

ORIGINAL CONTRIBUTION

Stable, Oscillatory, and Chaotic Regimes in the Dynamics of Small Neural Networks With Delay

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Abstract—*In this paper we consider simple neural network models consisting of two to three continuous nonlinear neurons, with no intrinsic synaptic plasticity, and with delay in neural signal transmission. We investigate the different dynamic regimes which may exist for these "minimal" neural network structures. Examples of stable, oscillatory (periodic or quasi-periodic), and chaotic regimes are reported and analyzed. For chaotic regimes, classical characteristics such as bifurcation diagrams, sensitive dependence on initial conditions, Lyapunov exponents, pseudo phase space attractors, are presented. It is shown that the dynamic regime of a network can be changed through modifications of either internal or external parameters, such as a synaptic weight or an external neuron input. The resulting dynamic regimes offer frameworks to represent various neural functions. For instance, oscillatory regimes provide a mechanism to implement controllable neural oscillators. The sensitive dependence on initial conditions, which is shown to exist even for very small networks, sets a limit to any long term prediction concerning the evolution of the neural system, unless the network adjust its parameters through plasticity in order to avoid chaotic regimes.*

Keywords—Neural network, Dynamics, Stability, Unstability, Oscillator, Quasi-periodicity, Chaos, Delay.

1. INTRODUCTION

Complex dynamic evolutions, that lead to chaotic regimes, recently have been experimentally observed in neural systems (Babloyantz & Destexhe, 1986; Babloyantz & Salazar, 1985; Holden, Winlow, & Haydon, 1982; King, Barchas, & Huberman, 1984; Skarda & Freeman, 1987). In contrast, in theoretical modeling of neural systems, the emphasis has been put mainly on either stable or cyclic behaviors (Grondin, Porod, Loeffler, & Ferry, 1983; Hirsch, 1989). Nevertheless, a few theoretical models have been proposed, that illustrate the existence of chaos in neural networks (Choi & Huberman, 1983; Guevara, Glass, Mackey, & Shrier, 1983; Riedel, Kühn, & van Hemmen, 1988; van der Maas, Verschure, & Molenaar, 1990). These models, to display chaotic behavior, generally rely on complex architectures, or complex equations for both neuron and synapse dynamics, or they incorporate stochastic elements. Sometimes also, the quantities which exhibit chaotic evolutions in these models, have no direct physiological interpretation. An example of this is

found in van der Maas et al. (1990), where chaos appears in the evolution of the sum of the absolute values of the synaptic weights of a network.

In this paper we consider small neural circuits that contain no more than two or three nonlinear neurons. The equations governing these models are classical in neural modeling, although the investigation of their unstable behaviors has seldom been undertaken. Each neuron has a sigmoid transfer function, and a continuous positive and bounded output activity that evolves according to weighted sums of the activities in the network. In order to focus the analysis on the dynamics of neuron activities, no intrinsic synaptic plasticity is incorporated. No special conditions, like symmetry, are imposed to restrict synaptic values. We then study, through numerical simulations, the time evolution of the output activities of the neurons. We report and analyze the different dynamic regimes which can be observed for these quantities under various conditions. In particular, we show direct evidence of the possibility of chaotic regimes in individual neuron output activities, in very small networks. Some biological implications of the results are discussed.

2. STRUCTURE AND DYNAMICS OF THE NETWORKS

We consider small neural networks, consisting of two or three neurons, connected as depicted in Figure 1.

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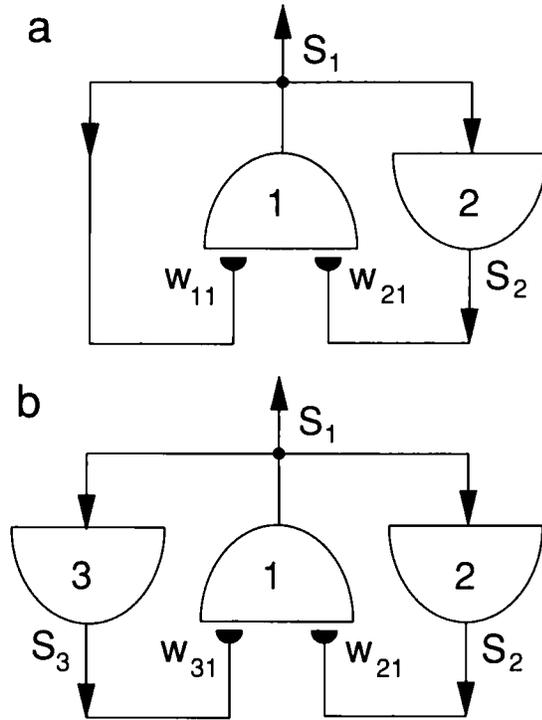


FIGURE 1. Structure of the two neural networks investigated here.

$S_i(t)$ is the output activity of neuron i at time t , and w_{ij} is the weight of the synaptic connection from neuron i to neuron j . The neurons have a sigmoid transfer function, whose expression, for neuron i , is:

$$f_i(V) = (1 + \exp - \beta_i(V - \theta_i))^{-1}. \quad (1)$$

Both the threshold θ_i and the slope β_i of the sigmoid are considered as adjustable parameters for neuron i .

We chose a discrete-time dynamics for the evolution of the activities, that seeks to represent the effect of delays in the transmission of neural signals.

