PHYSICAL REVIEW E **66**, 026212 (2002)

Possible neural coding with interevent intervals of synchronous firing

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(Received 12 December 2001; published 23 August 2002)

Neural networks composed of excitable neurons with noise generate rich nonlinear dynamics with spatiotemporal structures of neuronal spikes. Among various spatiotemporal patterns of spikes, synchronous firing has been studied most extensively both with physiological experimentation and with theoretical analysis. In this paper, we consider nonlinear neurodynamics in terms of synchronous firing and possibility of neural coding with such synchronous firing, which may be used in the ‘‘noisy brain.’’ In particular, reconstruction of a chaotic attractor modeling a dynamical environment is explored with interevent intervals of synchronous firing from the perspective of nonlinear time series analysis and stochastic resonance.

DOI: 10.1103/PhysRevE.66.026212 PACS number(s): 05.45.Xt, 87.18.Sn, 07.05.Mh

I. INTRODUCTION

It is widely believed that information in the brain is carried by neuronal spikes or action potentials. But the problem of how the information is encoded in these spikes remains unsolved. The most commonly accepted hypothesis is that firing rates of spikes encode the information. However, the possibility of spatiotemporal spike coding on the basis of spike timing, interspike intervals (ISIs), and mutual correlation of spikes from different neurons is currently being explored from a viewpoint of nonlinear neurodynamics (see Refs. [1,2] for background reviews). In fact, a single neuron has peculiar nonlinear dynamics with a threshold, which can be described by nonlinear dynamical systems like the Hodgkin-Huxley equations [3] and the FitzHugh-Nagumo equations [4]; such nonlinear dynamics generates various dynamical behaviors including the deterministic chaos [5].

In this paper, the possibility of spatiotemporal spike coding is considered particularly from the standpoint of nonlinear time series analysis [6]. To approach this problem, we analyze response characteristics of a neural network composed of the FitzHugh-Nagumo neurons when they are forced by a chaotic stimulus that models dynamical input from an environment. In particular, we study how the dynamical structure of the chaotic input is encoded into interevent intervals (IEIs), where the event is defined by timing of synchronous firing in the neural network.

II. IS THE CORTICAL NEURON AN INTEGRATOR OR A COINCIDENCE DETECTOR?

Spike timing and ISIs of real neurons are highly variable and irregular [7]. Whether variability and irregularity of neuronal spikes carry significant information or are just noise that should be smoothed away for good estimation of firing rates is an intriguing question. Related to this question, the problem of whether the cortical neuron serves as an integrator or a coincidence detector [8] has recently been revisited as a very important research topic [7,9]. It is usually understood that the integrator neuron and the coincidence detector neuron contribute to rate coding and spatiotemporal spike coding, respectively [1,9].

In this light, theoretical analysis of ISI reconstruction [10–13] is interesting because these results imply that a kind of spatiotemporal spike coding is possible even with the perfect integrator neurons that generate spikes by integrating the input signal $S(t)$ without any leak during interspike intervals; each interspike interval is equal to the ‘‘short-term’’ averaged $1/S(t)$ times the threshold [11].

III. METHODS OF ATTRACTOR RECONSTRUCTION

Mees *et al.* [14] showed that deterministic chaos of squid axon response can be detected by building a nonlinear dynamical model directly from noisy electrophysiological data without any *a priori* model. Applicability of the nonlinear time series analysis to ISI data has been also intensively explored by analyzing ISIs of various neuronal models stimulated by chaotic input [10–13], where a chaotic system is used as a model of a dynamical environment whose complex behavior is neither purely random nor perfectly predictable. In the case of the perfect integrator neuron without any *leak*, Sauer [10] showed that the geometrical structure of a chaotic system can be reconstructed with delay coordinates of ISI sequence data.

