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**DYNAMICAL BEHAVIOUR OF THE FIRING  
IN COUPLED NEURONAL SYSTEM**



**INTERNATIONAL  
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EDUCATIONAL,  
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International Atomic Energy Agency  
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IN COUPLED NEURONAL SYSTEM \***

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**ABSTRACT**

The time interval sequences and the spatio-temporal 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 large numbers of neurons shows a complex spatio-temporal pattern structure. As the coupling strength increases, the numbers of phase locked neurons increase and the time interval diagram shows temporal chaos and a bifurcation in the space. The dynamical behaviour is also verified by the Lyapunov exponent.

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## 1 Introduction

Aspects of the dynamical behaviour 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, 2, 3, 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, 9, 10, 11]. Moreover, statistical analysis 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 (HS) [13]. They found that there are three types of phase for the network: 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 spatio-temporal patterns of firings in a coupled neuronal system which presents a complex dynamical behaviour of the neural activity. The outline of this paper

is as follows. In section II, we describe the models of the coupled network. In section III we present and discuss the results. In section IV a summary is given.

## 2 A coupled neuronal network

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

$$\frac{dX_i}{dt} = f_1(X_i, Y_i, Z_i) = Y_i - aX_i^3 + bX_i^2 - Z_i + I_i + \sum_{j=1, j \neq i}^N J_{ij}S_j(t), \quad (1)$$

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

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

The Hindmarsh-Rose neuron of three variable model is a modification of Fitzhugh's B.v.P. (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  $j$ -th neuron on the  $i$ -th neuron is modeled in Eq.(1) by an impulse current to the  $i$ -th neuron, proportional to the synaptic strength  $J_{ij}$ , generated when the  $j$ -th neuron is active. The neuron is active whenever its membrane potential exceeds a threshold value  $X^*$ ,

$$S_j(t) = \theta(X_j(t) - X^*), \quad (4)$$

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  $I$ :

$$\frac{dX_i}{dt} = f_1(X_i, Y_i, Z_i) + I + J S_j(t) \quad (5)$$

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

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

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

To characterize the dynamical behaviour 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  $\delta_n$  values we can know that if the firing pattern is a train of bursts of one spike (period-1), the  $\delta_n$  will have an unique value. For a train of bursts of  $n$  spikes (period- $n$ ), we get  $n$  different values for  $\delta_n$ . For a train of bursts of undetermined number of spikes (chaotic), the  $\delta_n$  will show a spread of values. In this paper we have also studied the spatio-temporal 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 used in Ref. [13]. The spatio-temporal 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  $i$ -th 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 spatio-temporal patterns of a network with a large numbers 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 are not changed. 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 Refs. [14].

### 3 Results and discussion

#### 3.1 The firing of a single neuron

Firstly, 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 the Eqs.(5-7) with  $J = 0$ . In Fig.1, we plot the time interval  $\delta_n$  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  $\delta_n$  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  $\delta_n$ . 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 encode for the information process is different for the different firing states.

#### 3.2 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 Fig.2(a)-2(c), we show the time intervals of the firings  $\delta_n$  against the stimulus  $I$  for the coupling strength  $J = 0.5, 1.0$  and  $3.5$ , respectively. 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 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 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 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 enable the neuron to be stimulated with a repetitive firing. If the coupling is larger than a certain value, there is no more chaotic firing.

#### 3.3 The Spatio-temporal patterns of a coupled network

Now we turn to 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]: asynchronous stationary state, synchronized oscillations and synchronized chaos. Here in this paper, we are interested in the spatio-temporal patterns and the time intervals of the firings of the network as showed in Fig.3 for the coupling strength  $J = 0.5, 3.0$  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 behaviour 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 spatio-temporal 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 bursts consisting of one, two, three and four spikes, and an intermittency to chaotic state, as well as a reversed bifurcation to 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  $n$  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 one which means that all the neurons are chaotic. In Fig.3(c) we have showed 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. But, 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 noise. The activity of most of the neurons tends to synchronize with this periodic current  $I_s(t)$ . We call this a quasi-synchronization. From the time interval figure showed in Fig.3(c), the bifurcation region is extended to the whole network and a lot of points are distributed irregularly

near the two main values of  $\delta_n$  for each neurons. As our conclusion, such an irregular spatio-temporal behaviour, is definitely chaotic since the time interval sequences against the local neurons can be recognized as an attractor for the network.

In Fig.3(e) and Fig.3(f) we presented the results for  $J = 6.0$ . From the spatio-temporal 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 behaviour, 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 behaviour of the independent neurons for most of the values of  $I$  included in the interval  $1 \leq I \leq 5$ . An average over some set of periodically evolving variables will have in general at least quasiperiodic behaviour, 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  $I_{syn}(t)$ . 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  $I_{syn}(t)$  is impulse-like. The neurons are synchronized to this impulse-like 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).

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

## 4 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 studied in this paper), for example in the interspike interval distribution for a neuron in the spinal chord of a decerebrate cat, where there 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 spatio-temporal 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 neurons models, 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 spatio-temporal patterns, the strong coupling results in a spatio-order phase, or synchronized firing state of the neurons, while the temporal behaviour of the neurons is chaotic. The whole chaotic behaviour can not be accounted for by the finite size noise. The three phases for this coupled neuronal network are: (a) asynchronous stationary state ( $0 < J < 0.8$ ); (b) quasi-synchronized chaos ( $0.9 < J < 3.2$ ); (c) synchronized chaos ( $J > 3.2$ ). However, for more strong coupling, we can also expect to have a

non-chaotic activity of neurons, the fronts of activity appear in a regular time interval, since: a) the strong coupling increases the spatio-correlation which can have a complete synchronization of the neurons. 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 to note that for modelling 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 qualitatively results for the nonlinear behaviour are the same as the simple model.

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## Figure Captions

### Figure 1:

$\delta_n = T_{n+1} - T_n$ , the time interval sequences of the firing for a single neuron versus the external stimulus  $I$ . Results from simulations of one set of Eq.(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.

### Figure 2:

$\delta_n = T_{n+1} - T_n$ , the time interval sequences of the firing for two coupled neurons with the coupling strength  $J$  versus 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  $t = 2300$  are eliminated.

### Figure 3:

The spatio-temporal patterns: neuron,  $i$ , versus 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 numbers of the neurons  $N = 800$  were used.

### Figure 4:

The synaptic current  $I_{syn}$  versus time for a coupled network with the number of the neurons  $N = 10000$  and the coupling strength: (a)  $J = 0$ ; (b)  $J = 0.5$ .

### Figure 5:

Power spectra of the synaptic current  $I_{syn}$  for a coupled neuronal network with the number of the neurons  $N = 2400, 4800, 10000$  (from the top curve to the bottom one) and the coupling strength: (a)  $J = 0$ ; (b)  $J = 0.5$ .

### Figure 6:

The local maximum Lyapunov exponent  $\lambda_i$  versus the neuron,  $i$ . The time is followed to  $t = 9000$  and first  $t = 1000$  are eliminated for transient. (a)  $J = 0.5$ ; (b)  $J = 3.0$ .