The dynamics of the two-neuron network in Figure 1a is taken as:

$$S_1(t + \Delta t) = f_1[w_{11}S_1(t) + w_{21}S_2(t)], \quad (2)$$

$$S_2(t + \Delta t) = f_2[S_1(t)]. \quad (3)$$

To examine the influence of delays in various settings, we consider two possible types of dynamics for the three-neuron network in Figure 1b. The first one, which will be called "dynamics with full delay," is governed by:

$$S_1(t + \Delta t) = f_1[w_{21}S_2(t) + w_{31}S_3(t)], \quad (4)$$

$$S_2(t + \Delta t) = f_2[S_1(t)], \quad (5)$$

$$S_3(t + \Delta t) = f_3[S_1(t)]. \quad (6)$$

This dynamics assumes that delays are significant for all transmission paths.

The second one, called "dynamics with partial delay," assumes significant delays in only part of the

transmission paths (namely the incoming paths to neuron 1). It is governed by:

$$S_1(t + \Delta t) = f_1[w_{21}S_2(t) + w_{31}S_3(t)], \quad (7)$$

$$S_2(t + \Delta t) = f_2[S_1(t + \Delta t)], \quad (8)$$

$$S_3(t + \Delta t) = f_3[S_1(t + \Delta t)]. \quad (9)$$

Equations (1–9) endow the neurons with a continuous positive and bounded output activity. Such an output activity S_i is interpretable as a short-term average of the firing rate of the neuron. This mode of representation of neuron activities has frequently been assumed in modeling, (see Amari, 1989, for a recent example), and its relevance to describe information exchange in neural systems was previously mentioned (Hopfield, 1982).

Now, as we said, the relevance of a discrete-time dynamics for natural systems that involve continuous time, arises from the possibility of having significant delays in neural signal transmission along certain paths. In such a case, if neurons in a circuit change their outputs at a given time, it is only after a finite transit time that these changes of activity are received by other neurons as inputs capable of inducing, in turn, evolution of their own outputs. The transmission delays can be attributed, for an important part, to delays in synaptic responses. In the framework of the present model, a train of action potentials with given short-term average frequency $S_i(t)$ is emitted by a neuron i . In the presence of transmission delay, this train begins to be felt by another neuron j after a time Δt , after which time, as a response, the receiving neuron j starts to emit its own train of action potentials with its own short-term average frequency represented by $S_j(t + \Delta t)$. The transmission delay Δt is of partially stochastic character, it is modelled here in eqns (2–9) by a single parameter interpretable as an average transmission delay, and with an appropriate choice of the unit of time, we shall take now on $\Delta t = 1$.

To complete the justification of the relevance of a discrete-time dynamics, one can add that this assumption has emerged as a convenient and fruitful choice in neural modeling since the early days (Little & Shaw, 1975; McCulloch & Pitts, 1943). On this basis, spin glass-like neural networks (Amit, 1989; Hopfield, 1982) have been extensively developed. These models provide a most valuable paradigm to represent and interpret learning and retrieval of information capabilities in neural systems. The present model brings elements to further characterize such neural networks, especially when two major constraints are relaxed in the direction of higher biological plausibility, that is when neuron activities are allowed to vary continuously and when synaptic symmetry ensuring stability breaks.

The salient feature with the model summarized in eqs (1–9) and the simple architectures of Figure 1, is that qualitatively quite different dynamic regimes can

be observed for the neuron activities. By varying the parameters β_i , θ_i , and w_{ij} of a network, stable, oscillatory, and chaotic regimes are accessible. This is demonstrated by the results presented in the following sections.

3. PROPERTIES OF THE THREE NEURON NETWORK

3.1. Dynamics with Partial Delay

For the network of Figure 1b, let us consider the dynamics with partial delays of eqns (7–9), with the following fixed values for the parameters: $\beta_1 = \beta_2 = 7.0$, $\beta_3 = 13.0$, $\theta_1 = 0.5$, $\theta_2 = 0.3$, $\theta_3 = 0.7$, and $w_{21} = 1.0$. The remaining adjustable parameter w_{31} , will serve as a control parameter to change the dynamic regime of the system. Interesting behaviors arise when the synapse w_{31} is given negative values, to supplement with an inhibitory action on neuron 1, the excitatory action of w_{21} . In such a case, the competition of the inhibitory and excitatory actions in the network can yield complex dynamics, as we shall see.

We can focus on the time evolution of $S_1(t)$, the output of neuron 1. For low values of $|w_{31}|$ (w_{31} is negative), $S_1(t)$ rapidly reaches a stable activated state, as exemplified by Figure 2a for $|w_{31}| = 0.3$. For higher

