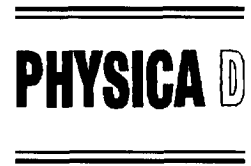




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Synchronous oscillatory activity in assemblies of chaotic model neurons

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Abstract

Recent physiological evidence signals the presence of synchronous oscillatory behavior over distances of some millimeters in several parts of the brain of mammals. These oscillations are customarily explained in terms of the synchronization of coupled limit cycle, relaxation or pulsed oscillators. Following the suggestion by Freeman that perceptive processes might be shaped by the intrinsically chaotic activity of the brain, it is shown that the synchronous oscillatory activity of assemblies of neurons can also be retrieved from model neurons exhibiting chaotic behavior. This is achieved by the coexistence of appropriate synchronizing connections and the effect of external stimuli. The effect of the latter is to suppress chaos in the corresponding sensory neuron, yielding a particular periodic behavior.

1. Introduction

In the recent years evidence from physiological studies has accumulated indicating the existence of synchronous rhythmic activity in different areas of the brain of some mammals, like cats and monkeys. These studies include the olfactory bulb [1], thalamo-cortical spindle rhythms [2], the visual cortex [3], the olivocerebellar system [4], hippocampal rhythms, and somatomotor cortices, among others [5]. Moreover, it has been suggested [6–8] that this synchronous activity may have a role in solving the so-called binding problem. This problem is related to the fact that processing of information is scattered among different areas of the brain, while it is not clear how this information is linked, as it appears that there is not any privileged part of it in which all the information

is centralized. The processing through synchronous oscillations would be related to the use of a temporal code: those neurons firing synchronously at one level of the cortex would be processing parts of the same percept. Thus, a given neuron could be engaged in processing information corresponding to different percepts, and the brain could achieve a high degree of parallelism. The existence of synchronous oscillations tends to favor the view that the processing of information in the brain is carried by populations of neurons, and not by individual cells [8]. On top of it, it appears that there is some kind of hierarchical processing of information, in which the different levels of the cortex successively bind several aspects of a given percept in cascade. For instance, in the case of the visual system one would first group low-level details of the scene, while in a higher level features like the distinction between figures and ground would be processed.

Regarding the properties of individual neurons, classical studies of the squid giant axon [9], then

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followed by studies of mammalian spinal motoneurons [10], have lead to the widespread view that neurons fire in the form of action potentials in response to some external stimulus, being these potentials produced by a transient inward Na^+ current followed by an outward K^+ current. These motor neurons exhibit a simple threshold dynamics, firing when the stimulus exceeds some value. Thus, it has been considered that complexity in the mammalian brain arises exclusively from the different connectivities of these *ideal* neurons, that are connected in such a way that all the incoming pulses add in a simple linear fashion. In the case of such excitable models the appearance of overall oscillations can be traced back to the entrainment of excitatory and inhibitory connections. One could even obtain aperiodic oscillations in this fashion, as shown by Freeman [11], who obtained results in agreement with his experimental observations for the olfactory bulb.

This simple view of neurons in the central nervous system has been recently challenged, starting from studies on invertebrate neurons [12], that are more amenable to a detailed study, and later confirmed on other systems (see Ref. [13] for a review). From these studies it emerges that these neurons can exhibit a richer behavior, while the idea that the dendritic tree is electrically passive, allowing to add in a more or less linear way the synaptic potentials, needs to be altered [13]. One of the consequences of the dendritic excitability is the so-called low-threshold Ca^{2+} conductance [14], that is essentially inactivated at the membrane resting potential and deinactivated by membrane hyperpolarization, breaking this one of the dogmas of neurophysiology, namely that membrane depolarization from the resting potential increases excitability, whereas membrane hyperpolarization decreases it. Thus, in certain cases an otherwise sub-threshold depolarization can produce action potentials if superimposed on either a depolarizing or a hyperpolarizing membrane potential change, allowing central neurons to exhibit sustained oscillations (limit cycle behavior). In this context it is to be understood that these oscillations are associated to self-sustained rhythmic firing in the absence of any synaptic input.

Some theoretical studies [15] have focused on the analysis of the conditions under which some kinds

of models with biological relevance, including limit-cycle, relaxation, and pulsed oscillators, may yield synchronized behavior, like the role of excitatory and inhibitory couplings, time delays, etc. Classical neural networks [16] customary involve all-to-all coupling and integrate-and-fire schemes, ultimately involving a minimum location procedure. Neural networks that are more realistic from the physiological viewpoint, and that make use of synchronous oscillatory behavior have been already introduced in the context of visual processing [17,18]. A problem with this approach is how do these neurons desynchronize in preparation for a new percept. So far the problem has been solved in some ad hoc way, e.g. by considering some spatially correlated form of noise [18].

