. Since the NS neuron has a decay similar to that of an excitable LIF neuron, we postulate that g takes the same form as Eq. (17). Substitution of Eq. (17) into Eq. (22) then yields

$$A=\frac{ab}{b-1}, \quad B=\left(\ln\frac{a+b-1}{ab}\right)^{-1},$$

$$D=1, \quad \text{and} \quad \Delta\phi=\ln b \Big/ \ln\frac{a+b-1}{ab}. \tag{23}$$

Compatibility conditions of $A>0$ and $B>0$ are satisfied. Finally, ϕ is represented by

$$\phi=g(x)=\ln\frac{ab}{ab-(b-1)x} \Big/ \ln\frac{a+b-1}{ab}+1. \tag{24}$$

As a result, we can expect phase dynamics similar to that of an excitable LIF neuron when $x(t)<0$,

According to Eq. (21), x certainly falls into $x(t)\geqslant 0$ in a finite time. This encourages us to define $1\leqslant\phi<\ln b/\ln[(a+b-1)/(ab)]+1$ (for $0\leqslant x<a$) by using Eq. (24) to describe whole phase dynamics. We should then determine the phase shift per iteration $\Delta\phi$ when $\phi\geqslant 1$. For $\phi\geqslant 1$, substituting

$$x=g^{-}(\phi)=\frac{ab}{b-1}\left\{1-\left(\frac{ab}{a+b-1}\right)^{\phi-1}\right\}, \tag{25}$$

into

$$\Delta\phi=g\left(\frac{x}{b}+a-1\right)-\phi,$$

we have

$$\Delta\phi=-\ln\left\{\frac{1}{b}+\frac{b-1}{ab}\left(\frac{a+b-1}{ab}\right)^{\phi-1}\right\} \Big/ \ln\frac{a+b-1}{ab}. \tag{26}$$

As is expected, $\Delta\phi<0$ for $\phi\geqslant 1$, corresponding to the resetting of x immediately after firing.

The single NS neuron approaches an identical stable periodic solution for any initial conditions $x(0)$ [40]. In our phase description, the phase shift $\Delta\phi$ is constant when $0\leqslant\phi<1$. The contractive property of Eq. (21) is represented in the contracting phase shift dynamics when $\phi\geqslant 1$; differentiating Eq. (26), we have

$$-1<\frac{d\Delta\phi}{d\phi}<0. \tag{27}$$

To capture the way of convergence to a periodic solution using the phase dynamics, we consider a distribution of the phase whose support is included in $[0,\ln b/\ln[(a+b-1)/(ab)]+1]$. We start from these initial conditions. The phase space can be divided into a finite number of connected regions according to the number of steps it takes for the neuronal state to satisfy $\phi>1$. The phase density in a region remains unchanged until the neuron fires. When $\phi>1$ is realized, the region contracts, and the contracted region is pulled back into $\phi\in[0,1)$. Then the region again drifts toward $\phi>1$ under iterations. In the course of iterations, the density restricted to a region contracts every time the neuron fires. The number of points that asymptotically have positive density is the same as the number of regions. These points form the periodic solution of Eq. (21). We note that this picture is obtained even if we do not persist in phase description; we can conclude the convergent property based on the factor $1/b$ in Eq. (21). The reason we adopt the phase description is that it enables us to investigate collective behavior of coupled NS neurons easily. Spike couplings can be interpreted as phase jumps and we can make use of results