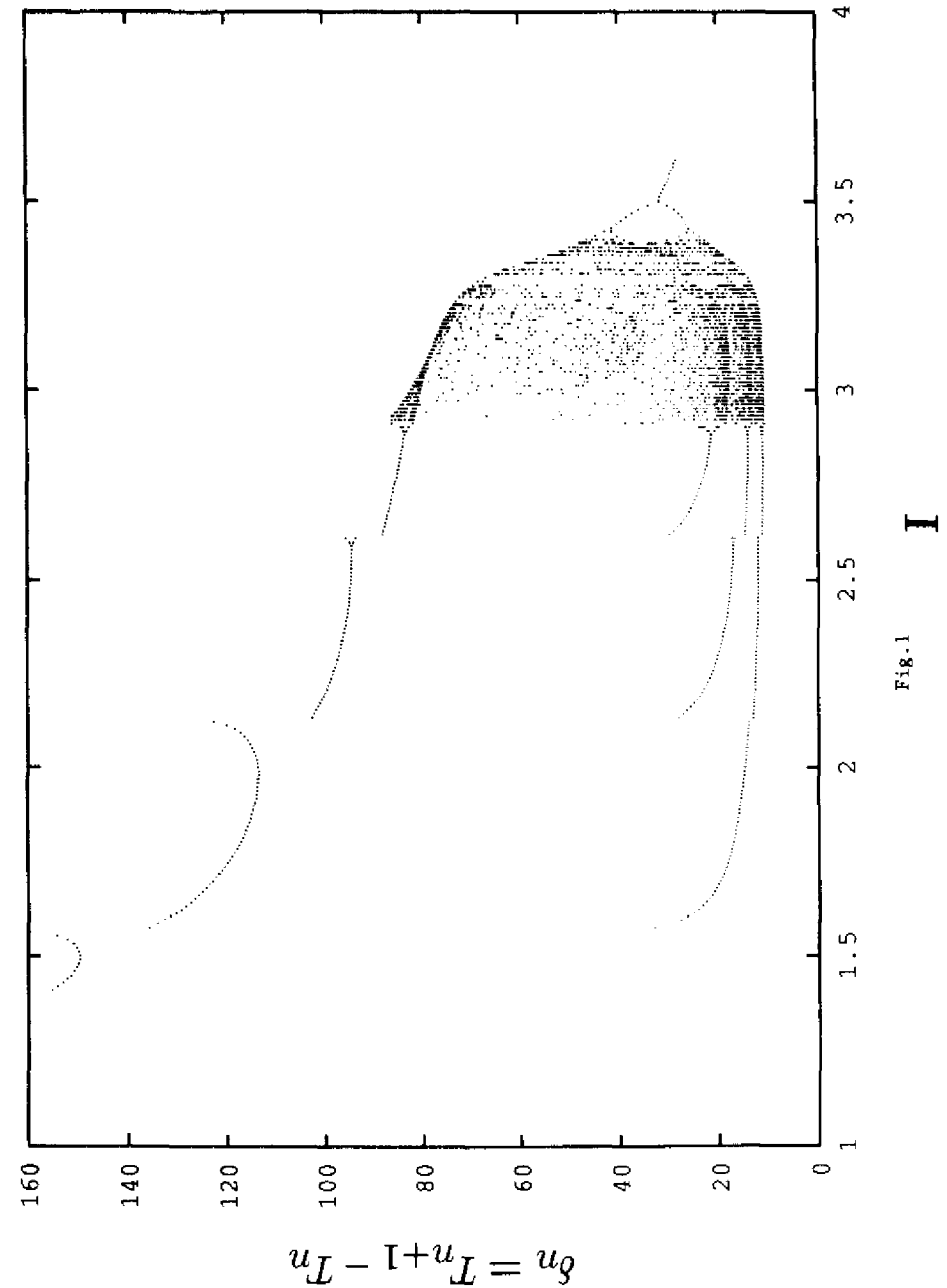
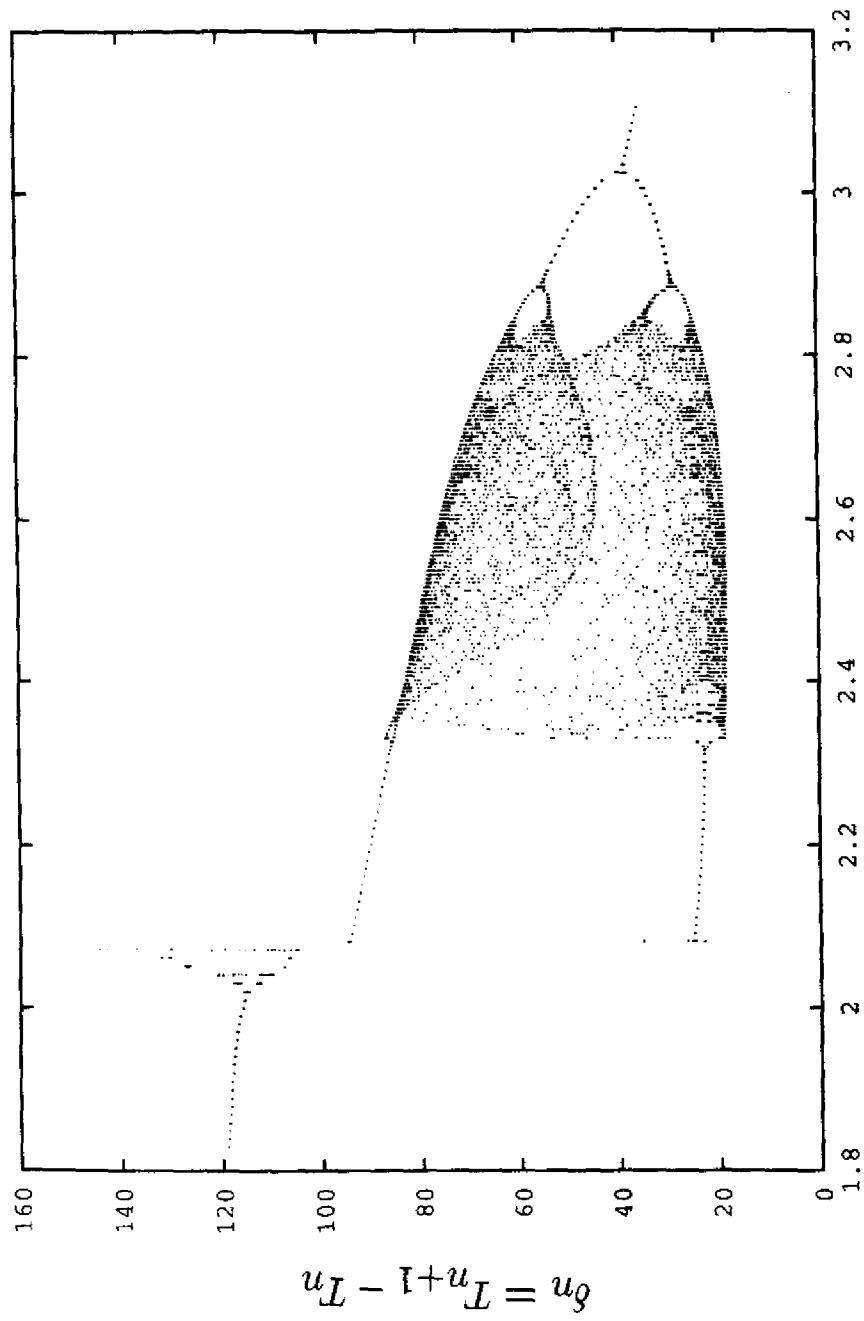
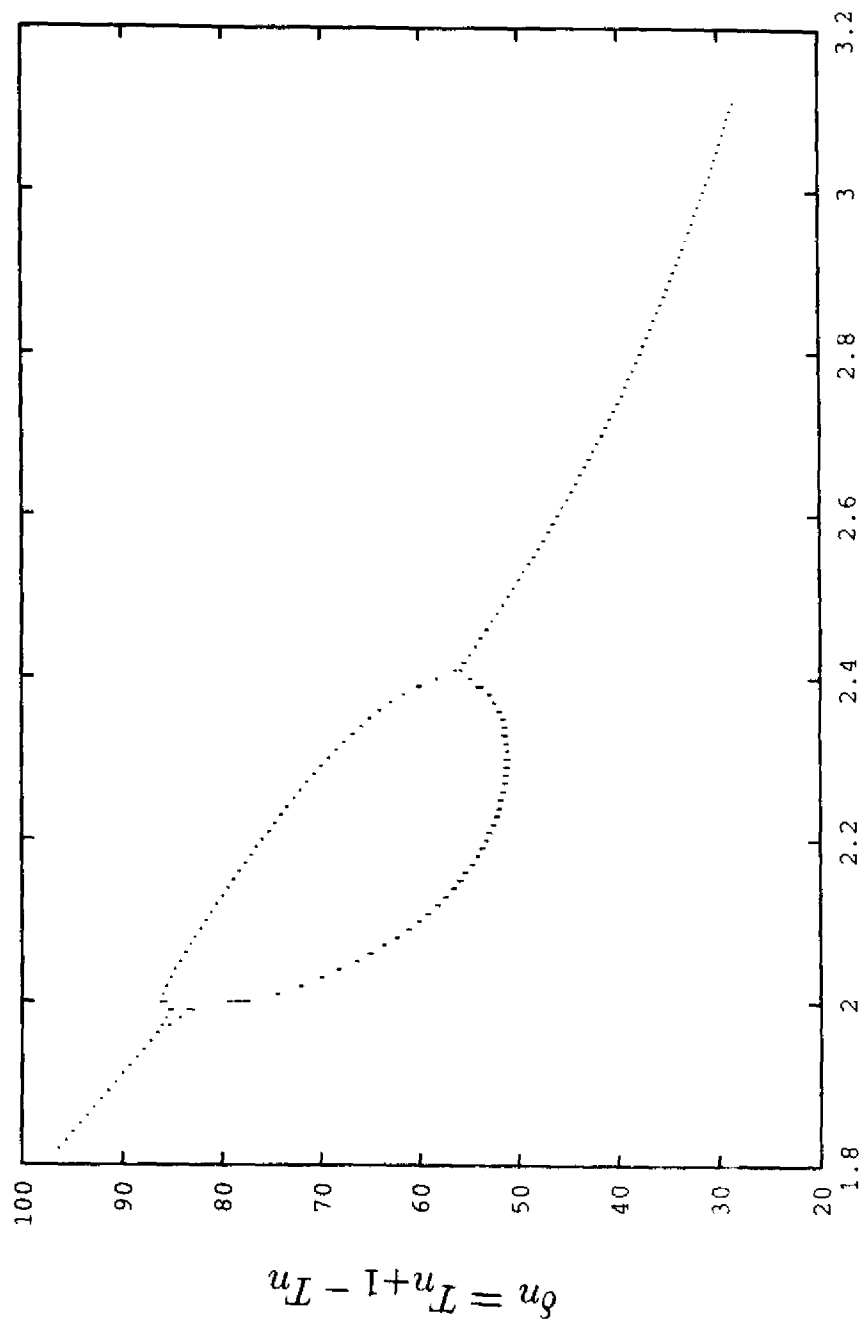