The aim of the present contribution is to look at this problem from a different perspective, namely by using Freeman's remark [19] that brain activity might be shaped by deterministic chaos. In fact, deterministic chaos has also been found in some measurements of the EEG [20]. The possible usefulness of using model neurons that are in the chaotic regime has been already discussed [21] in the context of processing visual information by considering a different model to that employed in this work. Deterministic chaos may offer a mechanism for desynchronization through the use of the broadband properties of the chaotic signals instead of resorting to some structured form of noise. In the present study we shall combine the evidence in Ref. [13] together with Freeman's hypothesis [19] to assume that isolated neurons in the central system may exhibit chaotic behavior.

In the framework of Freeman's suggestion the rest state of the brain is chaotic, and the response to a certain external stimulus would be a given periodic pattern. In his view this would happen through a transition from the chaotic attractor to a limit cycle that would coexist with it. The process of incorporation of new percepts would occur through the deformation of the system such as to incorporate these as new alternative dynamical behaviors. These ideas are very interesting from the qualitative point of view, but recent findings in the field of nonlinear dynamical systems may be able to couch them in more precise terms. The key

idea is the possibility of controlling chaos, as proved by Ott, Grebogi, and Yorke (OGY) [22,23].

The idea is to look at the strange attractor as the superposition of a very large number of unstable periodic orbits (or cycles) [24], consisting chaos control in the stabilization with small time-dependent perturbations of one of these orbits. This is a very attractive hypothesis for the coding and retrieving of information in the brain, although a practical difficulty is that the implementation of the OGY method in the case that the dynamical equations are known is quite involved (one needs to define a suitable Poincaré plane and solve an eigenvalue problem at each crossing with it). A number of applications to the control of chaos in experimental systems has appeared in the literature [25], including mechanical, electrical, and chemical systems, a laser, heart tissue, including a more recent studied that has focused on chaotic neurons [26]. While these methods work by applying suitable perturbations to some system parameter, in this work we shall use an alternative simpler method [27], in which suitable perturbations are applied to the dynamical variables of the system. This method has been recently applied to chaos suppression in a neural network [28].

Another point is that if one considers the activity of individual neurons to be chaotic, it is hard to see how could one obtain synchronized behavior, due to the sensitive dependence on the initial conditions that characterizes deterministic chaos. However, some theoretical predictions [29], later proved in a practical setting by Pecora and Carroll (PC) [30,31], have shown the possibility of synchronizing chaotic systems by connecting them in a special way (see also [32]). The kind of dynamical behavior that one obtains is still chaotic, but the linked systems become synchronized after some transient behavior.

In the present work, we shall consider a discrete (difference-equation) two-variable model suggested in Ref. [33], and that has been shown to agree with the experimental results of Ref. [34]. This model exhibits deterministic chaos for certain values of the parameters. The plausibility of this behavior is also supported by the fact that more sophisticated mathematical models of bursting neurons [35] also exhibit deterministic chaos in certain regimes of parameters [36]. The

variables of the model are an activation (transmembrane potential) and a recovery variable, while the individual neurons are connected through one-way selective coupling, in such a way that synchronized behavior may arise. In particular, neurons will be linked by using a recently introduced [32] variant of the PC method. This is to be considered as a toy model with no direct physiological counterpart, as membrane potentials do not generally link neurons, except in the sparse occurrences of gap junctions within the mammalian nervous system. Thus, this kind of model can be seen as an *electrical network* representation of real neuron assemblies.

The present paper is organized as follows. In Section 2 the model and the chaos suppression and synchronization methods used in this work are briefly discussed. The results obtained in this work are presented in Section 3, while Section 4 contains the main conclusions stemming from the present paper.

2. Model and method

Individual neurons have been represented through a two-variable finite difference-equation model (or map) introduced in Ref. [33], and found to agree, at least qualitatively, with the experimental return map reported in Ref. [34]. This map is written in the form

$$\begin{aligned}x_{n+1} &= x_n^2 \exp(y_n - x_n) + k, \\y_{n+1} &= ay_n - bx_n + c,\end{aligned}\quad (1)$$

where x is related to an instantaneous transmembrane membrane potential, while y corresponds to a generalized recovery variable. For the parameters given in Ref. [33] the model exhibits either fixed-point (quiescent) or limit-cycle (periodic) behavior. However, in the present work the parameters have been chosen [37] in such a way that the system exhibits deterministic chaos.