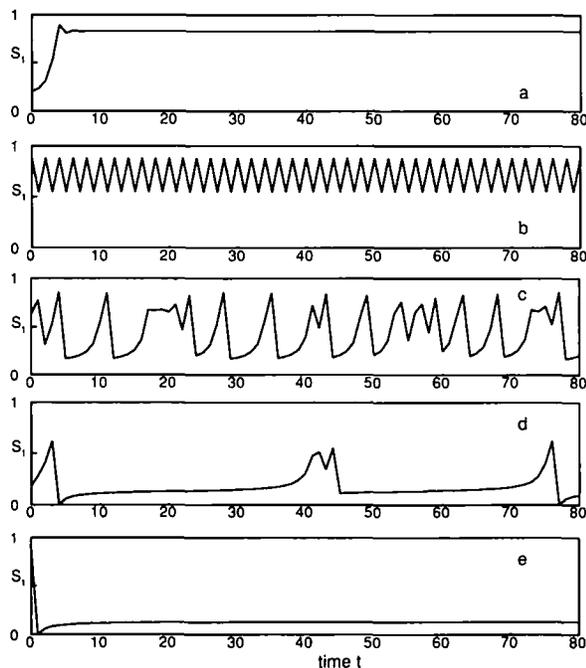


FIGURE 2. Time evolutions of the output activity $S_1(t)$ showing different accessible dynamic regimes for neuron 1 of Figure 1b, for decreasing values of the synaptic weight w_{31} : (a) Stable activated, for $w_{31} = -0.3$. (b) Periodic, for $w_{31} = -0.5$. (c) Chaotic, for $w_{31} = -0.8$. (d) "Bursting" chaotic, for $w_{31} = -5.0$. (e) Stable inhibited, for $w_{31} = -8.0$. The other parameters of the network are: $\beta_1 = \beta_2 = 7.0$, $\beta_3 = 13.0$, $\theta_1 = 0.5$, $\theta_2 = 0.3$, $\theta_3 = 0.7$, and $w_{21} = 1.0$.

values of $|w_{31}|$ a periodic regime of $S_1(t)$ can be reached, as Figure 2b shows for $|w_{31}| = 0.5$. When $|w_{31}|$ is further increased the periodic regime transforms into a chaotic regime, which subsists over a wide range of values of $|w_{31}|$. Figures 2c and 2d show two examples of the chaotic evolution of $S_1(t)$, obtained for $|w_{31}| = 0.8$, and $|w_{31}| = 5.0$, respectively. For high values of the inhibitory synapse $|w_{31}|$, the dynamics returns to a stable regime in which $S_1(t)$ converges to a fixed inhibited state, as illustrated in Figure 2e for $|w_{31}| = 8.0$.

The route by which the system evolves from a stable regime to a chaotic regime as $|w_{31}|$ increases, consists of a cascade of period doublings, depicted by the bifurcation diagram in Figure 3. This type of bifurcation diagram is a characteristic way by which a system can evolve towards chaos. It is found in simple mathematical models exhibiting deterministic chaos, as for instance the so-called logistic map (Schuster, 1988).

The inverse route, leading from chaos to a stable inhibited state as $|w_{31}|$ further increases, passes through intermittency, with chaotic bursts of activity separated by intervals of quasi-stability of increasing durations. An interval of quasi-stability is understood as an interval in which the variation of $S_1(t)$ between to successive time steps, does not exceed a given small threshold. Let T_{stab} be the maximum duration of these intervals of quasi-stability encountered in a signal $S_1(t)$ having the global appearance of Figure 2d. In Figure 4 is plotted the value of T_{stab} recorded for a given value of $|w_{31}|$, against $|w_{31}|$. We found that this variation of T_{stab} as a function of $|w_{31}|$ can be fitted by a power law of the form $(w_c - |w_{31}|)^{-\gamma}$, with $w_c = 7.63$ and $\gamma = 0.67$. The transition between the chaotic regime and the stable regime as $|w_{31}|$ increases, thus appears to be similar to a phase transition in solid state physics. It is possible to define an order parameter as $1/T_{\text{stab}}$, which is zero in the stable regime, and nonzero in the chaotic regime. The phase transition (of second order) occurs for a critical value w_c of the control parameter $|w_{31}|$, and the variation of the order parameter is a power law with critical exponent γ .

From a biological standpoint, such a behavior of the network in the region before w_c is interesting, as it provides a model in which a signal shows bursts of activity (see Figure 2d) with a repetition rate modifiable through the value of a synaptic weight. The outcome of such behavior is an *internally controllable neural oscillator*.

Another element which clearly indicates the presence of chaos, is the sensitive dependence on initial conditions in the time evolution of $S_1(t)$. In a chaotic regime, once the attractor of the dynamics has been reached after a few iterations, the distance between two distinct sequences of iterates rapidly diverges (see Figure 5a), at least within the limit of the size of the attractor itself. Figure 5b shows the time evolution of the distance $D(t) = |S'_1(t) - S_1(t)|$ between two distinct trajectories $S_1(t)$

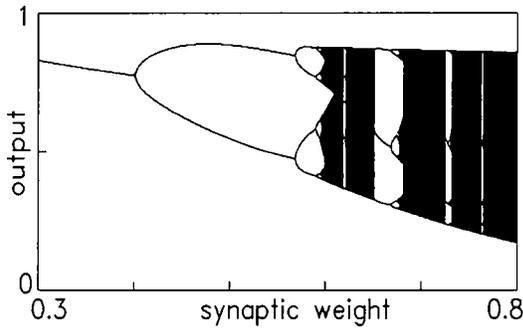


FIGURE 3. Bifurcation diagram of the output activity $S_1(t)$ of neuron 1 of Figure 1b, as a function of synaptic weight $|w_{31}|$, and showing the evolution of the dynamics from stability to chaos through a cascade of period doublings.

and $S'_1(t)$ on the attractor, for the value $w_{31} = -0.8$ of the control parameter. In a semilogarithmic plot, the points which can be fitted to a straight line, reveal the exponential divergence of the trajectories. The slope of the line gives a Lyapunov exponent of 0.62 for the dynamics. This type of exponential divergence of the trajectories is characteristic of chaotic systems, and is also a property of the deterministic chaotic logistic map (Bergé, Pomeau, & Vidal, 1986).