A neuron fires a spike when the membrane potential crosses a threshold. From the firing times of the neuronal spikes $\{T_1, T_2, \ldots, T_N\}$, the ISI sequence data can be obtained as

$$\{t_i = T_{i+1} - T_i, \quad i = 1,2,\ldots,N-1\}. \tag{1}$$

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With the ISI data, the dynamical structure of the chaotic input is reconstructed in a d-dimensional delay-coordinate space [15] as follows:

$$\boldsymbol{u}(i)=(t_i,t_{i-1},t_{i-2},\ldots,t_{i-d+1}). \tag{2}$$

In the present study, accuracy of the ISI reconstruction or interevent interval (IEI) reconstruction (see Sec. V) of chaotic dynamics is measured by the normalized prediction error (NPE). First, we divide the ISI or IEI data into two parts. From the first part of the data, a predictor $\tilde{f}:R^d \rightarrow R^d$, which approximates the data dynamics as $\boldsymbol{u}(i+1)\approx \tilde{f}(\boldsymbol{u}(i))$ is constructed. For the predictor $\tilde{f}$, a local linear predictor [10,16] is used in this paper. Then, for the second part of the data, nonlinear prediction is carried out. Namely, for a given initial state $\boldsymbol{u}(i)$, the s-step future state $\boldsymbol{u}(i+s)$ is predicted as $\tilde{\boldsymbol{u}}(i+s)=\tilde{f}^s(\boldsymbol{u}(i))$ with s iterations of the predictor $\tilde{f}$. The NPE $\mathcal{E}$ is finally calculated as the following normalized root-mean-square error:

$$\mathcal{E}=\frac{\langle (t_i-\tilde{t}_i)^2\rangle^{1/2}}{\langle (t_i-\overline{t})^2\rangle^{1/2}}, \tag{3}$$

where $\tilde{t}_i$ and $\overline{t}$ are the predicted values of the ith ISI or IEI and the average of $\{t_i\}$, and $\langle\cdot\rangle$ stands for the average over time series. In the following numerical experiments, the reconstruction dimension d, the prediction step s, and the number of the data N are fixed at $(d,s,N)=(4,1,5001)$ unless specified otherwise.

IV. NONLINEAR NEURODYNAMICS AND RECONSTRUCTION WITH INTERSPIKE INTERVALS

Since leaky components inevitably exist in biological neurons of the real brain, effects of the leak on ISI reconstruction should be analyzed in order to consider the ISI reconstruction as a possible mechanism of neural coding in the brain.

Racicot and Longtin [11] studied ISI sequence data generated from different neuronal models such as leaky integrate-and-fire neurons and clarified short-term deterministic predictability of the ISI data. Segundo *et al.* [17] applied the nonlinear analysis to ISI data recorded from synaptically inhibited crayfish pacemaker neurons and categorized the discharge forms. Richardson *et al.* [18] recorded ISI data from a rat cutaneous mechanoreceptor neuron stimulated by chaotic input and reported that the deterministic structure of the chaotic input can be preserved in the ISI data. Suzuki *et al.* [19] also found both numerically and experimentally that significant determinism is detectable from the ISI data generated by the leaky integrator neuron model and cricket wind receptor cells, which are stimulated by chaotic input. Furthermore, Castro and Sauer [12] observed improvement of the ISI reconstruction by adding stochastic noise to the FitzHugh-Nagumo neuron with subthreshold chaotic input. Castro and Sauer [13] considered reconstruction of chaotic dynamics with the period-parameter plots too.

The present study focuses on the result of Castro and Sauer [12] because the property is related to stochastic resonance phenomena that may contribute to detection of weak input stimuli by biological systems [20,21] and possibly to higher brain functions.

