PHYSICAL REVIEW E VOLUME 47, NUMBER 4 APRIL 1993

Dynamical behavior of the firings in a coupled neuronal system

Wei Wang
The International Center for Theoretical Physics, P.O. Box 586, 34100 Trieste, Italy
and Physics Department, Nanjing University, Nanjing 210008, People's Republic of China

G. Perez
The International Center for Theoretical Physics, P.O. Box 586, 34100 Trieste, Italy

Hilda A. Cerdeira
The International Center for Theoretical Physics, P.O. Box 586, 34100 Trieste, Italy
and Universidade Estadual de Campinas, Instituto de Fisica, 13081 Campinas, São Paulo, Brazil

(Received 27 October 1992)

The time-interval sequences and the spatiotemporal patterns of the firings of a coupled neuronal network are investigated in this paper. For a single neuron stimulated by an external stimulus I, the time-interval sequences show a low-frequency firing of bursts of spikes and a reversed period-doubling cascade to a high-frequency repetitive firing state as the stimulus I is increased. For two neurons coupled to each other through the firing of the spikes, the complexity of the time-interval sequences becomes simple as the coupling strength increases. A network with a large number of neurons shows a complex spatiotemporal pattern structure. As the coupling strength increases, the number of phase-locked neurons increases and the time-interval diagram shows temporal chaos and a bifurcation in the space. The dynamical behavior is also verified by the behavior of the Lyapunov exponent.

PACS number(s): 87.10.+e, 05.45.+b

I. INTRODUCTION

Aspects of the dynamical behavior of a coupled neuronal system, such as the synchronized patterns of neural activity which result from the cooperative dynamical properties, have attracted considerable interest over recent years [1–4]. Some experimental results have been obtained in the olfactory system, the visual cortex, and other brain areas. Local groups of neurons responding to a common stimulus display synchronized activity, and neurons responding to separate stimuli are also phase locked [5,6]. It has been suggested that the selective synchronization of neural activity serves as a mechanism for binding spatially distributed features into a coherent object [5,7]. It has also been well known for decades that a major component of sensory information is transmitted to the brain using a code based on the time intervals between firings of neurons, that is, action potentials or spikes [8–11]. Moreover, statistical analyses of experimentally obtained spike trains have concluded that the time intervals contain a significant irregular component [12]. It is thus important to investigate how the sensory information is encoded and how this process is affected by the irregular firings.

Recently an investigation of synchronized chaos in a network model of bursting neurons responding to an inhomogeneous stimulus has been made by Hansel and Sompolinsky [13]. They found that there are three types of phases for the network: an asynchronous stationary state, synchronized oscillations, and synchronized chaos. They concluded that the mechanism for generating the synchronized chaotic state in their network model is the long-range positive interactions in a population of neurons with a distribution of local driving currents.

In this paper, we are interested in the dynamical properties of the time-interval sequences and the spatiotemporal patterns of firings in a coupled neuronal system which presents a complex dynamical behavior of the neural activity. The outline of this paper is as follows. In Sec. II we describe the models of the coupled network. In Sec. III we present and discuss the results. In Sec. IV a summary is given.

II. A COUPLED NEURONAL NETWORK

A network of coupled Hindmarsh-Rose neurons [14] is represented by the following equations [13]:

$$\frac{dX_i}{dt}=f_1(X_i,Y_i,Z_i)+I_i+\sum_{\substack{j=1\\ j\neq i}}^{N} J_{ij}S_j(t)$$

$$=Y_i-aX_i^3+bX_i^2-Z_i+I_i+\sum_{\substack{j=1\\ j\neq i}}^{N} J_{ij}S_j(t)\ , \tag{1}$$

$$\frac{dY_i}{dt}=f_2(X_i,Y_i,Z_i)=c-dX_i^2-Y_i\ , \tag{2}$$

$$\frac{dZ_i}{dt}=f_3(X_i,Y_i,Z_i)=r[s(X_i-X_0)-Z_i]\ . \tag{3}$$

The Hindmarsh-Rose neuron of the three-variable model is a modification of Fitzhugh's Bonhoeffer–van der Pol model [15,16], with the property that each action potential is separated by a long interspike interval typical of real neurons. That is, each neuron is characterized by three time-dependent variables: the membrane potential X_i, the recovery variable Y_i, and a slow adaptation current Z_i. The external inputs are given by I_i. In the coupled neuronal network, the effect of the firing activity of the jth neuron on the ith neuron is modeled in Eq. (1) by an impulse current to the ith neuron, proportional to the synaptic strength J_{ij}, generated when the jth neuron is active. The neuron is active whenever its membrane potential exceeds a threshold value X^*,