The existence of different dynamic regimes for the neural network in Figure 1b with partial delay, can be understood on the basis of the iteration map for $S_1(t)$ which follows from eqns (7-9) with $\Delta t = 1$:

$$S_1(t + 1) = f_1[w_{21}f_2(S_1(t)) + w_{31}f_3(S_1(t))]. \quad (10)$$

A typical form of this map is represented in Figure 6. This form can be varied in many different ways by alteration of the parameters β_i , θ_i , and w_{ij} . A general

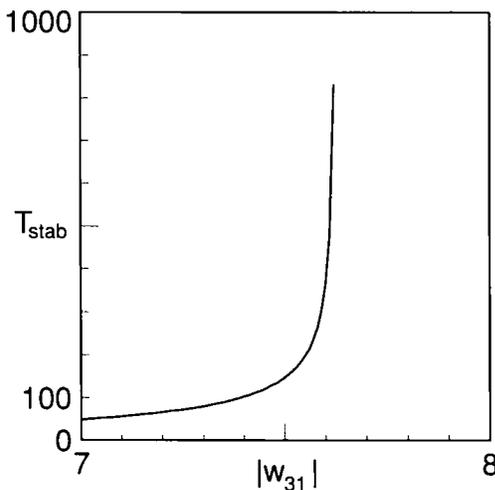


FIGURE 4. Quasi-stability period T_{stab} of the output activity $S_1(t)$ of neuron 1 of Figure 1b, versus synaptic weight $|w_{31}|$. This evolution is interpretable as a phase transition with order parameter $1/T_{stab}$ occurring at the critical value $w_c = 7.63$ of the control parameter $|w_{31}|$. With such a dynamics the network behaves as an internally controllable neural oscillator.

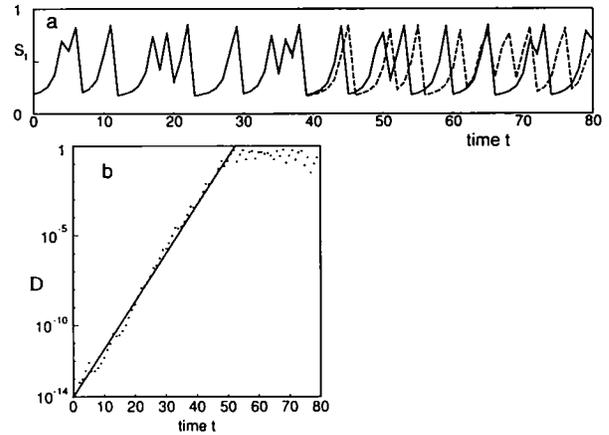


FIGURE 5. Sensitive dependence on initial conditions for the output activity $S_1(t)$ for conditions of Figure 2c: (a) Divergence of two distinct sequences of iterates separated at $t = 0$ by a distance of 10^{-12} . (b) Time evolution of the distance $D(t)$ between two distinct sequences of iterates separated at $t = 0$ by a distance of 10^{-14} ; the exponential divergence of the trajectories can be characterized by the slope of the line which gives a Lyapunov exponent of 0.62 for the dynamics.

condition that ensures the existence of unstable dynamics, is to have a nonmonotone map which intersects the first bisecant with a slope whose absolute value is always larger than 1. This condition can be fulfilled over wide parameter ranges, and the values assigned to the parameters in the examples presented here are merely illustrative, and by no means critical for the existence of oscillatory or chaotic regimes.

Such a first order nonmonotone iteration map forms the basis of the chaotic behaviors of many simple mathematical models, as for instance the logistic map (Bergé et al., 1986; Schuster, 1988). In these mathematical models the nonmonotone nonlinearity is built-in from the start; here in our neural networks it arises

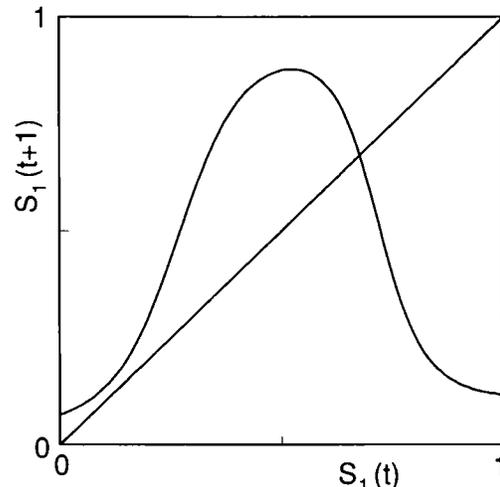


FIGURE 6. Nonmonotone iteration map that results from eqn (10), with the parameter values $\beta_1 = \beta_2 = 7.0$, $\beta_3 = 13.0$, $\theta_1 = 0.5$, $\theta_2 = 0.3$, $\theta_3 = 0.7$, $w_{21} = 1.0$, and $w_{31} = -0.8$.

from the interactions of monotone nonlinear neurons with appropriate signs for the couplings.

We note in Figure 6, the presence of a “canal” between the iteration map and the first bisecant for low values of S_1 . As the control parameter $|w_{31}|$ is increased, this canal becomes narrower and narrower. As a result, the iteration of the dynamics spends more time in the region of small values of S_1 . This leads to a behavior of $S_1(t)$ that is characterized by long intervals of low activity separated by short bursts of high activity, as displayed in Figure 2d. The reduction of the width of the canal to zero then creates a stable fixed point in the dynamics. This type of behavior is known as intermittency in the mathematical theory of chaotic systems (Bergé et al., 1986), and is also a property of the logistic map (Schuster, 1988).