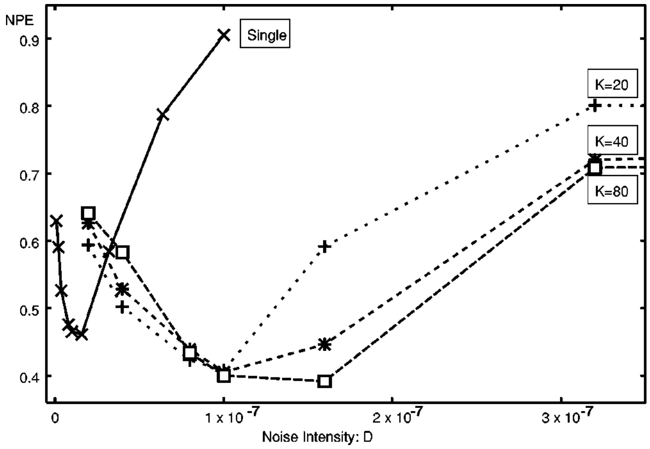

FIG. 1. NPE of ISI or IEI data generated by a network of the FHN neurons with noise. The number of neurons is varied as $K=1$ (single), 20, 40, and 80.

The FitzHugh-Nagumo (FHN) neuron model with noise is described as follows [4,12]:

$$\begin{aligned}\epsilon\dot{v}&=-v(v-0.5)(v-1)-w+S(t)+\xi(t),\\ \dot{w}&=v-w-0.15,\end{aligned} \tag{4}$$

where v is the membrane potential and w is the recovery variable; $\xi(t)$ is *Gaussian* white noise with $E[\xi(t)]=0$ and $E[\xi(t)\xi(s)]=2D\delta(t-s)$ with the noise intensity D. The neuron receives weak *subthreshold* input $S(t)=0.075+0.0092x(t)$ from variable x of the Rössler equations [22], $\dot{x}=\tau(-y-z)$, $\dot{y}=\tau(x+ay)$, $\dot{z}=\tau[bx+z(x-c)]$, where the parameter values are fixed at $(a,b,c,\tau)=(0.36,0.4,4.5,0.5)$. As reported by Castro and Sauer [12], the response characteristic of the FHN neuron shows a single sharp minimum NPE on increasing the noise intensity D, at which the optimal ISI reconstruction of chaotic dynamics is realized (see the "single" case of Fig. 1).

V. NONLINEAR NETWORK DYNAMICS AND RECONSTRUCTION WITH INTEREVENT INTERVALS OF SYNCHRONOUS FIRING

Although reconstruction of an input attractor with ISI data generated by a single neuron provides an intriguing mechanism of temporal spike coding, global dynamics at the level of neural networks rather than local dynamics at the level of single neurons should be considered because neurons in the brain, especially in the cortex, interact with each other massively. For example, Watanabe and Aihara [23] showed that neural networks composed of coincidence detector neurons generate rich dynamical phenomena with spatiotemporal structures of neuronal spikes, which include spatiotemporal chaos. Among various spatiotemporal spike patterns, synchronous firing has been most extensively studied both by

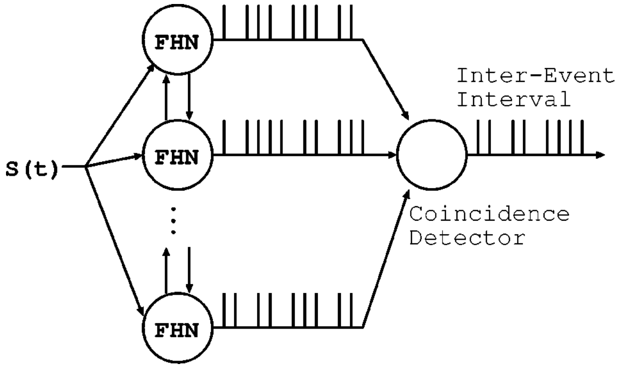

FIG. 2. A schematic diagram of a network composed of the globally coupled FHN neurons with noise. The coincidence detector neuron receives spike trains from all the FHN neurons and fires when and only when a large enough number of incident spikes are received almost simultaneously. This coincidence detector neuron is introduced as an observer for coincidence of input spikes, namely, synchronous firing in the network.

physiological experimentation (for example, see Refs. [24,25]) and by theoretical analysis (for example, see Refs. [25,26]).