Chaos suppression is achieved by applying proportional pulses to the system, and in the case of two-dimensional maps $x_{n+1} = F(x_n, Y_n)$; $y_{n+1} = G(x_n, y_n)$ like (1), the method is applied in the form [38]

$$\begin{aligned}x_{n+1} &= F(x_n, y_n)(1 + \lambda_x \delta_{m,p}), \\y_{n+1} &= G(x_n, y_n)(1 + \lambda_y \delta_{m,p}),\end{aligned}\quad (2)$$

where $\delta_{m,p}$ is Kronecker's delta and $m \equiv n \pmod{p}$, reflecting the fact that the perturbations are applied every p iterations, while λ_x and λ_y are the intensity of the proportional perturbations applied to the system variables x and y , respectively.

It was mentioned before that the connections between the neuron models used in the present work are one-way, although they are not strictly of the PC [30] type. Within the PC method one splits the response system to be synchronized with the drive in two subsystems, and one of these subsystems is shared between the two connected systems. In particular, in the case of Eq. (1) (x) is the only stable subsystem in the PC sense. This fact implies that by using the PC connection scheme it is impossible to construct a network of interconnected neuron units, because if one injects, say, $y(t)$ from the first unit into the second, and then again $y(t)$ from the second into the third one, and so forth, the result would be a series of neuron units driven by the same signal, coming from the drive, and not a cascade [31] of them. Any other possibility consisting in the introduction of $x(t)$ at some point would not lead to synchronized behavior.

Thus, in the present work we shall resort to the connection method introduced in Ref. [32], being the idea to inject the driving signal at a particular place of the evolution equations of the response, such that it yields synchronized behavior. This synchronized behavior can be rigorously analyzed in the framework of the so-called transverse Lyapunov exponents, that measure the time evolution of differences between the two systems. One of the advantages of this method is the possibility of building a nontrivial network comprising many low-dimensional chaotic units, something that can be specially significant in the case that these units represent neurons, and even more if one recalls that the neurons are two-dimensional. In the case of (1) the following connection can be shown to exhibit synchronized behavior (see below)

$$\begin{aligned} x_{n+1} &= x_n^2 \exp(y_n - x_n) + k, \\ y_{n+1} &= ay_n - bx_n + c, \\ x'_{n+1} &= x_n^2 \exp(y'_n - x_n) + k, \\ y'_{n+1} &= ay'_n - bx'_n + c, \end{aligned} \tag{3}$$

where the place at which the driving signal enters has been underlined. Two different connections to be called upon later are the following ones

$$\begin{aligned} x'_{n+1} &= (x'_n)^2 \exp(\underline{y}_n - x'_n) + k, \\ y'_{n+1} &= ay'_n - bx'_n + c \end{aligned} \tag{4}$$

and

$$\begin{aligned} x'_{n+1} &= (x'_n)^2 \exp(y'_n - x'_n) + k, \\ y'_{n+1} &= a\underline{y}_n - bx'_n + c, \end{aligned} \tag{5}$$

where it is to be noticed that in (4) and (5) only the response system is reported.

3. Results

First of all, we shall test the versatility of method (2) in suppressing deterministic chaos in the case of a single neuron (1). Thus, in Fig. 1 three different periodic orbits have been stabilized, corresponding these to periods 4, and two different period-12 behaviors, although other periodic orbits could be also stabilized with parameter values in the same range.

The first connection to be presented consists of four model neurons linked through (3) in a cascade, such that the first neuron drives the second one, and analogously between the second and third, and third and fourth ones (see Fig. 2). In all the results reported in this work, all the neurons start always from randomly chosen initial conditions, and a transient in which they evolve independently is shown. Thus, the neurons are linked after the first vertical dotted line, and it can be seen that they exhibit synchronized chaotic behavior after a certain transient. After the second vertical dotted line pulses in x and y are applied to the first neuron, and after another transient the ensemble oscillates synchronously, while exhibiting periodic behavior. This result just proves the main thesis of the present contribution: that one may conciliate the finding of oscillatory synchronous activity corresponding to groups of neurons and the hypothesis by Freeman that the activity of the brain at rest is chaotic. One may understand the *propagation* of regular behavior from the first to the rest of neurons in the light