3.2. Dynamics with Full Delay

For the dynamics with full delay in the network of Figure 1b, the qualitative dynamic properties are preserved. Stable, oscillatory, and chaotic regimes also exist, and bifurcation diagrams as shown in Figure 3 can be observed. However, no first order iteration map exists with full delay. Instead, eqns (4–6) lead to the second order iteration map for $S_1(t)$:

$$S_1(t + 2) = f_1[w_{21}f_2(S_1(t)) + w_{31}f_3(S_1(t))]. \quad (11)$$

The resulting dynamics of $S_1(t)$ can be viewed as consisting of two interlaced time sequences, which are separately initialized, and each governed by a first order map of type (10).

The plotting of $S_1(t + 1)$ against $S_1(t)$ for the dynamics with full delay, generally will yield a phase trajectory that densely fills a finite portion of the accessible phase space region. Figure 7 shows the attractor described by a phase trajectory after the initial transient has vanished. The plot was obtained with the parameters set to $\beta_1 = \beta_2 = 7.0$, $\beta_3 = 13.0$, $\theta_1 = 0.5$, $\theta_2 = 0.3$, $\theta_3 = 0.7$, $w_{21} = 1.0$, and $w_{31} = -0.8$. Such an attractor does not uniformly fill the phase space region it occupies, as it would be the case if the values of S_1 were purely random.

To characterize the structure of the attractor, we have computed the correlation function of the attractor, with its classical definition as given in Bergé et al. (1986). We start with a series of $N + n$ successive values of S_1 , and we represent a point i in a n -dimensional phase space by the vector \mathbf{S}^i of components $[S_1(i), S_1(i + 1), \dots, S_1(i + n - 1)]$. We denote by $|\mathbf{S}^i - \mathbf{S}^j|$ the euclidian distance of two points i and j . The correlation function $C(r)$ then follows as:

$$C(r) = \frac{1}{N^2} \sum_{i,j=1}^N \Gamma(r - |\mathbf{S}^i - \mathbf{S}^j|), \quad (12)$$

where Γ is the Heaviside function, such that $\Gamma(x) = 0$ if $x \leq 0$ and $\Gamma(x) = 1$ if $x > 0$.

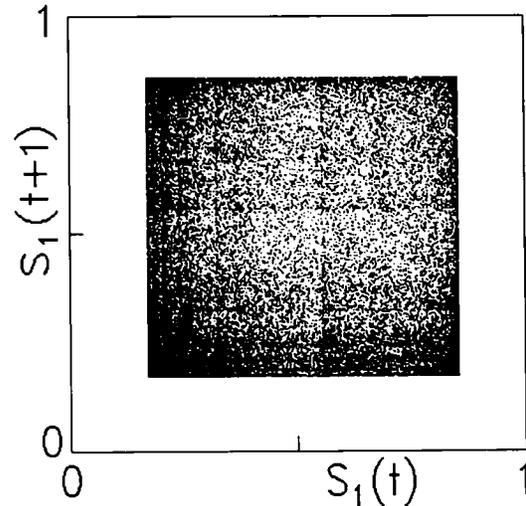


FIGURE 7. Pseudo phase space attractor for iteration map (11) with the parameter values $\beta_1 = \beta_2 = 7.0$, $\beta_3 = 13.0$, $\theta_1 = 0.5$, $\theta_2 = 0.3$, $\theta_3 = 0.7$, $w_{21} = 1.0$, and $w_{31} = -0.8$. The attractor does not uniformly fill the phase space region it occupies, as it would be the case with a purely random process.

We have verified that for the data points plotted in Figure 7, $C(r)$ varies as r^{-d} , for small r 's. When the dimension n of the phase space was increased, a saturation for the exponent d was observed, as shown in Figure 8. The saturation value $d = 2$ is interpreted as the correlation dimension of the attractor. We note that the form of iteration map (11) ensures that the phase trajectory lies on a two-dimensional manifold, and consequently that d cannot be found larger than 2. The finding of a noninteger value for d would have revealed a fractal attractor on the two-dimensional manifold. With $d = 2$ here, the attractor itself is a two-dimensional manifold. The saturation of the correlation dimension d as the phase space dimension n is increased, is typical of deterministic chaotic systems. It can be observed for instance in fluid turbulence (Bergé et al., 1986). In contrast, a stochastic system like random noise would show no such saturation, but a continued increase of d with n .

The same type of attractors that densely fill a finite portion of the phase plane, have been experimentally observed in biological neural systems. Babloyantz and Destexhe (1986) report similar attractors obtained from electroencephalograms of epileptics, for which the characterization based on the correlation function gives a correlation dimension of 2.05 ± 0.09 . A different attractor (see Figure 9), obtained with $\beta_3 = 23.16$ this time, clearly exhibits in its structure self-similarity typical of fractal sets.