$$S_j(t)=\Theta(X_j(t)-X^*) , \tag{4}$$

where $\Theta(x)=1$ if $x \geq 0$ and $\Theta(x)=0$ if $x<0$.

We first consider a network consisting of only two neurons that respond to a common external stimulus I:

$$\frac{dX_i}{dt}=f_1(X_i,Y_i,Z_i)+I+JS_j(t) , \tag{5}$$

$$\frac{dY_i}{dt}=f_2(X_i,Y_i,Z_i) , \tag{6}$$

$$\frac{dZ_i}{dt}=f_3(X_i,Y_i,Z_i) , \tag{7}$$

where $i=1,2$ and $j=2,1$, respectively.

To characterize the dynamical behavior of the time-interval sequences we record the successive times when the variable X crosses the $X=0$ line from above. That is, we define T_n by $X(T_n)=0$ and $X(T_n^-)>0$. After this, the time intervals $\delta_n=T_{n+1}-T_n$ can be obtained for all firings. From these δ_n values we can know that if the firing pattern is a train of bursts of one spike (period-1), the δ_n will have an unique value. For a train of bursts of n spikes (period-n), we get n different values for δ_n. For a train of bursts of undetermined number of spikes (chaotic), the δ_n will show a spread of values. In this paper we have also studied the spatiotemporal patterns of the firings for coupled neuronal network, Eqs. (1)–(3), with the numbers of neurons $N=800$. We used a uniform distribution for the stimulus I_i, with $1 \leq I_i \leq 5$ (i.e., $I_i=1+4i/N$). This distribution is the same as that used in Ref. [13]. The spatiotemporal patterns of the firings are obtained by plotting the neural activity, i.e., the firing time $t=T_n$, as defined before, with a point in the time axis against the space, i.e., the location of the ith neuron.

All the numerical calculations are done by using a modified fourth-order Runge-Kutta method. In the study of the time-interval sequences of the firings for a single and two coupled neurons, the time steps were chosen as $\Delta t=0.0125$. We first run the program to $t=2300$ to discard the transient and then followed the time to $t=3800$ or longer. To get the spatiotemporal patterns of a network with a large number of neurons, the time step was chosen to be $\Delta t=0.1$. We have also done some calculations with smaller steps, finding that the patterns do not change. All parameters are held constant at $a=1.0$, $b=3.0$, $c=1.0$, $d=5.0$, $s=4.0$, $r=0.006$, and $X_0=-1.6$, which are the values used in Ref. [14].

III. RESULTS AND DISCUSSION

A. The firing of a single neuron

First, in this section, we present results for the time-interval sequences for firing when there is no coupling between the neurons in the network. In this case, we only need to study one set of equations, Eqs. (5)–(7), with $J=0$. In Fig. 1, we plot the time interval δ_n against the stimulus I. From Fig. 1, we can see that when $I<1.32$, there is no spike since the stimulus I is too small to stimulate the neuron from its stable quiescent state with $X=X_0<0$. As I increases there is a train of regularly spaced spikes, the period-1 state. There is only one δ_n value for each I value when $1.32<I<1.57$. When $1.57<I<2.13$, there are periodic bursts of two spikes per burst, i.e., a period-2 state. For this case, in Fig. 1, there are two values of δ_n. Then it follows period-3 and period-4. At $I=2.83$, there is an intermittency transition to chaos. Finally, there follows a reversed period-doubling cascade to a period-1 state again. This is due to the fact that for a large stimulus I, the system is in a high-frequency repetitive firing state. The code for the information process is different for the differing firing states.

B. The firing of two coupled neurons

When the neurons in a network are completely synchronized and phase locked, we can use a simplified model of two coupling neurons to study the network since from Eqs. (1)–(3) all the states of neurons are equivalent and all the neurons are fired at the same time.