Here, we explore the possibility of extending the temporal spike coding with ISI data to more robust spatiotemporal coding with interevent intervals data, where the event is defined not by a single spike but by synchronous firing emergent in the neural network.

Let us consider a neural network composed of globally coupled neurons with noise, each of which is the same with the FHN neuron of Eq. (4). The network dynamics is given as follows (see Fig. 2):

$$\epsilon\dot{v}_i = -v_i(v_i-0.5)(v_i-1)-w_i+S(t) + \frac{C}{K}\sum_{j=1}^{K}(v_j-v_i)+\xi_i(t), \tag{5}$$

$$\dot{w}_i = v_i - w_i - 0.15, \tag{6}$$

where (v_i, w_i) are the state variables of the ith FHN neuron for $i=1,\ldots,K$; ξ_i is noise of the ith neuron with $E[\xi_i(t)]=0$ and $E[\xi_i(t)\xi_j(s)]=2D\delta(t-s)\delta(i-j)$; and K is the number of the neurons in the network. In this model, electrical connections with the coupling constant C are introduced.

In the network, each FHN neuron receives the common subthreshold chaotic input $S(t)$ and generates spike trains at firing times $\{T_1(i), T_2(i), T_3(i), \ldots\}$ for $i=1,2,\ldots,K$. The network dynamics depends upon the coupling strength C. If the coupling is very weak, the neurons with noise tend to fire almost independent of each other. With increasing the value of C, we can observe synchronous firing due to network dynamics with interactions among neurons. We fix the value of C at 0.05 in the following analysis. Synchronous firing is defined as coincidence of the incident spikes from more than κK neurons (κ represents the coincidence ratio) to the coincidence detector neuron in Fig. 2 within a coincidence time window ρ. After firing, the coincidence detector neuron is absolutely refractory for a period ν.

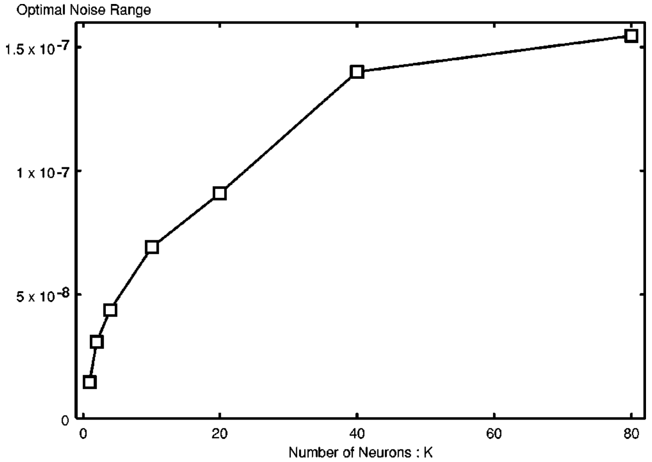

FIG. 3. An optimal noise range with NPE less than 0.5 increases as the number of the neurons increases from $K=1$ to $K=80$.

We call the intervals between adjacent events of synchronous firing as IEIs. With the IEI sequence data $\{t_i, i=1,\ldots,N-1\}$, the chaotic determinism is analyzed by the attractor reconstruction in the following d-dimensional delay-coordinate space:

$$\boldsymbol{u}(i)=(t_i, t_{i-1}, t_{i-2}, \ldots, t_{i-d+1}). \tag{7}$$

Figure 1 shows the NPE obtained from the IEI reconstruction by networks of neurons with $K=20$,40, and 80. The parameters for the coincidence detector neuron are set as $(\kappa,\rho,\nu)=(0.5,0.25,0.5)$. As the number of the neurons increases from $K=1$ to $K=80$, the range of optimal noise intensities defined as NPE less than 0.5 widens significantly as shown in Fig. 3. This implies that the network structure effectively facilitates the neural coding with synchronous firing and suppresses noisy components in a way that differs from population rate coding realized by a network structure with inhibitory coupling [27].