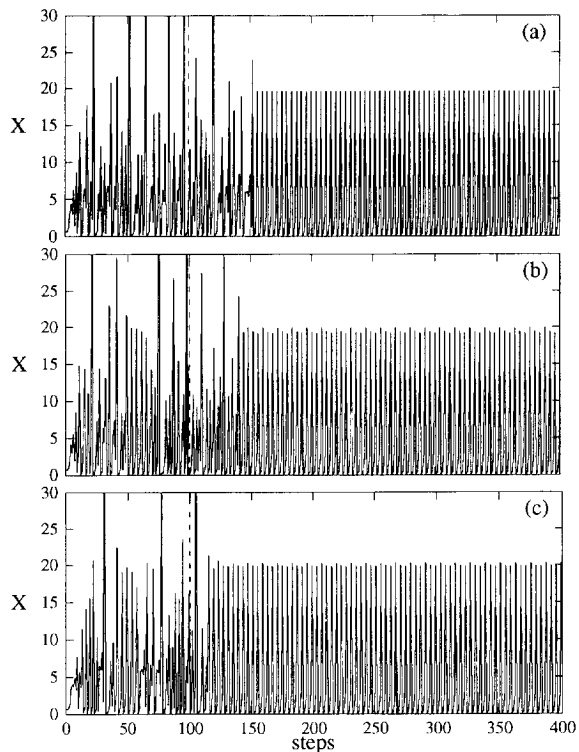


Fig. 1. Application of the chaos suppression algorithm (2) to model (1) (with the parameters given in Ref. [37]): (a) period-4 with $\lambda_x = \lambda_y = -0.017$ and $\Delta_n = 4$; (b) period-12 with $\lambda_x = \lambda_y = -0.028$ and $\Delta_n = 6$; (c) period-12 with $\lambda_x = \lambda_y = -0.035$ and $\Delta_n = 12$. The method (2) is applied after the vertical dotted line.

of recent results [39] showing that one can achieve synchronization between two systems with different parameters, even when one of them is in the chaotic region, while the other behaves regularly. However, the regular behavior that is induced in the response units is not necessarily identical to that of the drive (see Fig. 2), being this qualitatively explained in terms of the parameter mismatch of the systems [39] (after chaos is suppressed the drive effectively corresponds to the unperturbed system in a different parameter region yielding periodic behavior [38]).

Another connection that yields synchronized behavior between two neuron models (1) and (4). However, in this case it appears for some of the networks in which the units are connected exclusively through (4) one does not obtain a stable overall behavior, at variance of the case of connection (3) presented above.

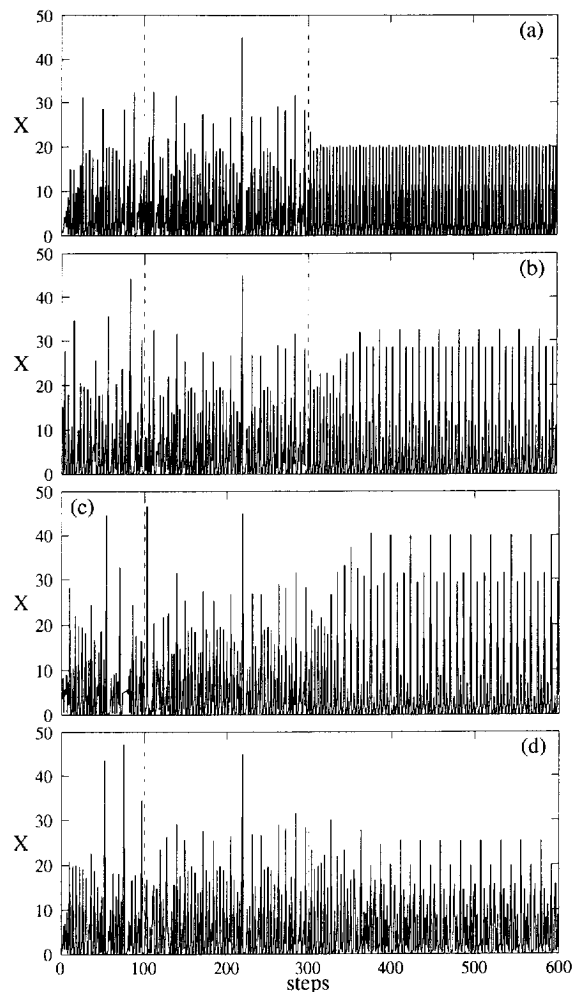


Fig. 2. Four identical model neurons (1) connected in cascade according to scheme (3), acting the second neuron as drive for the third one, and analogously between the third and fourth neurons (the parameters are those of Ref. [37]). The two connections are active after the first vertical dotted line, while after the second vertical dotted line the chaos suppression algorithm (2) is applied to the first unit ($\lambda_x - \lambda_y = -0.035$ and $\Delta_n = 12$).