In Figs. 2(a)–2(c) we show the time intervals of the firings δ_n against the stimulus I for the coupling strengths $J=0.5$, 1.0, and 3.5, repetitive. From these plots we can see that as the coupling increases, the complexity of the time-interval sequences becomes simpler. That is, as the coupling increases, the bifurcation regions

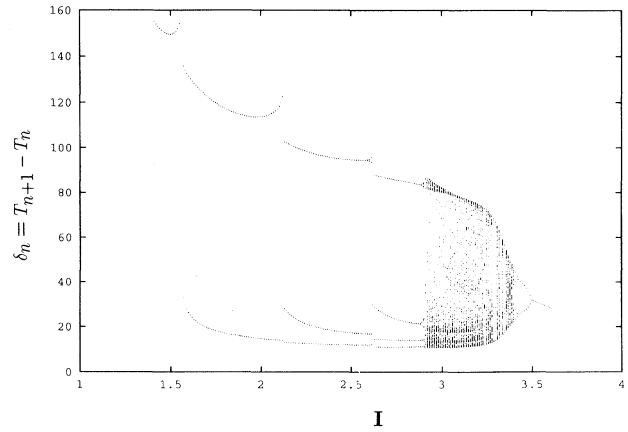

FIG. 1. $\delta_n=T_{n+1}-T_n$, the time-interval sequences of the firing for a single neuron vs the external stimulus I. Results from simulations of one set of equations, Eqs. (5)–(7), with $J=0$, and the time step $\Delta t=0.0125$ were used. For each I value, the time is followed to $t=5000$ and the first $t=2300$ are eliminated for transient.

become narrower. When the coupling is low, for example, in the case of $J = 0.5$, the firing of the system keeps most of the features of the single neuron, the case of $J = 0$. There is a bifurcation to a low-frequency repetitive firing state consisting of a train of regular spaced spikes, and a region of chaotic firing, as well as a reversed period-doubling cascades to a period-1 state [see Fig. 2(a)]. However, when $J = 1.0$, the bifurcation region is small [see (Fig. 2(b)] and there are almost only period-1 and period-2 firing states. Finally, when $J = 3.5$, the bifurcation region disappears and there is only a period-1 repetitive firing state [see Fig. 2(c)]. Actually as the coupling increases, the effective stimulus $I' = I + JS_j(t)$ is increased, which enables the neuron to be stimulated with a repetitive firing. If the coupling is larger than a certain value, there is no more chaotic firing.