4. PROPERTIES OF THE TWO NEURON NETWORK

An even smaller neural structure, constituted by the network shown in Figure 1a, also exhibits several distinct dynamic regimes. The time evolution of the ac-

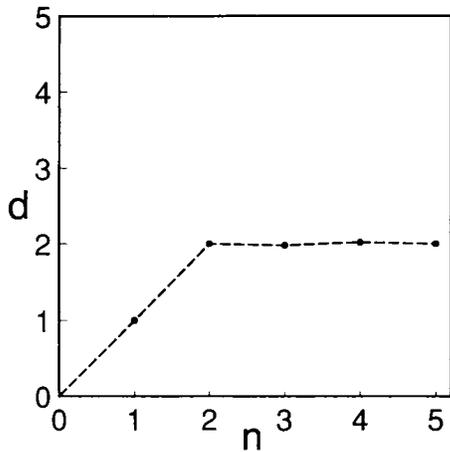


FIGURE 8. Correlation dimension d of the attractor of Figure 7 as a function of the phase space dimension n . The saturation of d with n is characteristic of deterministic chaotic systems.

tivities in this network are governed by eqns (2 and 3). Figure 10 shows different evolutions of the activity $S_1(t)$, obtained with the following fixed values for the parameters: $\beta_1 = 15.0$, $\beta_2 = 10.0$, $\theta_1 = 0.2$, $w_{11} = 0.6$, and $w_{21} = -0.4$. The control parameter is now θ_2 , the threshold of neuron 2. For low values of θ_2 , neuron 2 exerts a strong inhibiting action on neuron 1 through the negative synapse w_{21} , maintaining $S_1(t)$ in a stable inhibited state (Figure 10a). As θ_2 is increased, the inhibitory action of neuron 2 diminishes, and $S_1(t)$ experiences oscillatory regimes (Figs. 10b–10d). For large values of θ_2 , there is no longer a significant inhibiting action from neuron 2, and $S_1(t)$ attains a stable activated state (Figure 10e).

It is interesting to note that the *oscillatory* regimes displayed by the network are not necessarily *periodic*.

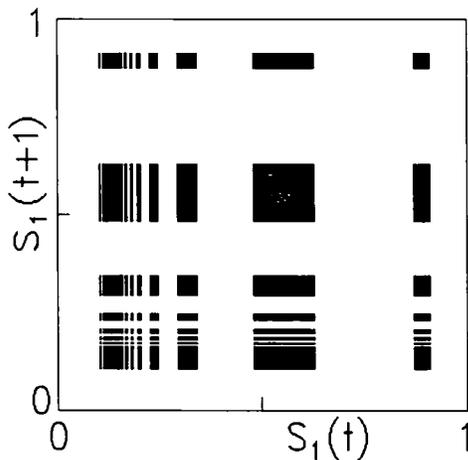


FIGURE 9. Pseudo phase space attractor for iteration map (11) with the parameter values $\beta_1 = \beta_2 = 7.0$, $\beta_3 = 23.16$, $\theta_1 = 0.5$, $\theta_2 = 0.3$, $\theta_3 = 0.7$, $w_{21} = 1.0$, and $w_{31} = -0.8$. The attractor displays self-similarity typical of fractal sets.

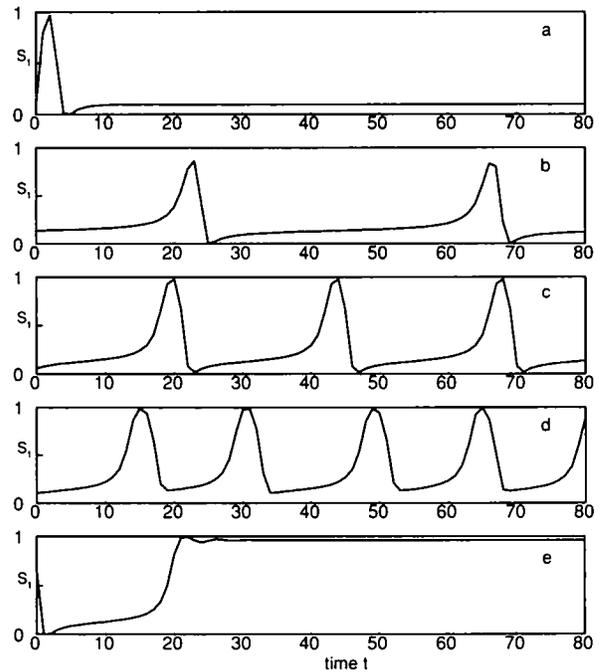


FIGURE 10. Time evolutions of the output activity $S_1(t)$ showing different accessible dynamic regimes for neuron 1 of Figure 1a, for increasing values of the synaptic threshold θ_2 : (a) Stable inhibited, for $\theta_2 = 0.5$. (b) Quasi-periodic, for $\theta_2 = 0.6$. (c) Periodic, for $\theta_2 = 0.75$. (d) Quasi-periodic, for $\theta_2 = 0.85$. (e) Stable activated, for $\theta_2 = 1.0$. The other parameters of the network are: $\beta_1 = 15.0$, $\beta_2 = 10.0$, $\theta_1 = 0.2$, $w_{11} = 0.6$, and $w_{21} = -0.4$.

but also may be *quasi-periodic*. For instance, the signal $S_1(t)$ in Figure 10c is strictly periodic, with a period of 24 time steps, whereas the signals $S_1(t)$ in Figs. 10b and 10d are only quasi-periodic (i.e., they do not exhibit exact periodicity). This difference appears clearly on the autocorrelation signals presented in Figure 11. For the periodic $S_1(t)$ in Figure 10c, the corresponding autocorrelation signal in Figure 11a is periodic with the same period as $S_1(t)$, and exhibits peaks of magnitude 1 every time the delay is an integer multiple of the period. In contrast, for the quasi-periodic $S_1(t)$ in Figure