However, this connection will be discussed later in the context of several connections coexisting in the same system. A qualitatively different behavior is the one obtained if one considers (5). When one connects two neuron models in this form, the behavior that one has is not synchronized. However, if one drives with the same signal a series of model neurons with different initial conditions, it is possible to see that these driven neurons exhibit after some transient identical behavior

comparing one to each other, although this behavior is different to the one of the drive unit (see Fig. 3). If chaos is suppressed in the drive unit, this induces chaos suppression in the response neurons. It is to be remarked that this kind of *synchronized behavior among the responses*, that has in common with synchronization that it also suppresses the effects of the sensitivity to initial conditions present in chaotic systems, is not present in any of the other nonsynchronizing connections.

It may happen that in some circumstances neurons exhibit organized patterns of activity in the absence

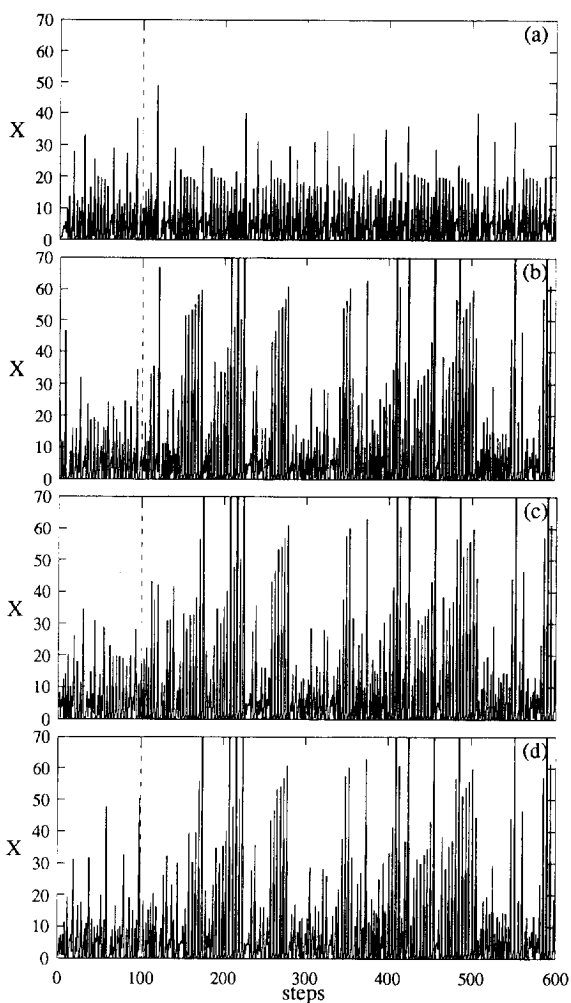


Fig. 3. Four identical model neurons (1) connected such that the first one drives the other three accordingly to scheme (5), (see Ref. [37] for the parameters). The connection is active after the vertical dotted line.

of external stimuli, and indeed we have considered a set of neurons connected in a circular way, such that there is a feedback and the last neuron influences back the first one. In particular, the case of three neurons in which one has a cascade with (3) in the order $1 \rightarrow 3$, while a cascade with (5) coexists in the order $3 \rightarrow 1$, or in more precise terms,

$$\begin{aligned}
 x_{n+1} &= x_n^2 \exp(y_n - x_n) + k, \\
 y_{n+1} &= ay'_n - bx_n + c, \\
 x'_{n+1} &= x_n^2 \exp(y'_n - x_n) + k, \\
 y'_{n+1} &= ay''_n - bx'_n + c, \\
 x''_{n+1} &= (x'_n)^2 \exp(y''_n - x'_n) + k, \\
 y''_{n+1} &= ay''_n - bx''_n + c.
 \end{aligned}
 \tag{6}$$

Fig. 4 shows the outcome of a simulation in which three neurons connected in the form (6) have achieved self-organization, in the sense that they yield periodic behavior in the absence of any external perturbation.