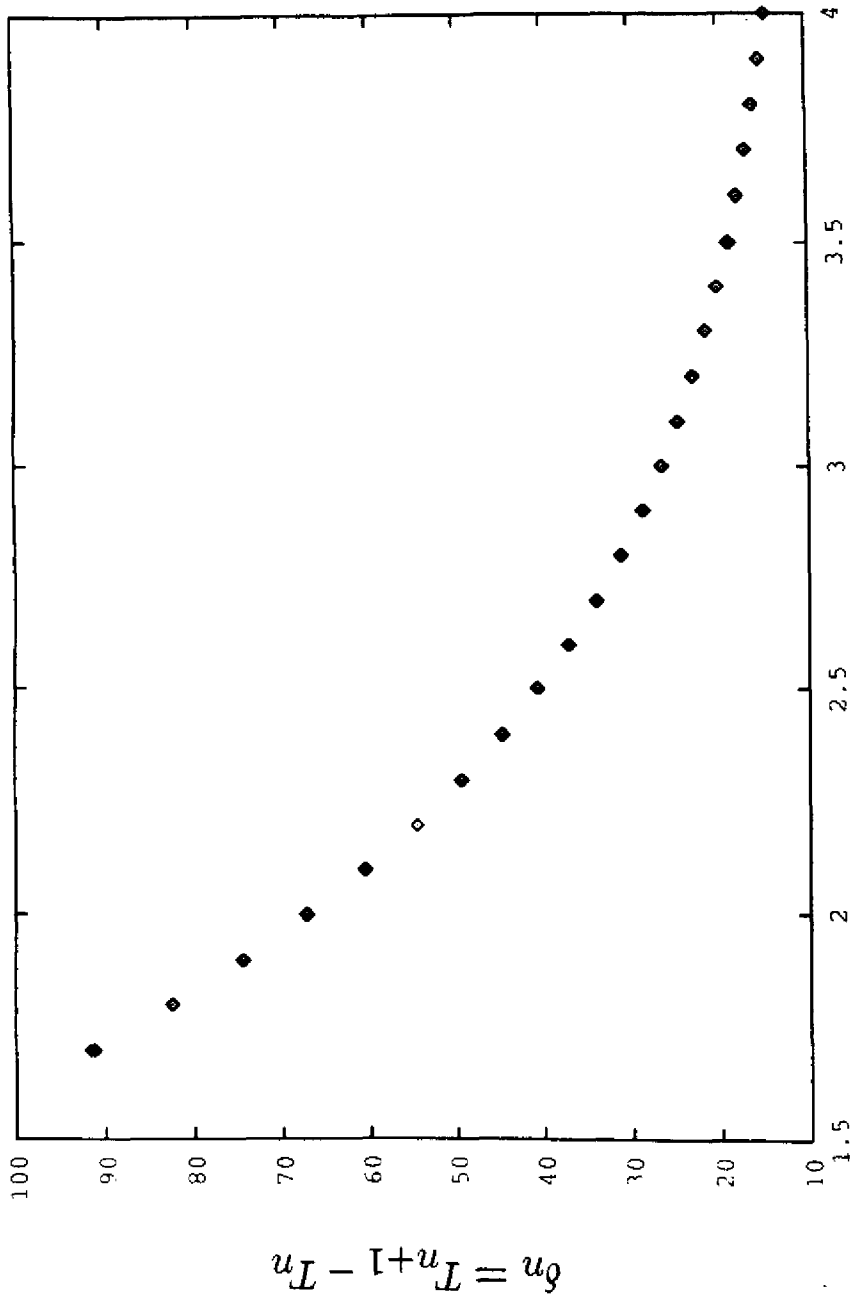
Fig.1



I  
Fig. 2(a)



I  
Fig. 2(b)