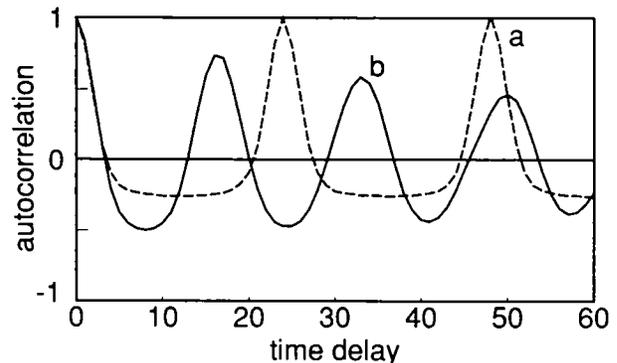


FIGURE 11. Autocorrelation signal of output activity $S_1(t)$, for: (a) the periodic regime of Figure 10c, (b) the quasi-periodic regime of Figure 10d.

10d, the corresponding autocorrelation signal in Figure 11b shows no periodicity. Nevertheless, it also contains peaks (separated here by about 16 time steps), which characterize the “quasi-period” of $S_1(t)$, but whose magnitudes uniformly decay as the delay increases. The quasi-periodicity as it is observed here may result from the incommensurability of the iteration time step Δt and an underlying possible period of oscillation in the system. However, in the framework of this model Δt is not arbitrary, but represents an average delay for transmission of activity from one neuron to another. Quasi-periodicity may thus be expected to be an actual property of the systems which are modelled here.

The period (or quasi-period) of the oscillatory signal $S_1(t)$ can be continuously modified, within a certain range, by alteration of the value of the control parameter. Figure 12 shows the variation of the period, or quasi-period, T , of $S_1(t)$ as a function of the control parameter θ_2 .

The role of control parameter played by the threshold θ_2 could be played identically by an external input signal, which would be applied to neuron 2 endowed with a fixed threshold, to act as an offset signal. In such a situation, the neural network considered here can be interpreted as representing an *externally controllable neural oscillator*.

A second order iteration map that governs the time evolution of $S_1(t)$, can be deduced. From eqns (2 and 3) with $\Delta t = 1$, it follows:

$$S_1(t + 1) = f_1[w_{11}S_1(t) + w_{21}f_4(S_1(t - 1))]. \quad (13)$$

A pseudo phase space attractor for the system can be obtained by plotting the values of $S_1(t + 1)$ against $S_1(t)$ once the initial transient has vanished. Figure 13 shows this plot for the signal S_1 in Figure 10d. In Figure 13, the points are not distributed randomly in the

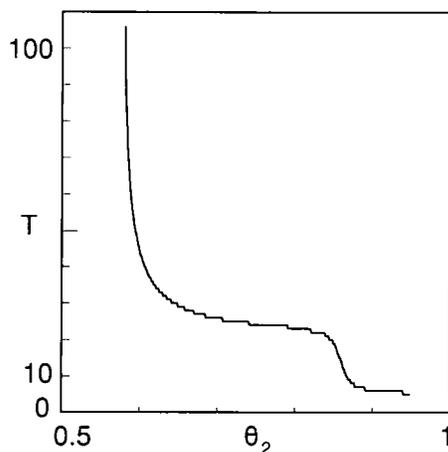


FIGURE 12. Continuous variation of the period or quasi-period T of the output activity $S_1(t)$ of neuron 1 of Figure 1a, as a function of neuron threshold θ_2 . With such a dynamics the network behaves as an externally controllable neural oscillator.

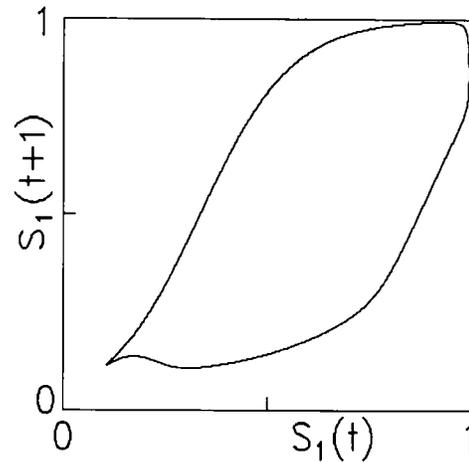


FIGURE 13. Pseudo phase space attractor resulting from the iteration map (13) with the parameter values $\beta_1 = 15.0$, $\beta_2 = 10.0$, $\theta_1 = 0.2$, $\theta_2 = 0.85$, $w_{11} = 0.6$, and $w_{21} = -0.4$. This type of attractor is characteristic of a quasi-periodic dynamics.

pseudo phase plane; instead, they all lie on a curve in this plane. This outcome is characteristic of the presence of quasi-periodicity in the system (Bergé et al., 1986). For a quasi-periodic regime, the points of the pseudo phase space attractor fill the curve in a continuous fashion, whereas for a periodic regime only a finite number of points appear on the curve. Comparable cyclic phase space trajectories have been derived from a theoretical model of the olfactory bulb (Freeman, 1987).

5. DISCUSSION OF THE RESULTS

The dynamic behaviors of small neural networks that we report here, can be compared to those of simple mathematical models based on time-iterated nonlinear equations and exhibiting deterministic chaos (May, 1976). As we mentioned throughout their analysis, our network models share several properties with these simple mathematical models. Such similarities are conveyed by characteristics like bifurcation diagrams, sensitive dependence on initial conditions, strange attractors, which are in fact the signatures of deterministic chaos itself. Beyond these similarities, our network models show some specificities of their own.