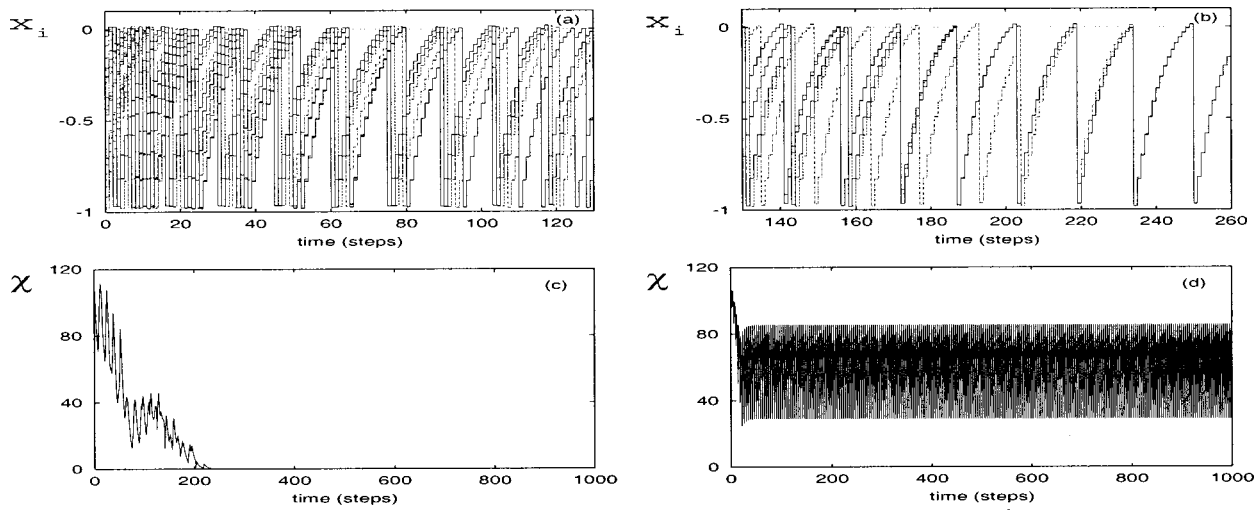

FIG. 5. (a), (b) Behavior of 30 NS neurons coupled by spikes with strength $\epsilon=0.005$ when $a=0.02$, $b=1.15$, and the internal period P of the single neuron is 20 (steps). (c) Behavior of the synchronization parameter $\chi(t)$ corresponding to (a) and (b). (d) Behavior of the synchronization parameter $\chi(t)$ when $a=0.18$, $b=1.15$, $\epsilon=0.01$, and $P=4$ (steps).

obtained for LIF neurons since the definition of the phase of the NS neuron is closely related to that of phase of a LIF neuron.

Our next step is to introduce pulse coupling. We denote the state of the ith neuron at time t by $x_i(t)$. We assume that the ith neuron fires when $x_i(t)\geqslant 0$. When it fires, it sends a spike with the amplitude ϵ at the next time to all the neurons except itself. The uniform synaptic delay is considered in this framework. $x_i(t)>0$ is automatically reset to $x_i(t+1)<0$ at the next step. The couplings are uniform and all to all. The phase return map $\tau(\phi)$ for $\phi<1$ is calculated using Eqs. (24) and (25) as

$$r(\phi)=g[g^{-1}(\phi)+\epsilon]$$

$$=\ln\left\{\left(\frac{a+b-1}{ab}\right)^{1-\phi}-\frac{b-1}{ab}\epsilon\right\}\Bigg/\ln\frac{a+b-1}{ab}+1.$$

Consequently,

$$\frac{d\tau}{d\phi}=\left\{1-\frac{(b-1)\epsilon}{ab}\left(\frac{ab}{a+b-1}\right)^{1-\phi}\right\}^{-1}>1, \qquad (28)$$

which assures that the behavior of pulse-coupled NS neurons receiving a feedback spike is expansive. In contrast, according to Eq. (27), we know that the NS neurons have the tendency to converge to a periodic solution and form clusters around the periodic points. The actual dynamics are determined by the tradeoff between these two effects, which are influential when $\phi<1$ and $\phi\geqslant 1$, respectively.

If random initial conditions are taken, we can expect $x_i(t)$'s $(1\leqslant i\leqslant N)$ to be distributed randomly at first. The ith neuron receives $N-1$ feedback spikes during its successive firings in this stage. For an appropriately large ϵ, the expanding effect is larger than the contracting one. Accordingly, the internal states of neurons travel in a ergodic manner like those of oscillatory LIF neurons. In the course of iterations, some neurons occasionally fire simultaneously. We assume that the ith neuron and the jth neuron fire simultaneously. We note that the absorption is not absolute; generally speaking, $x_i(t)$ and $x_j(t)$ do not take the same value even if they have fired simultaneously. However, we note that the phase variables corresponding to $x_i(t+1)$ and $x_j(t+1)$ are close and that the neurons receive interactive spikes at $t+1$. Accordingly, the expanding effect at $t+1$ is weaker for the ith and jth neurons than for the other neurons since $(d^2\tau)/d\phi^2>0$. If the contracting effect surpasses the expanding effect, then the ith and the jth neurons synchronize asymptotically. The lack of absolute refractoriness is partially compensated by the property of the network that the interactions among simultaneously firing neurons are weaker than those among the other neurons in the space of the phase variables. This property of the neural network is also regarded as the relative refractoriness. Even though the expanding effect still overwhelms the contracting effect at this stage, simultaneous firing of a larger number of neurons will cause contracting behavior. Thus, simultaneously firing neurons are likely to synchronize asymptotically to form a cluster with intracluster synchronization. On the other hand, clusters interact by pulse coupling. This interaction is essentially the same as that of oscillatory LIF neurons. In most cases, all the neurons finally synchronize. We can also observe avalanche phenomena since stronger interactions occur as cluster sizes become large. The time course of $N=30$ NS neurons coupled by spikes with strength $\epsilon=0.005$ is shown in Fig. 5(a) and Fig. 5(b) for $a=0.02$ and $b=1.15$. No noise is applied to neurons. Figure 5(c) shows the corresponding synchronization parameter $\chi(t)$ defined in Eq. (20). We can see that synchronization is achieved as a result of pulse couplings. For these parameter values, the period of the periodic solution of the single neuron is $P=20$ (steps).