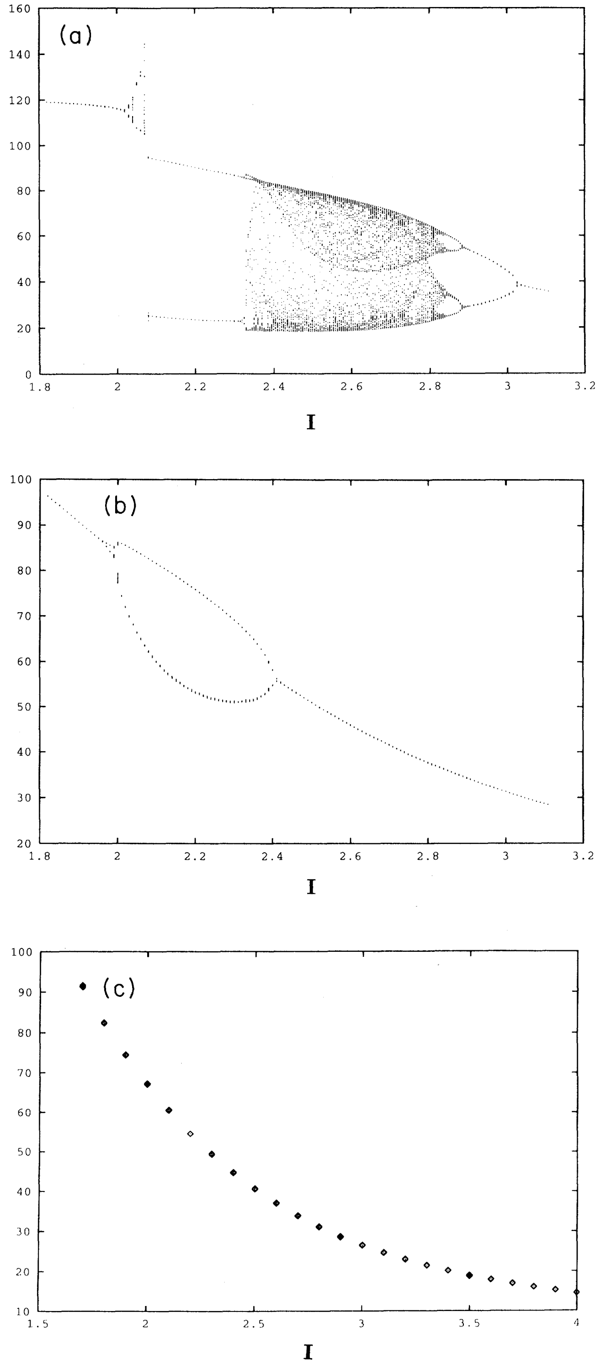

FIG. 2. $\delta_n = T_{n+1} - T_n$, the time-interval sequences of the firing for two coupled neurons with the coupling strength J vs the external stimulus I. (a) $J = 0.5$; (b) $J = 1.5$; (c) $J = 3.5$. The time step $\Delta t = 0.0125$ was used. For each value of I, the time is followed to $t = 5000$ with the first $t = 2300$ eliminated.

C. Spatiotemporal patterns of a coupled network

Now we consider a network consisting of N neurons with different values of I_i coupled globally by excitatory interactions, $J_{ij} = J/N$. Here we are using I_i distributed uniformly between 1 and 5, as before. Simulations of the network with $0 < J < 6.0$ revealed three phases [13]: an asynchronous stationary state, synchronized oscillations, and synchronized chaos. Here in this paper we are interested in the spatiotemporal patterns and the time intervals of the firings of the network as shown in Fig. 3 for the coupling strengths $J = 0.5$, 3.0, and 6.0, respectively. From these plots we can see that there are some structures of the firing state. For the lower stimulated region (the smaller i region) the firing period is longer, and for the higher stimulated region the period is shorter and the points become dense since for the high stimulus I, the neuron is repetitively fired. In addition, for some small groups, or clusters, of neurons, the activities have a synchronized behavior as they have the same frequency of firings, phase locked. Notice, however, that the actual time of firing within one of these clusters is widely distributed. When the coupling increases, the synchronization is expanded to a larger group of neurons, and finally to the whole network of neurons.

When $J = 0.5$, we can see from Fig. 3(a) that the pattern of firings can be divided into four regions: (1) nonfiring region for $(i < 60)$—there is no firings since the local effective stimulus $I' = I + \sum_j J_{ij} S_j(t)$ is too small and is not enough to stimulate the neurons from its quiescent state; (2) periodic firing region for $(60 < i < 370)$—the firing is period-1 to period-4 but the time widths of these period-n bursts are different; (3) chaotic firing region for $(370 < i < 500)$—the firing is chaotic, the time interval is irregular and with no structure in the pattern. The total numbers of chaotic neurons is about $n = 130$, which takes about $n/N \simeq 16\%$ for the network; (4) the repetitive high-frequency firing region for $(500 < i < 800)$—for this region, the pattern is regular. In Fig. 3(b), we have constructed a time-interval sequence versus the local neurons from the spatiotemporal pattern showed in Fig. 3(a). From this figure we can see that the time interval property is similar to Fig. 2(a). There is a bifurcation of a train burst consisting of one, two, three, and four spikes, and an intermittency to chaotic state, as well as a reversed bifurcation to a period-1 firing state. The difference is that this bifurcation is in the neuronal space and not in J as seen before.