**I** Fig. 2(c)

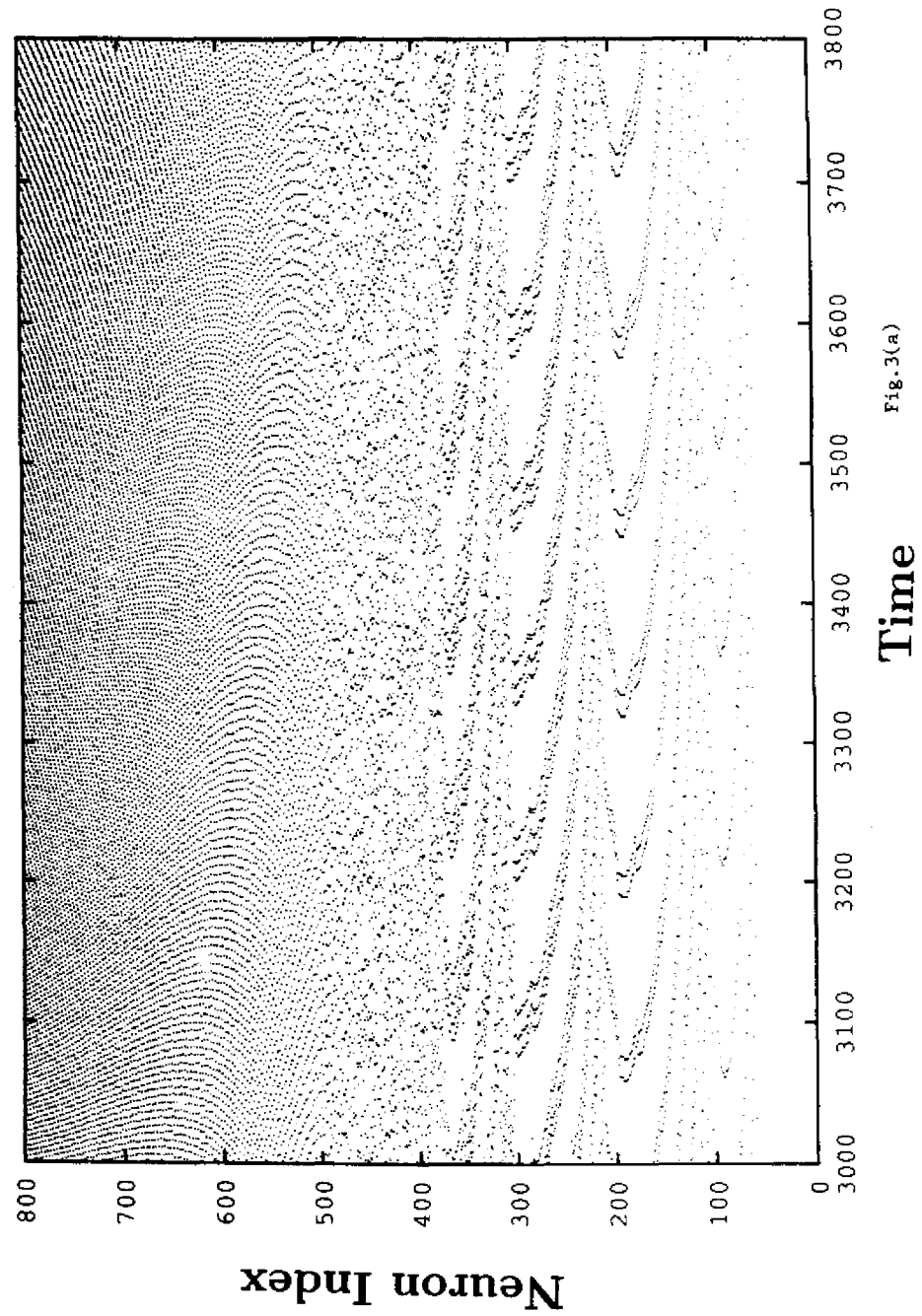


Fig. 3(a)