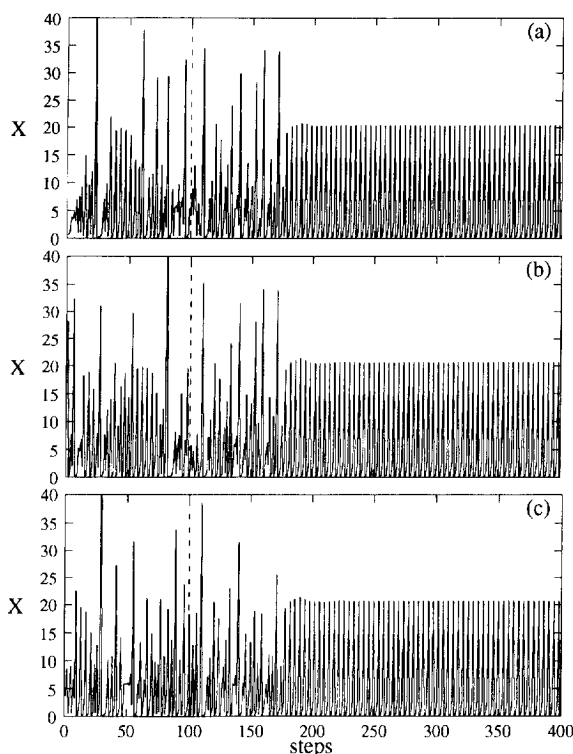


Fig. 4. Three identical model neurons (1) with a feedback connection accordingly to scheme (6), that implies connection (3) in the sense $1 \rightarrow 3$ and connection (5) in the sense $3 \rightarrow 1$. The connections are active after the vertical dotted line (see Ref. [37] for the parameters).

If one considers an ensemble composed out of many neurons, it is well known that each of them can be connected to a large number of its neighbors. We have considered the possibility that a neuron is connected simultaneously to other neurons. This can be illustrated with four neurons in which two of them receive signals from the other two in the form:

$$\begin{aligned}
 x_{n+1} &= x_n^2 \exp(y_n - x_n) + k, \\
 y_{n+1} &= ay_n - bx_n + c, \\
 x'_{n+1} &= x_n^2 \exp(y'_n - x_n) + k, \\
 y'_{n+1} &= ay'_n - bx'_n + c, \\
 x''_{n+1} &= x_n^2 \exp(y''_n - x_n) + k, \\
 y''_{n+1} &= ay''_n - bx''_n + c, \\
 x'''_{n+1} &= (x_n''')^2 \exp(y'''_n - x_n''') + k, \\
 y'''_{n+1} &= ay'''_n - bx'''_n + c,
 \end{aligned}
 \tag{7}$$

where, in particular, the first unit drives the second and third neurons through connection (3), while the fourth unit drives the same neurons through connection (4). The result, illustrated in Fig. 5, is that the second and third neurons become synchronized one to each other, but not necessarily with any of the driving systems. The outcome appears to come from the combined effect of both driving systems, although in other examples some connections appear to be more active than other ones, something that could be somehow related to the existence of activatory and inhibitory connections in classical networks.

Neurons studied in physiological experiments are never completely identical, and, on the other hand, the presence of some noise is unavoidable. Thus, from the point of view of any theoretical study it is interesting to study the situation in which one links model neurons whose parameters differ. In particular, Fig. 6 contains the results obtained when one connects several neurons with a certain degree of parameter mismatch. The result is that they are still able to synchronize, not being specially sensitive to the parameter difference (although in agreement with the results of Ref. [39] the height of the peaks will not be identical). An interesting situation can be the case in which the corresponding response neuron exhibits quiescent (fixed point) behavior. The result, shown in Fig. 7, is that the drive neuron first imposes its chaotic behavior after they are connected, while both of them become periodic when