First of all the quantities in our models are not mere mathematical variables, as they often appear in investigations of deterministic chaos. Here the quantities are interpretable in neurophysiological terms: the chaotic variables are neuron output activities, the control parameters are synaptic weights or external neuron inputs (equivalent to neuron thresholds). When related to biological systems, the concepts of deterministic chaos have been first applied to ecology, population dynamics, genetics, biochemistry (May, 1976). It is only recently that they have been applied to neural networks, and very few models have put in light the possibility of chaos

in individual neuron output activities, with control through a single synaptic weight, in very small neural circuits.

Another specificity of our network models compared to simple mathematical chaotic models as those described for instance in May (1976), is that for these later models, the nonlinearities on which they rely to generate chaos are essentially nonmonotone nonlinearities. This feature is essential for these systems to display chaos. In contrast, with neural networks, the basic nonlinearities in the system are that of the neuron input-output transfer functions, which are intrinsically monotone nonlinearities. Therefore, it is not *a priori* obvious, if, and how, chaos may show up in these systems, especially when their size is small. We exemplify here how feedback of excitatory and inhibitory activities, in networks incorporating no more than two or three neurons, can lead to the onset of chaos.

Another element that appears to be essential for the existence of chaos in the networks discussed here, is the presence of finite delays (partial delays are sufficient) in eqns (2–9). Examples are known of continuous-time equations with very smooth and stable solutions, that, when approximated by discrete-time iterated equations can give way to chaotic evolutions. These conditions do not apply for the description of the networks we present here. We believe that there are no continuous-time equations with stable and smooth solutions, which could describe adequately the neural network dynamics, and for which eqns (2–9) would represent discrete-time approximations. Neural functioning is not smooth, but rather controlled by “discrete” events such as spike emissions, spike arrivals on a synaptic terminal, sudden release of a neurotransmitter, opening of ionic channels. The finite delays in eqns (2–9), interpreted as explained in Section 2, express a property inherent to the neural systems, where driving events appear at discrete times. The chaotic behaviors which then follow in certain conditions can thus be considered as bearing relevance for the description of the dynamics of the neural networks. They cannot be seen as mere artifacts introduced by discrete time in the dynamics of systems that otherwise would be smooth and stable.

The results presented in Sections 3 and 4 show that qualitatively different dynamic regimes can exist in neural networks, even with very simple structures. Stable, oscillatory (periodic and quasi-periodic), and chaotic regimes are observable. It is interesting to note that this dynamic variability results from the sole evolution of the neuron activities. No intrinsic synaptic plasticity need be incorporated to obtain complex dynamic behaviors. This contrasts with recent models, in which the joined effects of neuron dynamics and synapse dynamics are put in play, in order to generate chaotic evolutions in a neural network (van der Maas et al., 1990).

The neural networks modelled here represent what can be viewed as “minimal structures” that give rise to complex dynamic behaviors. As was mentioned above, properties of the networks that appear to be crucial for the existence of unstable or chaotic regimes, are feedback of excitatory and inhibitory actions transmitted with delays. For the purpose of demonstration, in the present paper, these properties were concentrated in neural networks of very reduced size. Neural structures as simple as that depicted in Figure 1 can be identified in certain biological networks (e.g., in the cerebellar cortex at the level of the granule and Golgi cells (Ito, 1984)). If large populations of neurons are considered, the presence of feedbacks and delays is very probable. Jitter in individual signal delays is also probable in large neuron assemblies. Coherent oscillations that require durable synchronization of neuron activities may be more difficult to maintain in large networks. However, chaotic dynamics, together with stable dynamics, that do not require such synchronization, may be expected to also exist in large neural networks for some ranges of their parameters. In any case, the results reported here show that stability is not, in general, granted in neural systems, even with simple structures. Specific tuning of the network parameters must be achieved in order to sustain stable patterns of activation, and conditions that yield instability are not at all unlikely.

The dynamic regime of a network can be changed through modifications of internal or external parameters, such as synaptic weights or external neuron inputs. Any one of the observed regimes possesses some degree of structural stability, for it can subsist over finite ranges of parameter values. With such properties, the different dynamic regimes of a neural network, can provide a basis for various “cognitive” functions. *Stable regimes*, that are the most often evoked, usually to represent memory processes, may not be the only regimes useful for neural information processing. *Oscillatory regimes* offer schemes for the control of rhythmic biological functions such as respiration or locomotion. A question that is raised at this point, and that we are currently investigating, is the question of the determination of the synaptic connections, or the synaptic plasticity mechanisms, that could yield a neural oscillator with specific repetition rate and signal form. The role of *chaotic regimes* in biological neural systems is not yet fully perceived, although different possibilities already have been suggested (Skarda & Freeman, 1987; Yao & Freeman, 1990). Anyhow, it is now clear, both from experimental and theoretical evidence, that chaotic dynamics can exist in neural systems, even with quite simple structures, as demonstrated here. The possibility of chaotic dynamics in neural networks, introducing sensitive dependence on initial conditions, imposes a limit to any long term prediction concerning

the evolution of the system. This applies, unless an explicit mechanism is implemented by the network to adapt its parameters in order to avoid chaos, by synaptic plasticity through learning for instance.

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