As the coupling strength J increases, the number of n

of neurons being chaotic also increases. For example, when $J=1.5$, the number n is about $n=700$, which takes about $n/N \simeq 90\%$ of the neurons in the network. For $J=2.0$ this factor is almost 1, which means that all the neurons are chaotic. In Fig. 3(c) we have shown the case for $J=3.0$, an intermediate coupling. We can see that the nonfiring region has disappeared and there is a spatially correlated oscillation for the neurons. However, the oscillation is not phase locked in the whole network and only in some very small regions there is a phase locked activity. The synaptic current $I_s(t)$ is periodic in t and very noisy. The activity of most of the neurons tends to synchronize with this periodic current $I_s(t)$. We call this a quasisynchronization. From the time-interval figure shown in Fig. 3(d), the bifurcation region is extended to the whole network and many points are distributed irregularly near the two main values of δ_n for each neuron. As our conclusion, such an irregular spatiotemporal

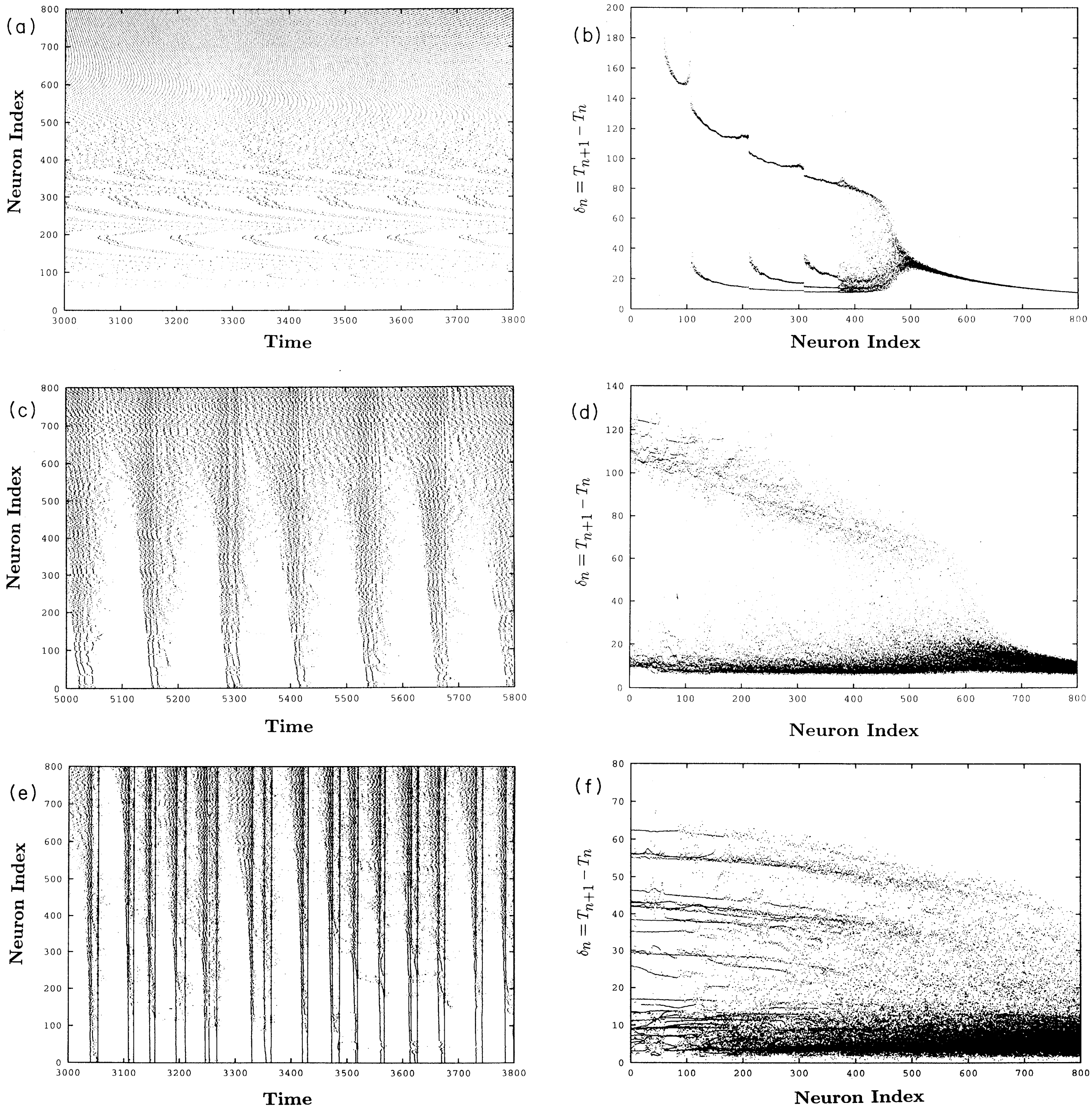

FIG. 3. The spatiotemporal patterns: neuron i vs the time intervals of the firing of spike for a coupled network with different coupling strength J: (a) and (b) $J=0.5$; (c) and (d) $J=3.0$; (e) and (f) $J=6.0$. The time step $\Delta t=0.1$ and the number of the neurons $N=800$ were used.

behavior is definitely chaotic since the time-interval sequences against the local neurons can be recognized as an attractor for the network.