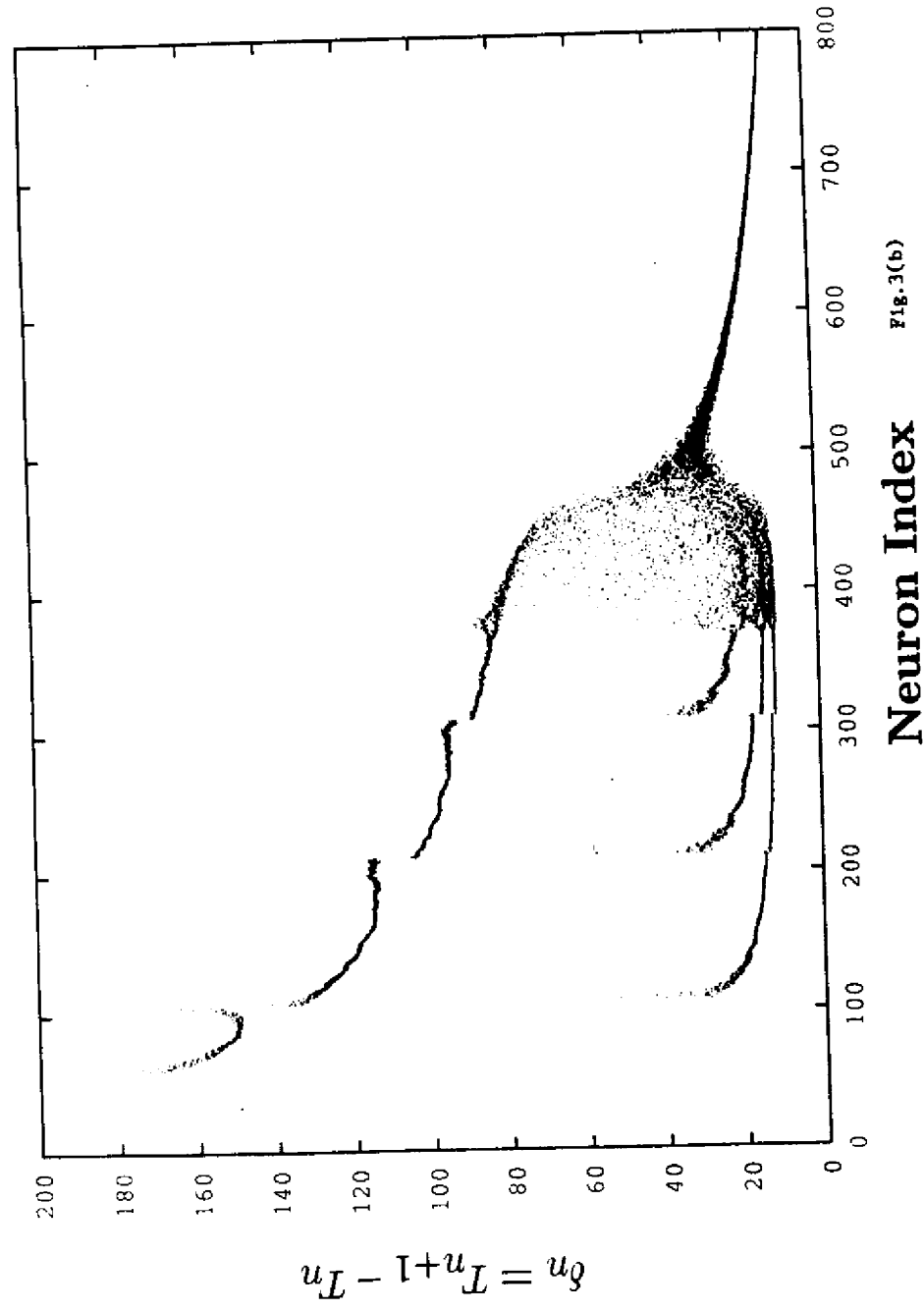


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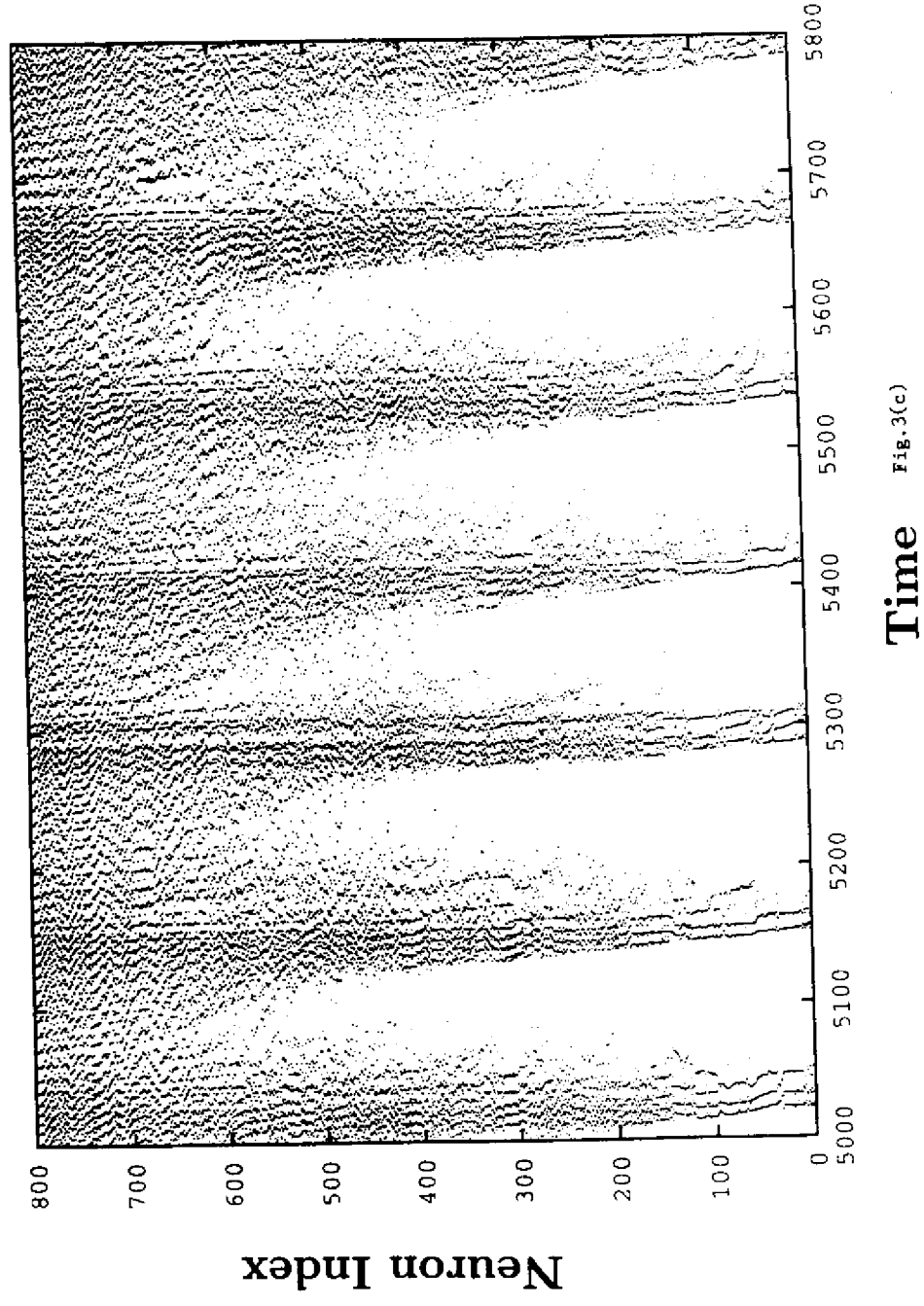
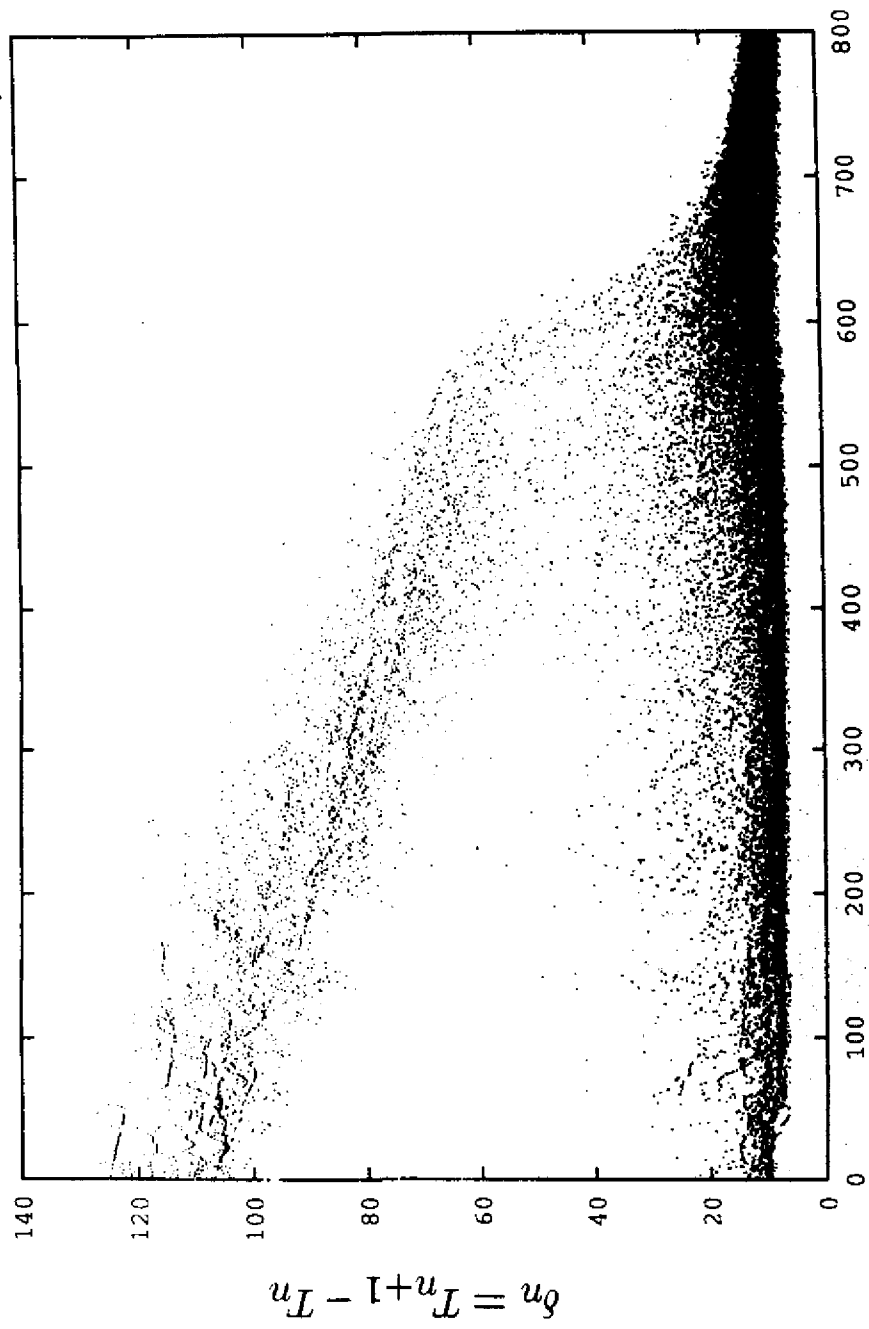
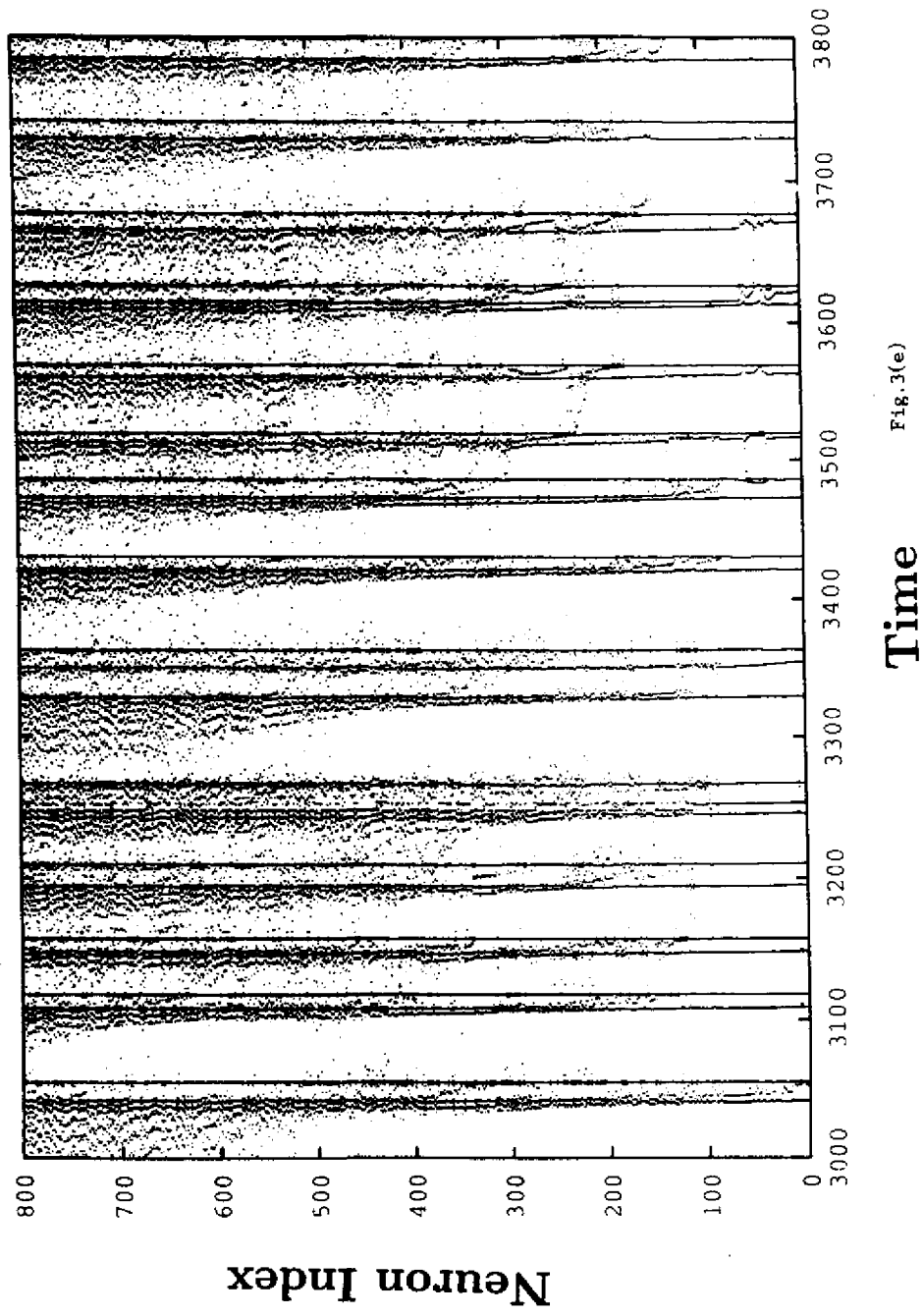