VI. CASE WITH SUPRATHRESHOLD INPUT

Next, we analyze a case of *suprathreshold input* rather than subthreshold input; namely, $S(t)=0.175+0.0092x(t)$. Figure 4 shows the NPE values obtained with the *suprathreshold* chaotic input, where the parameters of the nonlinear prediction are set as $(d,s,N)=(4,30,5001)$ and the parameters for the neural networks and the coincidence detector neuron are set as the same as in the *subthreshold* case. The solid line represents the NPE of the ISI data obtained from a single neuron, whereas the other lines indicate the NPE of the IEI data obtained from networks of neurons with $K=2$, 10, 20, and 40. For the ISI reconstruction by the single neuron, the NPE monotonically increases as the noise intensity D increases. This means that, in the case of *suprathreshold* input, noise in the neural dynamics simply deteriorates ISI reconstruction of the chaotic input.

As shown in Figs. 4 and 5, for the IEI reconstruction by the neural network model, the NPE monotonically decreases

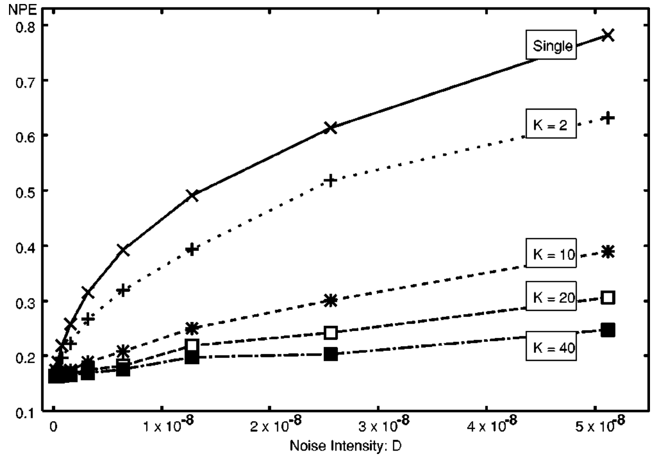

FIG. 4. NPE of the ISI or IEI reconstruction for *suprathreshold* chaotic input. The solid line indicates the ISI reconstruction by a single neuron, whereas the other lines indicate the IEI reconstructions by networks composed of neurons with $K=2$, 10, 20, and 40.

as the number of the neurons increases from $K=1$ to $K=1008$. This implies that the network structure contributes to improvement of the neural coding with synchronous firing also for the *suprathreshold* chaotic input and that better reconstruction of the original chaotic dynamics is realized. As demonstrated in Fig. 6, a smooth geometrical structure that resembles the original Rössler attractor is well reconstructed in the two-dimensional IEI space on the basis of IEI data generated by a network of 1008 FHN neurons with $D=5\times10^{-8}$.

VII. DISCUSSION

Synchronous firing in the neural network composed of the globally coupled FHN neurons has been analyzed in this paper from the viewpoint of neural coding. Synchronization itself has been widely studied in many systems [28,29]. Among various synchronous phenomena, the salient characteristic of the synchronous firing in the present model is that the IEI sequence data take continuous and nonperiodic values reflecting chaotic stimuli. Similar chaotic oscillation with synchronous firing is also observed by periodically stimulating a network composed of locally coupled FHN neurons [30] with respect to coherence resonance phenomena [31].