Figure 5(d) shows $\chi(t)$ when $a=0.18$, $b=1.15$, and $\epsilon=0.01$. In this case, full synchronization does not appear and the asymptotic collective behavior is a two-cluster state. The state of each NS neuron converges to the same periodic so-

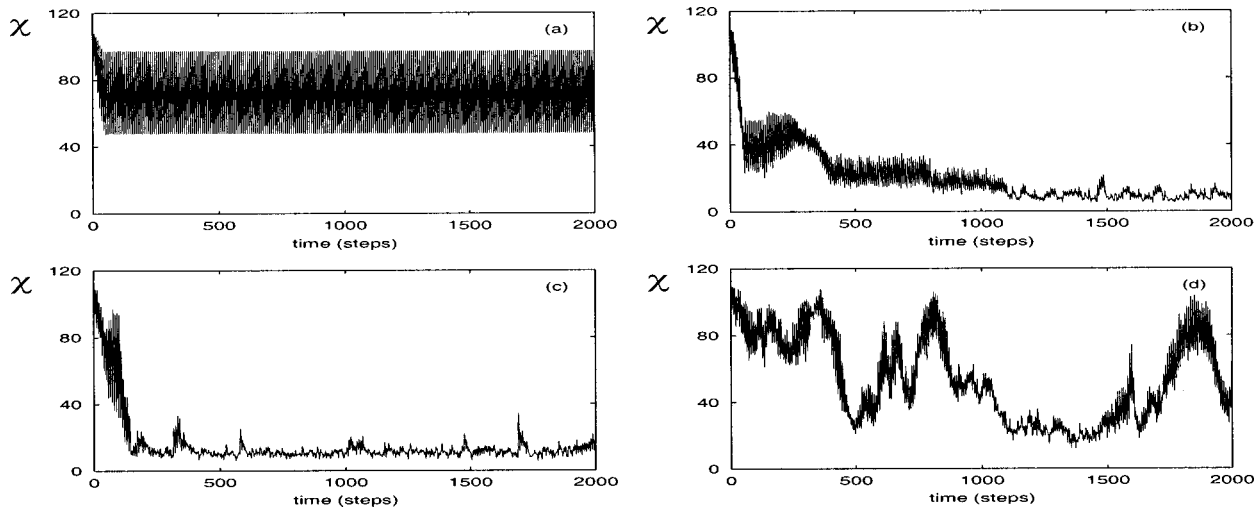

FIG. 6. Behavior of the synchronization parameter $x(t)$ for 30 NS neurons coupled by spikes with strength $\epsilon=0.005$ when $a=0.07$, $b=1.15$, and the internal period P of the single neuron is 8 (steps). Uniformly distributed independent noises with the dynamic range σ are applied to all the neurons. (a) $\sigma=0$ (step)$^{-1}$, (b) $\sigma=0.012$ (step)$^{-1}$, (c) $\sigma=0.018$ (step)$^{-1}$, and (d) $\sigma=0.028$ (step)$^{-1}$.

lution with $P=4$ (steps). Accordingly, the two clusters converge to the same periodic solution, but their phases are different. Each periodic point has the large attractive basin of the size $\sim 1/P$ in this case. Feedback spikes are not strong enough to propel neurons out of the basins. Nevertheless, we observe noise-induced full synchronization of coupled NS neurons. The noise enables a neuron to escape from an attractive basin of a clustered state. If the noise is strong enough to make the neurons get out of clusters but not so strong as to destroy intracluster synchronization, then full synchronization can be induced by noise. We performed a simulation in which we added uniformly distributed independent noises with the dynamic range σ to 30 neurons. The results when $a=0.07$, $b=1.15$, $\epsilon=0.005$, and $P=8$ (steps) are shown in Fig. 6. As Fig. 6(a) shows, without noise, the population falls into a clustered state with two clusters. This is because attractive basins of periodic points are relatively large compared to ϵ. The collective behavior can not escape out of the clustered state without noise. Figure 6(b) and Fig. 6(c), however, show that neurons synchronize when noises are applied. When $\sigma=0.012$ (step^{-1}) [Fig. 6(b)], each neuron first falls into one of five clusters at $t\cong 50$ (steps). The number of clusters decreases to three at $t\cong 350$ (steps), and to two at $t\cong 800$ (steps). Finally, the network state converges into one group at $t\cong 1100$ (steps). When $\sigma=0.018$ (step^{-1}) [Fig. 6(c)], full synchrony is realized in an earlier stage. The final state is the fully synchronous state deteriorated by continuously added noises. In these two cases, moderate strengths of white noises help the network state to go out of the clustered state. The state falls in the full synchronous state with a high probability since it is the most stable solution with the largest basin. Synchronization does not occur, on the other hand, when the noise amplitude is too large [$\sigma=0.028$ (step^{-1}) in Fig. 6(d)].