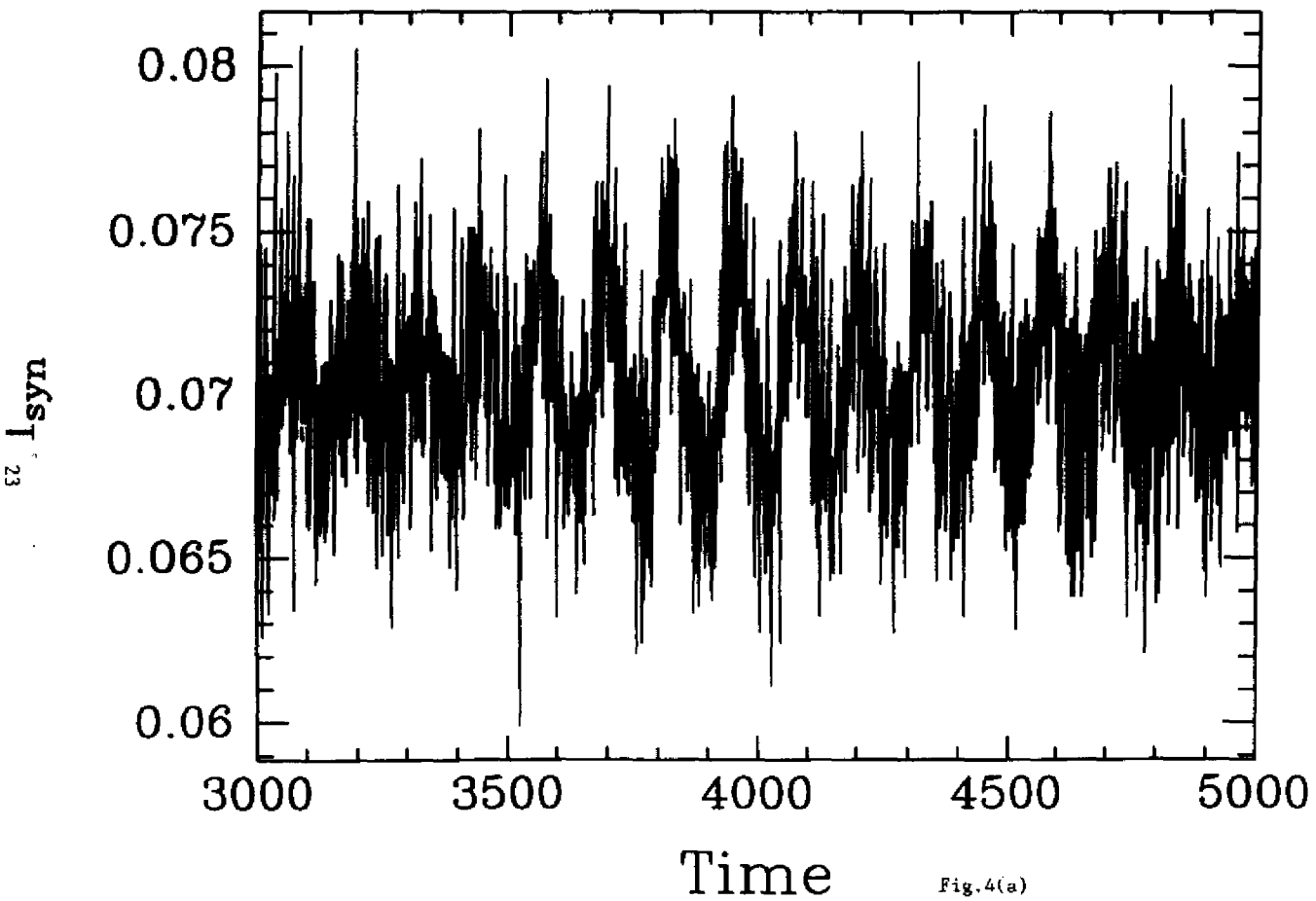
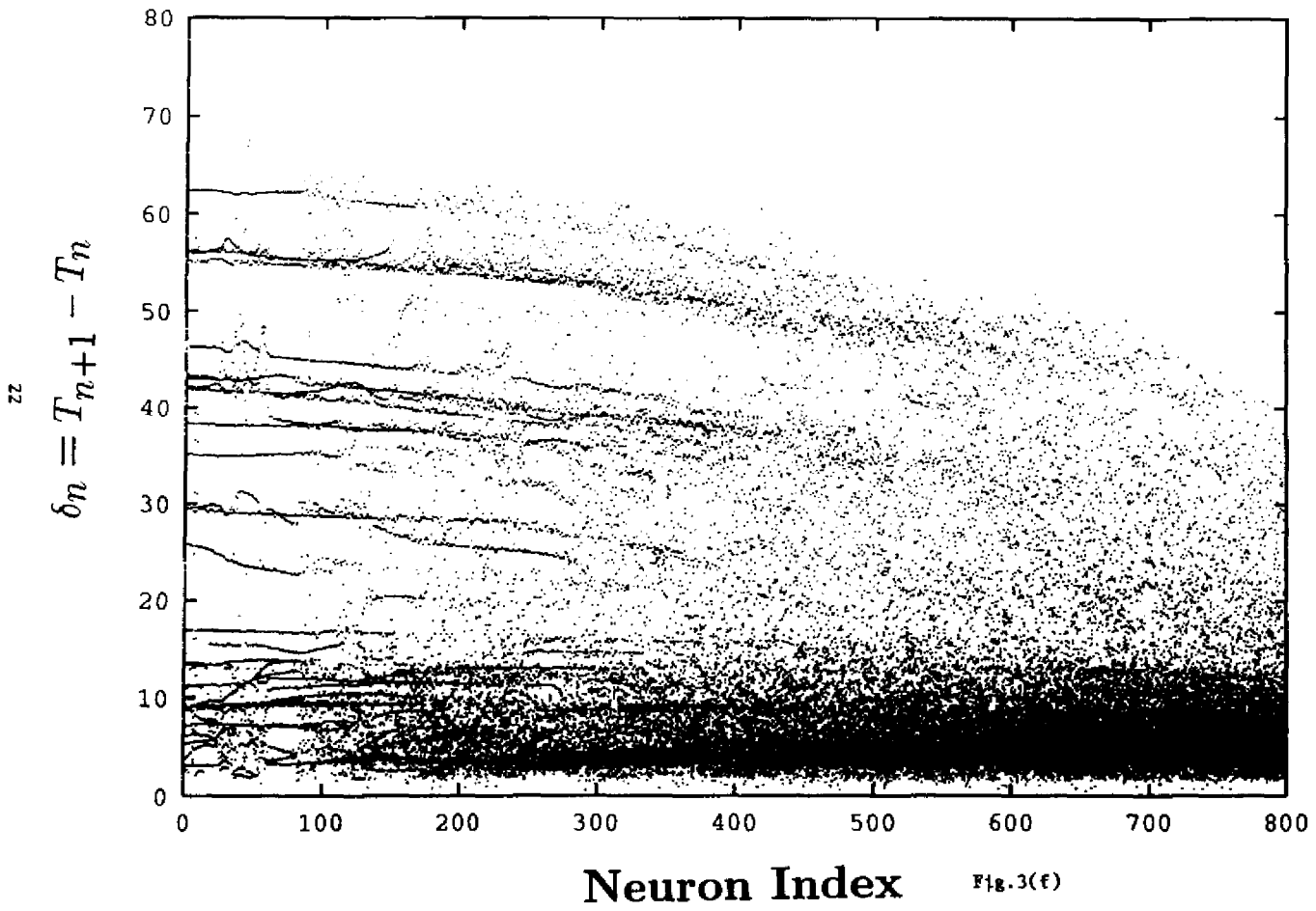
Fig.3(c)