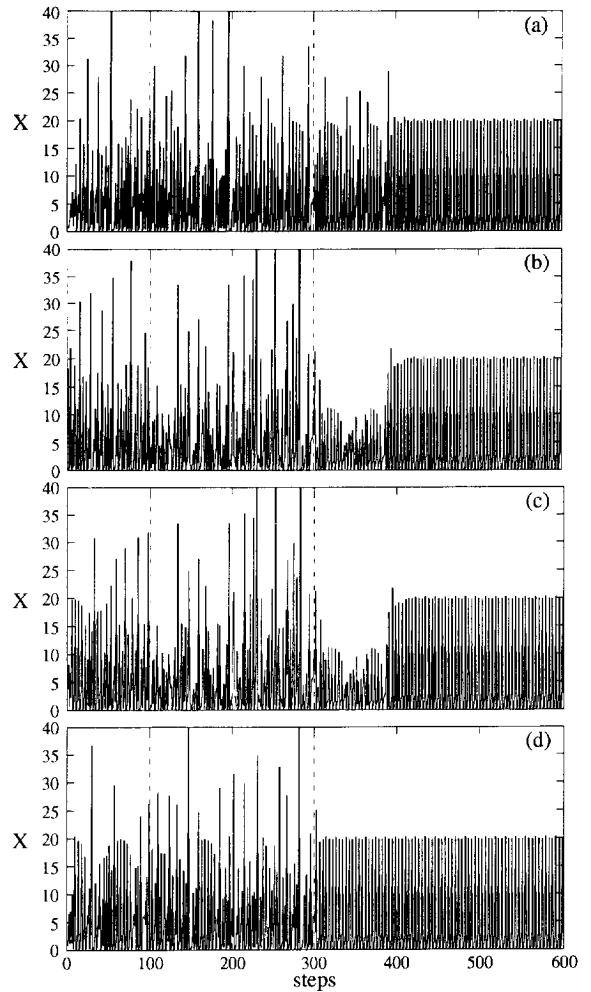


Fig. 5. Four identical model neurons (1) with a competitive connection accordingly to scheme (7). The connections are active after the vertical dotted line, while after the second vertical dotted line the chaos suppression algorithm (2) is applied to the first and fourth units with identical parameters (see Fig. 2 for the parameters).

an external stimulus is applied. This may be an alternative mechanism for preserving chaos [40], as chaos appears to be healthier than an excess of order in this context. Notice also the different scales for the heights of the peaks in Fig. 7, that should be also interpreted in terms of the parameter mismatch between the systems [39]. Analogous results have been obtained regarding the issue of noise, namely if some additive noise that alters the system variables in the form

$$x' = x + \gamma\alpha[0, 1]
 \tag{8}$$

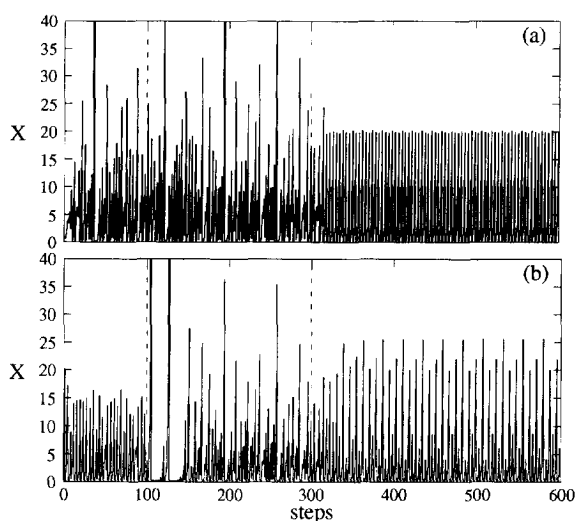


Fig. 6. Two model neurons (1) with different parameters connected accordingly to scheme (3). The connections are active after the vertical dotted line, while after the second vertical dotted line the chaos suppression algorithm (2) is applied to the first unit. The parameters of the first neuron, including those of the chaos suppression algorithm, are the same of Fig. 2, while those of the second neuron are $a = 1.045$, $b = 0.15$, $c = 0.5$, and $k = 0.17$.

is applied a pair of systems still become synchronized, being $\sigma[0, 1]$ a temporally uncorrelated (white noise) stochastic variable with gaussian distribution with zero mean and standard deviation equal to one. Thus, in Fig. 8 four identical model neurons have been considered in the presence of this kind of noise, acting the first as drive of the other three. The behavior of the four neurons is not identical although one could think that they are synchronized in a generalized sense [41], although in this case one has a stochastic contribution to the dynamics.

4. Conclusions

In the present contribution we have discussed the possibility that the observed physiological evidence of synchronized oscillations in different parts (olfactory bulb, visual cortex, etc.) of the brain of some mammals arise from the linking of neurons that exhibit deterministic chaos in isolated conditions. It is customary considered that these units are periodic, but in this work

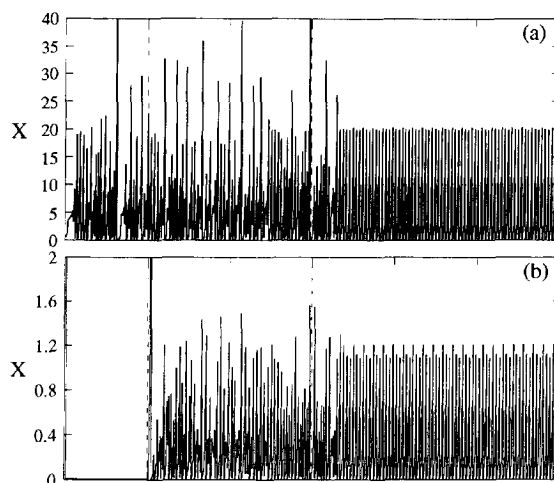


Fig. 7. Two model neurons (1) with different parameters connected accordingly to scheme (3): the second one has quiescent behavior, and it becomes chaotic under the influence of the drive neuron, until both become periodic under the influence of an external stimulus (introduced after the second vertical dotted line and modeled through (2)). The parameters of the first neuron and of (2) are the same of Fig. 2, while those of the second neuron are $a = 0.89$, $b = 0.6$, $c = 0.28$, and $k = 0.01$.