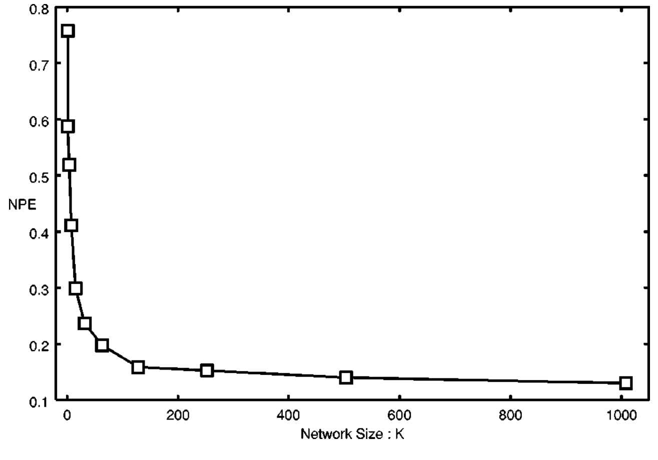

FIG. 5. NPE of the IEI reconstruction for the suprathreshold chaotic input with $D=5\times10^{-8}$ when the number of the neurons increases from $K=1$ to $K=1008$.

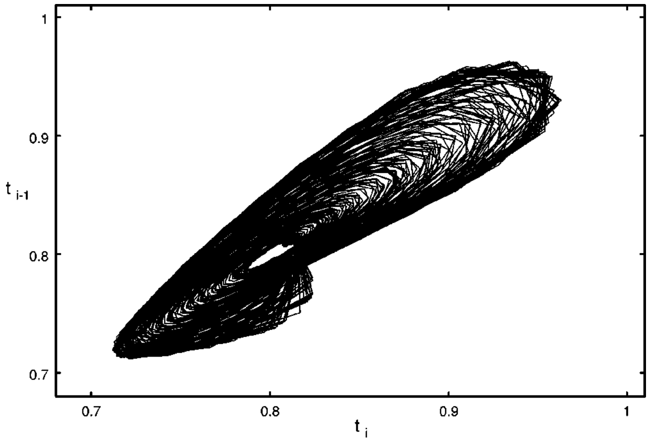

FIG. 6. Two-dimensional IEI reconstruction (t_i, t_{i-1}) of the Rössler attractor by the IEI data obtained from a network of 1008 neurons with $D=5\times10^{-8}$.

A kind of global coupling through electrical synapses is considered in this paper. Actually, rich electrical synapses up to distances of about 100 μm are found especially between cortical interneurons of fast-spiking cells and low-threshold-spiking cells and thought to contribute to the emergence of synchronization among such neurons [32]. It is probable that spatial distribution of electrical coupling is dependent on distances between neurons. Further, a variety of chemical synapses also coexist with electrical ones [32]. Generally speaking, local coupling and global coupling can produce different network dynamics as typically demonstrated by coupled map lattices and globally coupled maps [29]. In this respect, analysis on effects of the different network structures upon the IEI coding is an important future problem.

Another point to be carefully examined is a difference of the types of neurons. Both biological neurons and neuronal models are generally classified to class I and class II according to the repetitive firing characteristics [33–35]. Class-I neurons and class-II ones can be usually characterized by saddle-node bifurcations and Hopf bifurcations, respectively [34,35]. The FHN neuron model is a typical example of a class-II neuron. On the other hand, there are many cortical neurons that are thought to be of class I [35]. It should be noted that IEI coding has been also observed in a network composed of leaky integrate-and-fire neurons [36], whose response characteristics are similar to those of class-I neurons. It is also an important future problem to consider effects of the different neuronal types upon the IEI coding.

VIII. CONCLUSION

A neural network composed of the globally coupled FHN neurons with noise is introduced as a model that encodes dynamical information of chaotic input with IEI time series data. The numerical analysis demonstrated that the spatiotemporal neurodynamics can be used to realize a kind of neural coding with IEI data without fine tuning of the optimal noise level, as Collins *et al*. [21] showed in a summing stochastic resonance network with a kind of rate coding. The neural coding with IEI data is more robust than that with ISI data. These results imply the possibility that IEI neuronal data in the noisy brain retain dynamical information necessary for real-time estimation of time-dependent stimuli [37].

ACKNOWLEDGMENTS

This research was supported financially by CREST, JST. The authors thank Professor S. Amari for his warm encouragement, Professor H. Fujii for his valuable comments on electrical synapses and types of neurons, and N. Masuda and Dr. H. Suzuki for their helpful discussions.

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