Neuron Index Fig. 3(d)



Time Fig. 3(e)



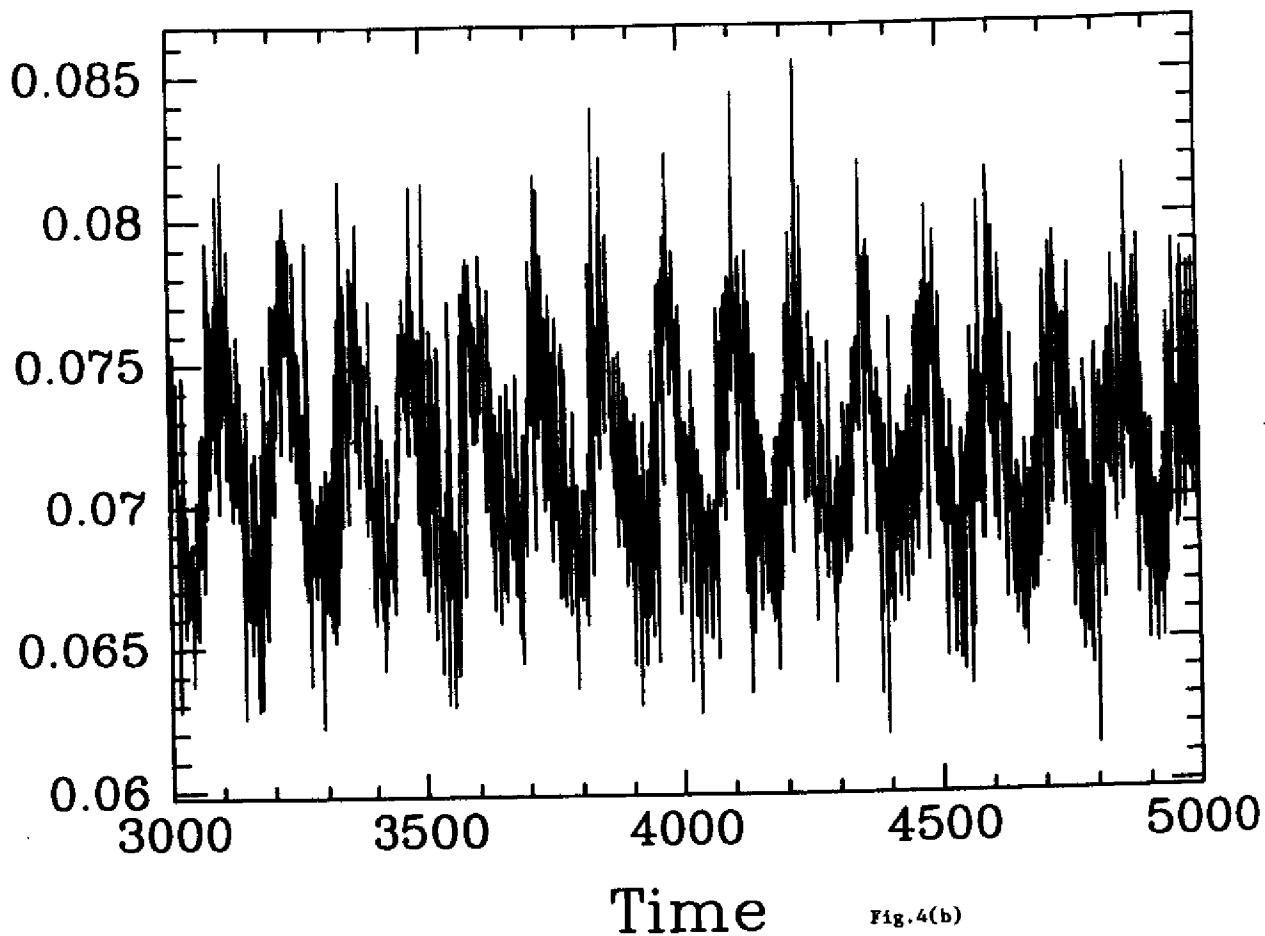


Fig.4(b)

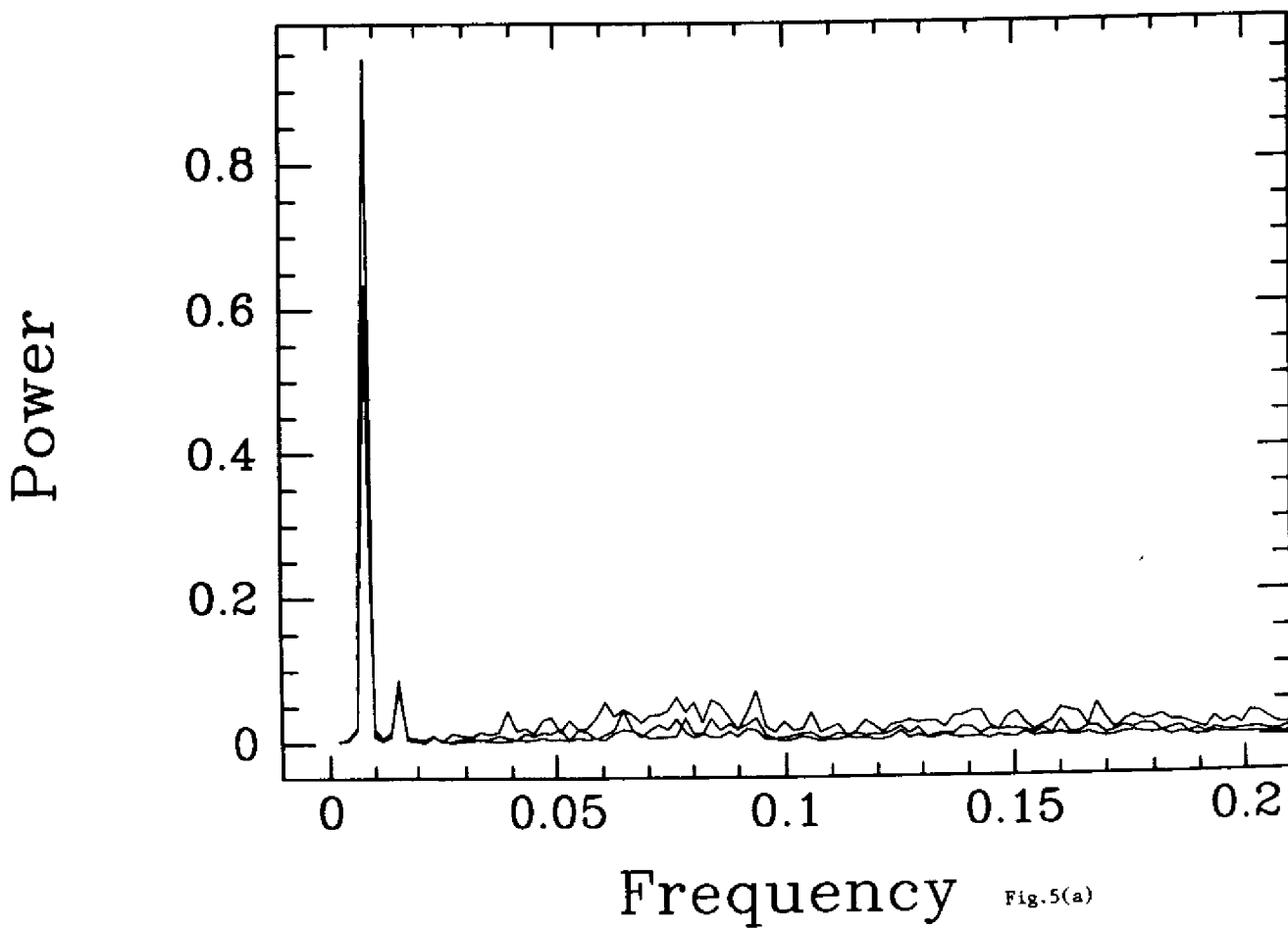


Fig.5(a)