we have followed Freeman's suggestion regarding the possible role of deterministic chaos in perceptive processes. The hypothesis is very attractive, because of the role that chaos may play in the generation of information [42]. Moreover, the hypothesis can be cast in a sound way from the viewpoint of dynamical systems theory by recalling that a strange attractor can be considered a reservoir of periodic behaviors, none of which dominates, rather than some kind of *noisy* behavior. The key in the process of information retrieval can be the idea of chaos control, namely the possibility of stabilizing one of the unstable periodic orbits that form a strange attractor. A second key idea is the possibility of synchronizing chaotic systems, apparently defying their sensitive dependence on the initial conditions.

These ideas are illustrated in the neural arena with a toy model, written in terms of a two-variable difference-equation, and that exhibits deterministic chaos in certain parameter ranges. The combined application of the ideas of chaos control and synchronization is able to yield a behavior that is completely analogous to the synchronized oscillations found by

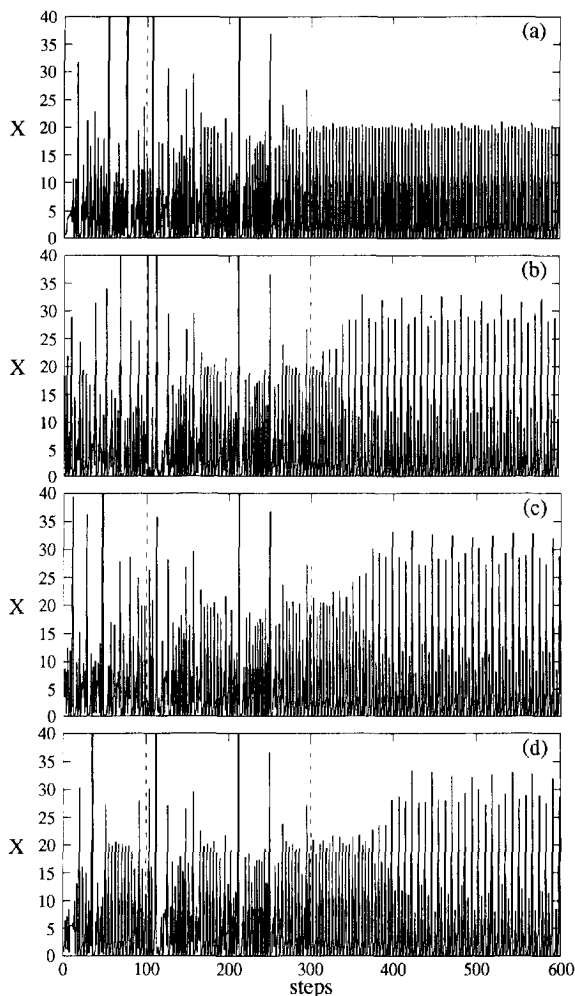


Fig. 8. Four identical model neurons (1) in the presence of external additive noise are represented. The first one drives the other three, that independent from each other. The connections are active after the vertical dotted line, while after the second vertical dotted line the chaos suppression algorithm (2) is applied to the first unit. The parameters of the neurons and of (2) are the same of Fig. 2, while for the external noise (8) one has $\sigma = 0.002$.

the physiologists. In addition, a number of different possibilities are explored, including the behavior observed when neurons receive several concurrent stimuli and possibility of synchronous oscillations in a network that does not receive any external stimulus. The robustness of this phenomenon against parameter mismatch and the presence of external noise has been also shown.

In this sense, the appearance of order in the network spontaneously, i.e., in the absence of any input, exhibits some similarities with the behavior observed in Globally Coupled Maps (GCM) [43], typically logistic maps in the chaotic regime with all-to-all coupling. Within this model one may find phenomena like synchronized chaos, synchronized oscillations, traveling waves, etc. GCMs were introduced as a mean-field-type extension of Coupled Map Lattices (CML) (see [44] for a review), for which the chaotic units are coupled locally in a diffusive fashion, and that are interesting models for many complex spatio-temporal phenomena. Thus, future work along the lines discussed in the present work could include either the study of coupled map lattices in which the local units represent neurons, such as is the case of the map employed in the present study, or the use of more realistic models of neurons in terms of differential equations in the study [45].

Acknowledgements

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