The noise-induced synchronization resembles coherence resonance (CR) [43–45] in the meaning that both are ordered states realized with the help of noise. For CR in continuous-time models, noise evokes coherent firing in neurons when biases are set at slightly subthreshold values. For instance, CR is observed in coupled FitzHugh-Nagumo neurons [44] and coupled Hodgkin-Huxley neurons [45]. Moreover, noise-induced synchronization in the NS neurons is also similar to simulated annealing. In simulated annealing, a global optimization problem is solved by noises whose strengths gradually decrease so that the internal state can get out of local optima. Clustered states are less stable than the fully synchronous state since clusters have smaller attractive basins than the fully synchronous state does. Noises are effective in driving the network out of quasioptimal clustered states.

V. DISCUSSIONS

A. Possible extensions

We have shown that networks of excitable LIF neurons without the delay and the NS neurons with the uniform delay become fully synchronized in most cases. We have proposed a phase-based framework for studying the pulse-coupled excitable neurons.

Though we have concentrated on the analysis of synchronized behavior in this paper, stable clustered solutions [17,22,26,27,32,33] and asynchronous states [18,20,34] have also been found in more general networks. This multistability is related to the superposition problem [17]. Investigations of more general cases are our future problem.

We must also pay attention to the role of external inputs. No matter whether suprathreshold or subthreshold, inputs have been supposed to be common to all the neurons in many studies, including ours. This simple supposition has enabled us to conclude that neurons synchronize even without interactions, entrained by external spikes. Though the synchronization without coupling is unrealistic [1], it is possible for those neurons that receive the same external inputs and mutual interactions through coupling to synchronize to form an assembly. The external inputs representing information signals can be nonuniform [46]. Synchronization in an

actual assembly may occur as a result of the combined effects of feedback interactions and entrainment by external inputs.

B. Contracting or expanding?

We comment on the possibility of realistic routes to synchronization. In a network of LIF neurons the aggregated phase variable Φ travels ergodically and chaotically until it reaches an attractive basin of absorption. Local stability of synchrony is based on absorption. The synchronization mechanism of nonleaky linear neurons is also based on ergodicity [25]. In a network of the FitzHugh-Nagumo neurons, on the other hand, the collected phase variable is contracting and there is no absolute absorption [33]. Synchrony would be achieved only in the limit of infinite time. The local volume around the stable point contracts on receiving external spikes.

Though ergodicity-based scenarios are mathematically perfect, their application to the synchronization of actual network of neurons is questionable because the assumption of absolute absorption is biologically implausible. If absorption is not absolute, small fluctuations caused by noises might grow because of the expanding dynamics. Furthermore, the proof of the synchronization is combinatorial and tells us nothing about the synchronization time. Synchronization may require a longer time than is biologically feasible. This situation is common to primitive chaos control techniques in which the controller must wait for a long time before the state falls near the desired fixed point [47]. Our analysis of excitable LIF neurons and the NS neurons is also subject to ergodicity-based evidence although more general routes to synchronization are suggested by analyzing the case of distributed interspike intervals of external inputs. Biological situations are between two extremes represented by the expanding and contracting dynamics.

C. Oscillatoriness and excitability

In oscillatory systems, the phase variable changes at a constant speed proportional to the internal frequency. In excitable systems, in contrast, the phase drifts in the negative direction when there are no external inputs. An external spike makes the phase jump towards the positive direction, compensating the negative phase drift. The phase has been defined so that both effects are almost balanced; the phase has a constant positive velocity on the average when the external spike arrives periodically with a prescribed period. In this way, excitable systems have been related to oscillatory systems. With the use of the results for oscillatory LIF neurons, we have proven that neurons synchronize when the interspike intervals of external input are less than a prescribed period. Full synchrony can be also realized in most cases with more general types of interspike intervals in which interspike intervals are more widely distributed.