In Figs. 3(e) and 3(f) we presented the results for $J = 6.0$. From the spatiotemporal pattern of the activity, we can see that the spatial structure is more ordered, i.e., all the neurons are phase locked together. But for the temporal behavior, the activity of the neurons is chaotic.

It should be noticed that for very small values of J (and even for $J = 0$), the synaptic current I_{syn} is not given by a constant plus noise. In fact, we have found that a periodic component, albeit of very small amplitude, appears for large values of N. This periodic component simply represents the effects of the oscillatory behavior of the independent neurons for most of the values of I included in the interval $1 \le I \le 5$. An average over some set of periodically evolving variables will have in general at least quasiperiodic behavior and is only in special cases that the periodic components balance perfectly and the average becomes a constant. There is of course a noisy component, coming from the chaotic neurons, but this component decays for large N. In addition, the introduction of the coupling acts as a positive feedback and tend to increase the periodic component. In Fig. 4 we plotted the periodicity of the synaptic current for (a) $J = 0$ and (b) $J = 0.5$, in a network of 10^4 neurons. It is clearly seen that the synaptic current is periodic even for $J = 0$. In Fig. 5 we show the corresponding power spectra of the synaptic current $I_{\mathrm{syn}}(t)$. As the number of neurons is increased, the noisy part decreases, but there still exists a peak of very low frequency which represents the periodicity of the synaptic current. However, in the case of large values of J, the synaptic current $I_{\mathrm{syn}}(t)$ is impulselike. The neurons are synchronized to this impulselike current. The fronts of the activity of the neuron encode the information at the same time (except for the high-I region there are some dilute activities).

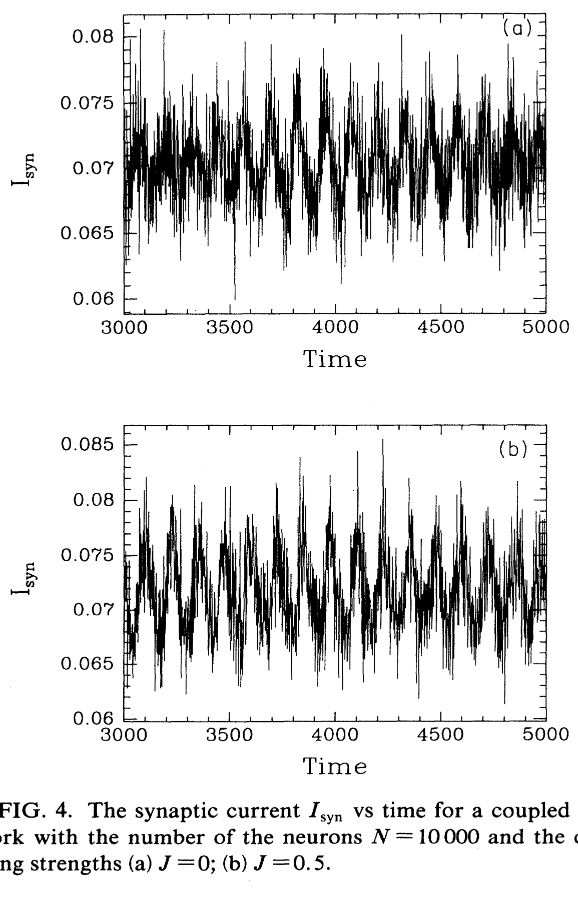

FIG. 4. The synaptic current I_{syn} vs time for a coupled network with the number of the neurons $N = 10\,000$ and the coupling strengths (a) $J = 0$; (b) $J = 0.5$.