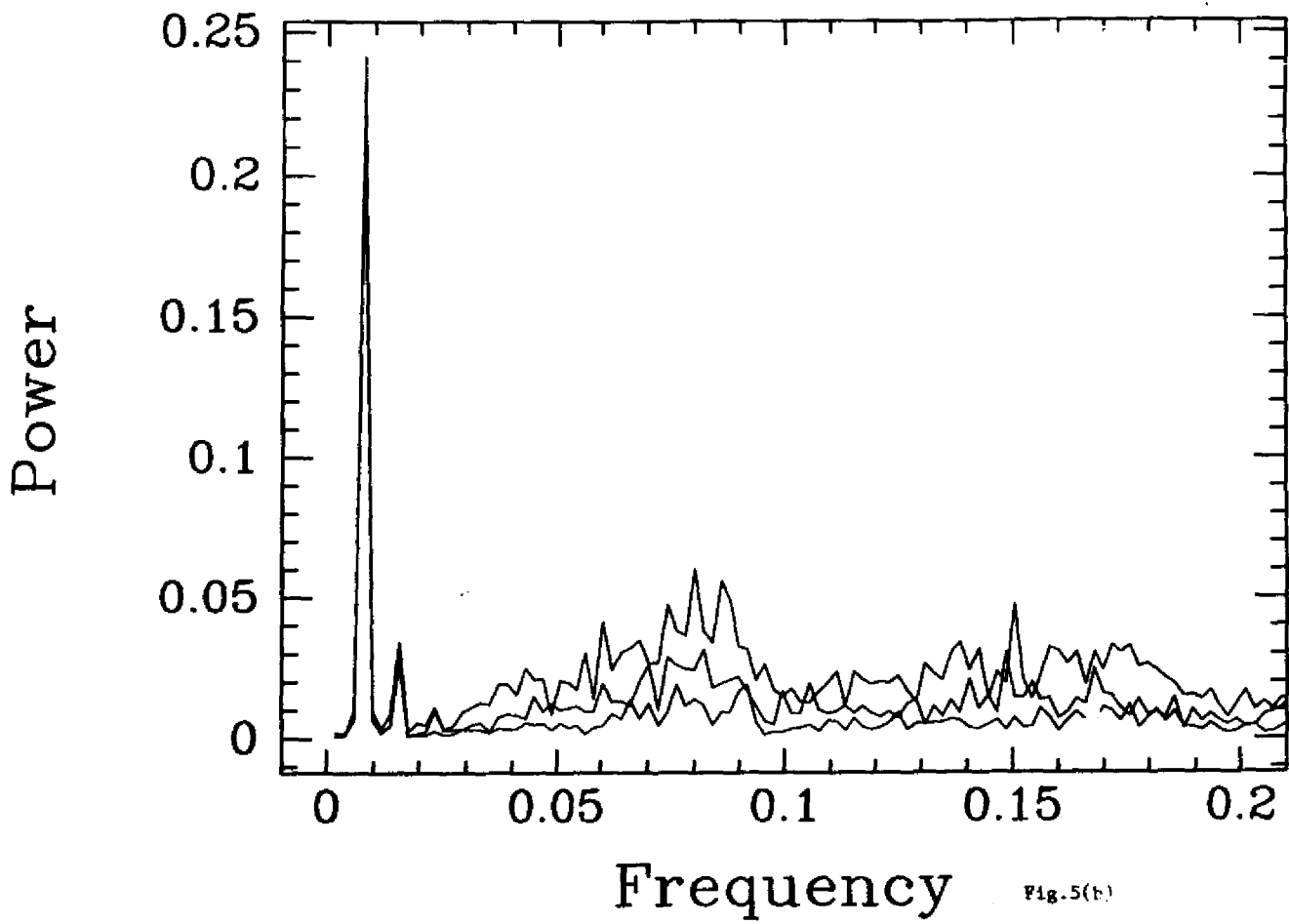


Fig.5(b)

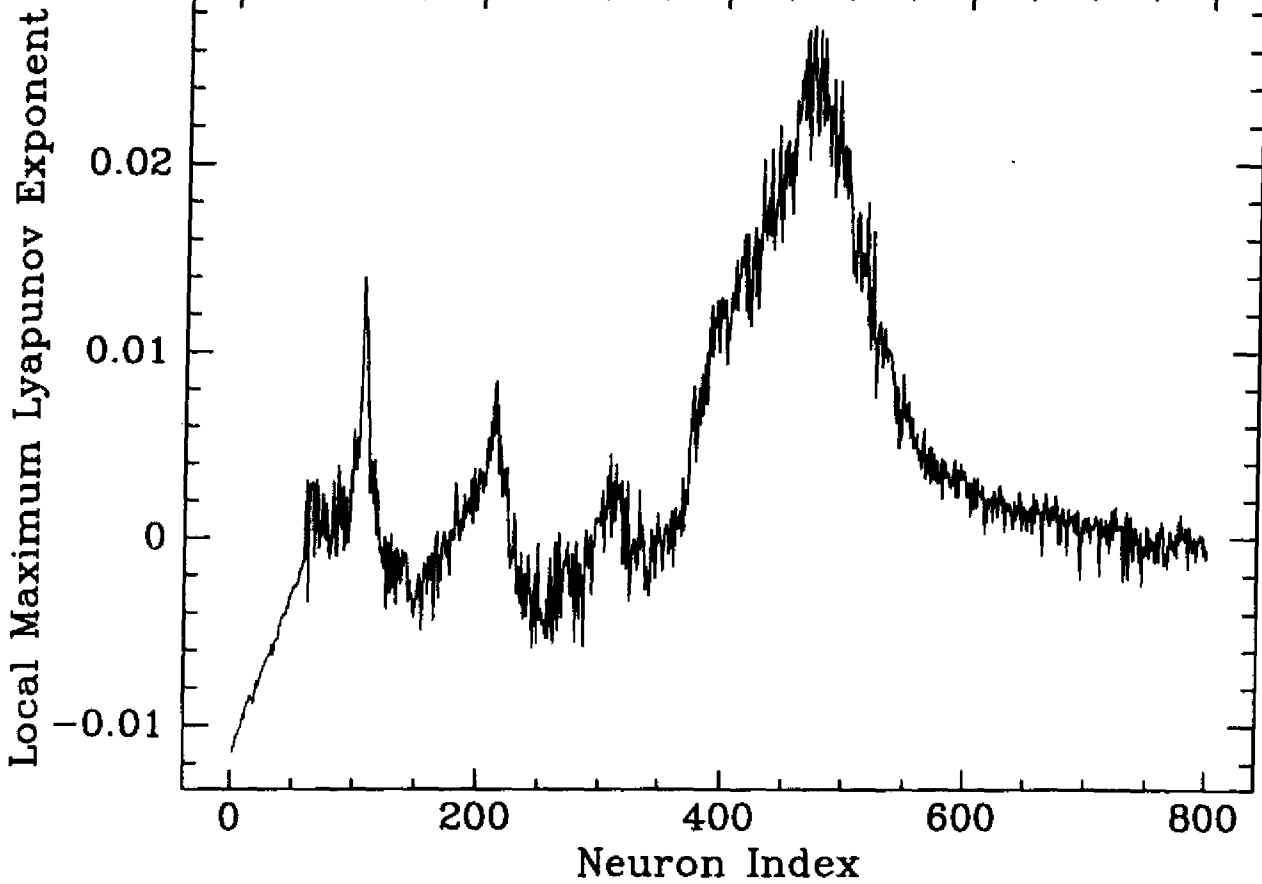


Fig.6(a)