Firing can be driven by suprathreshold biases. These biases may come into play, for example, when sensory neurons strongly respond to large external stimuli and when a living thing is carrying some mental or physical activities. On the other hand, a neuron is not an intrinsic self-sustained oscillator in most cases where firings are promoted by spike inputs from neurons outside a fixed assembly as well as by feedback spikes inside the assembly. The technique developed in this paper is also useful for analyzing dynamics of neuronal assemblies within a huge population, since we can look upon the neurons outside the assembly as an external source of spikes.

Another model to be noted is the nonleaky integrate-and-fire neuron that corresponds to the LIF neuron with $\gamma=\overline{\gamma}=0$. An arbitrarily small positive bias makes this kind of neuron a linear oscillatory integrator [25]. In the excitable case with a subthreshold bias, the state x does not change unless external spikes arrive. Networks of these excitable nonleaky neurons that spontaneously fire only by mutual exchanges of spikes were analyzed in Ref. [36], which showed that full synchronization occurs in most cases and clusters appear for some initial conditions. The phase variable for this neuron is discretized after transient activity; a neuron takes $m=\lceil h/\overline{\epsilon}\rceil$ states $0,1/(m-1),2/(m-1),\ldots,(m-2)/(m-1)$, and 1 where h is the threshold and $\lceil x\rceil$ denotes the roundup of x. We can easily show that the neurons synchronize if $\epsilon>h/N$ and $\overline{\epsilon}$ is comparatively larger than ϵ. Though we do not further examine this model here, we are interested in it since it is related to coincidence detector models [31,48]. A coincidence detector neuron fires if it receives more spikes than the threshold within a short time window. The coincidence detectors are usually at their resting potentials waiting for simultaneous input spikes. Each discrete phase value would correspond to the number of received spikes within the time window. However, the phase is at the resting states in most cases, and the phase description is not effective to express the dynamical behavior of coincidence detectors. Considerations of delay and of more general couplings are required for understanding the computational role of coincidence detectors [31,35,46].

APPENDIX: PROOF OF THE THEOREM

To prove the theorem, we assume $\sup \operatorname{supp} \rho(t)>t_0$, and then we can take $t_1>t_0$ such that $\rho(t_1)>0$. Accordingly, the interspike interval of external spikes is equal to t_1 with a positive probability. Then, without loss of generality, we can consider a situation in which external spikes arrive at $t=kt_1$, $(k=1,2,\ldots)$. Using Eq. (6),

$$x_i[(k+1)t_1]=[x_i(kt_1)+\overline{\epsilon}]e^{-\overline{\gamma}t_1}, \tag{A1}$$

where $x_i(kt_1)$ and $x_i[(k+1)t_1]$ are the internal states just before each external spike is received. Using Eq. (A1) with $k=0,1,\ldots,k-1$, we have

$$x_i(kt_1)=x_i(0)e^{-\overline{\gamma}kt_1}+\overline{\epsilon}e^{-\overline{\gamma}t_1}\frac{1-e^{-\overline{\gamma}kt_1}}{1-e^{-\overline{\gamma}t_1}}.$$

Accordingly, for every $\delta>0$, we can take k_1 such that

$$|x_i(k_1t_1)-\overline{x}|<\delta,$$

where

$$\overline{x}=\frac{\overline{\epsilon}e^{-\overline{\gamma}t_1}}{1-e^{-\overline{\gamma}t_1}}.$$

We assume that spikes arrive at an interval $t_2<t_0$ after k_1 external spikes have come. Then every $x_i(t)$ is pushed up faster than it decays, and eventually the ith neuron fires. We consider a neuron that at $t=k_1t_1$ has state $x(k_1t_1)=\overline{x}$ and assume that this neuron would fire after receiving k_2 more periodic external spikes of the period t_2. The state of the imaginary neuron just before receiving the k_2th spike satisfies

$$x(k_1t_1+k_2t_2)>h-\overline{\epsilon}.$$

N neurons fire synchronously at $t=k_1t_1+k_2t_2$ if we choose

$$\delta=x(k_1t_1+k_2t_2)-(h-\overline{\epsilon}),$$

since for every i it follows that

$$x_i(k_1t_1+k_2t_2)>x(k_1t_1+k_2t_2)-\delta>h-\overline{\epsilon}.$$

Once N neurons fire synchronously, they are synchronous in the future because $x_i(t)$ takes the same value for all i. This completes the proof.

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