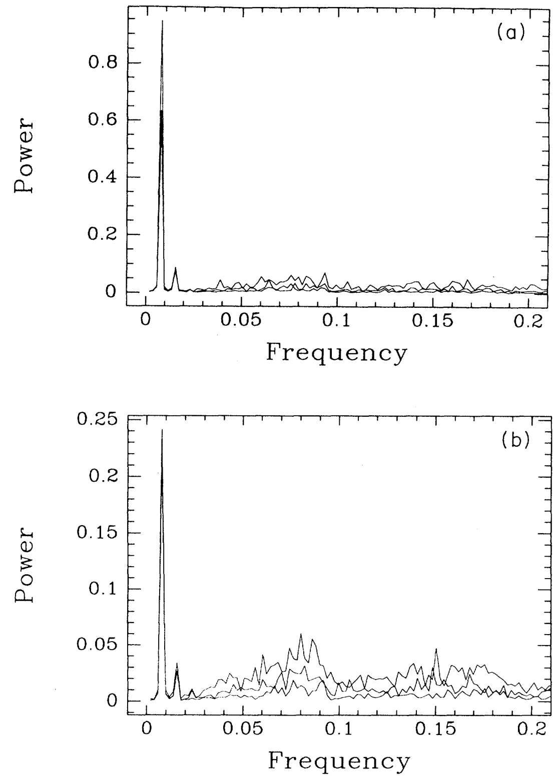

FIG. 5. Power spectra of the synaptic current I_{syn} for a coupled neuronal network with the number of the neurons $N = 2400, 4800, 10\,000$ (from the top curve to the bottom one) and the coupling strengths (a) $J = 0$; (b) $J = 0.5$.

Finally, in order to verify the chaotic behavior, we have also calculated the local maximum Lyapunov exponent λ_i against the neuron i as shown in Figs. 6(a) and 6(b), respectively. From these two figures, we can see that there are positive value of λ_i for the chaotic region and negative ones for periodic behavior. At the transitions between one phase-locking region and another, there are some small factors with positive λ_i.

IV. SUMMARY

Neuronal activity is well known to be noisy. This stochasticity is observed both during information transmission and spontaneously. One of the most obvious features of such stochasticity is in the uncertainty arising in the interspike interval (the time-interval sequences

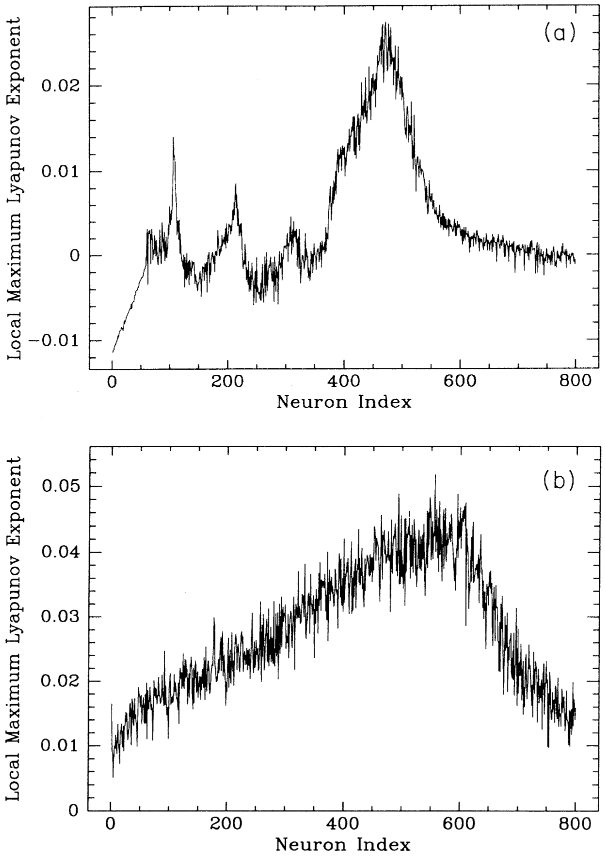

FIG. 6. The local maximum Lyapunov exponent λ_i vs the neuron i. The time is followed to $t=9000$ and the first $t=4000$ are eliminated for transient. (a) $J=0.5$; (b) $J=3.0$.

studied in this paper), for example, in the interspike interval distribution for a neuron in the spinal chord of a decerebrate cat, where they may be a variance of the order of 20% of the mean interval [17]. In this paper, we started from a model of coupled neuronal network without any noise and studied the time-interval sequences and the spatiotemporal patterns of the activities of the neurons. We found that (1) for a single neuron, or a network with zero coupling, the chaotic activities can exist for some range of the external stimulus [16]; (2) for a coupled two-neuron model, the chaotic activity is dominated by the coupling strength. For large coupling, the bifurcation region can disappear totally; (3) for a coupled network with an uniform distribution of the external stimulus, the activity of the neurons can be regular or irregular (chaotic). From the spatiotemporal patterns, the strong coupling results in a spatio-order phase, or synchronized firing state of the neurons, while the temporal behavior of the neurons is chaotic. The whole chaotic behavior cannot be accounted for by the finite-size noise. The three phases for this coupled neuronal network are (a) an asynchronous stationary state ($0<J<0.8$); (b) quasisynchronized chaos ($0.9<J<3.2$); (c) synchronized chaos ($J>3.2$). However, for more strong coupling, we can also expect to have a nonchaotic activity of neurons, the fronts of activity appear in a regular time interval, since (a) the strong coupling increases the spatiocorrelation which can have a complete synchronization of the neurons and (b) the effect of this very high coupling or the synaptic current is shifted to the local neurons, and it can result in a high-frequency repetitive firing of the neurons.

It is worth noting that for modeling more realistic neuronal network, one must consider the structure of the network. This can be done assuming the local coupling and stimulus are a function of the number of neurons, i.e., differently in the space. However, the qualitative results for the nonlinear behavior are the same as for the simple model.

ACKNOWLEDGMENTS

H.A.C. acknowledges support from the Instituto Nazionale de Fisica Nucleare (INFN). W.W. would also like to thank E. Canessa for valuable discussions.

---

[1] C. Skarda and W. J. Freeman, Behav. Brain Sci. **10**, 161 (1987).

[2] O. Sporns, G. Tononi, and G. M. Edelman, Proc. Natl. Acad. Sci. U.S.A. **88**, 129 (1991).

[3] H. G. Schuster and P. Wagner, Biol. Cybern. **64**, 77 (1990); **64**, 83 (1990).

[4] H. Sompolinsky, D. Golomb, and D. Kleifeld, Proc. Natl. Acad. Sci. U.S.A. **87**, 7200 (1990); Phys. Rev. A **43**, 6990 (1991).

[5] C. M. Gray, P. Konig, A. K. Engel, and W. Singer, Nature (London) **338**, 334 (1989).

[6] R. Eckhorn *et al.*, Biol. Cybern. **60**, 121 (1988).

[7] Ch. von der Malburg and W. Schneider, Biol. Cybern. **54**, 29 (1986).

[8] J. C. Eccles, *The Understanding of the Brain* (McGraw-Hill, New York, 1973).

[9] S. W. Kuffler, R. Fitzhugh, and H. B. Barlow, J. Gen. Physiol. **40**, 683 (1957).

[10] R. M. Siegel, Physica (Amsterdam) D **42**, 385 (1990).

[11] A. Longtin, A. Bulsara, and F. Moss, Phys. Rev. Lett. **67**, 656 (1991).

[12] H. C. Tuchwell, *Stochastic Processes in the Neurosciences* (SIAM, Philadelphia, 1989); A. V. Holden, *Models of the Stochastic Activity of Neurons,* Lecture Notes in Biomathematics Vol. 12 (Springer, Berlin, 1976); G. Sampath and S. K. Srinivasan, *Stochastic Models for Spike Trains of Single Neurons,* Lecture Notes in Biomathematics Vol. 16 (Springer, Berlin, 1977).

[13] D. Hansel and H. Sompolinsky, Phys. Rev. Lett. **68**, 718 (1992).

[14] J. L. Hindmarsh and R. M. Rose, Proc. R. Soc. London Ser. B **221**, 87 (1984).

[15] R. Fitzhugh, Biophys. J. **1**, 445 (1961).

[16] Wei Wang, J. Phys. A **22**, L627 (1989).

[17] J. G. Taylor, in *Neurodynamics,* edited by F. Pasemann and H.-D. Doebner (World Scientific, Singapore, 1991).