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**MODELING NEURONS BY SIMPLE MAPS**

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## Abstract

We introduce a simple generalization of graded response formal neurons which presents very complex behavior. Phase diagrams in full parameter space are given, showing regions with fixed points, periodic, quasiperiodic and chaotic behavior. These diagrams also represent the possible time series learnable by the simplest feed-forward network, a two input single-layer perceptron. This simple formal neuron behaves as an *excitable element* with characteristics very similar to those appearing in more complicated neuron models like FitzHugh-Nagumo and Hodgkin-Huxley systems: natural threshold for action potentials, damped subthreshold oscillations, rebound response, repetitive firing under constant input, *nerve blocking* effect etc. All this rich dynamics can be introduced in a very natural way in the current paradigm of networks of formal neurons. We show that networks of such elements are interesting models which lie at the interface of neural networks, CMLs, excitable media and self-organized criticality studies.

*Key words: neural networks, perceptron, time series, coupled map lattices, biological oscillators, excitable media, self-organized criticality, Farey tree.*

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## 1 Introduction

Although convergent dynamics (relaxation to fixed points) has been a dominant theme in studies of artificial neural networks [Hertz *et al.*, 1991], oscillatory behavior in network models is currently the object of increasing attention. Not only single neurons can behave as autonomous oscillators [Llinas, 1988] but also oscillatory *collective and synchronized* dynamics has been observed at different biological functional levels, for example in the visual [Gray *et al.*, 1989, Eckhorn & Schanze, 1991] and olfactory systems [Skarda & Freeman, 1987, Gelperin & Tank, 1990, Laurent & Davidowitz, 1994] in organisms situated at all branches of the phylogenetic tree. Such behavior has been conjectured to be an important clue for solving the feature-binding problem (how the brain links different perceptual signals to the same object) triggering a lot of theoretical and modeling work.

Since the standard networks of formal neurons (attractor networks with binary or graded response elements) are unable to capture this type of temporal behavior, researchers in this area have turned their attention to a variety of alternative elements to represent neurons or neural assemblies. These include phase oscillators [Sompölnsky *et al.*, 1991, Hansel & Sompölnsky, 1992, van Hemmen & Wreszinski, 1993, Arenas & Pérez Vicente, 1994, Matsuno *et al.*, 1994], excitable elements like FitzHugh-Nagumo system [Abbott, 1990, Kurrer *et al.*, 1991, Wallenstein, 1993, Gopalsamy & He, 1994], pulse-emitting units [Gerstner & van Hemmen, 1993, Abbott & van Vreeswijk, 1993] and binary elements with dynamical thresholds [Horn, 1993].

Other researchers, from the dynamical systems community, have proposed coupled map lattices (CML) as an alternative paradigm to consider synchronization, chaos and other spatio-temporal phenomena in biological neural networks [Kaneko, 1992, Chaté & Manneville, 1992]. The most studied models have as basic element the logistic map, which is a simple and well known system but has no neurobiological motivation.

In this work we propose a new formal neuron which is a 2-dimensional map (networks of these elements lie in the coupled map paradigm). This map is a very natural extension of the *graded response neuron*, the usual element of standard artificial neural networks. We call this map a *dynamical perceptron* (DP). Networks of dynamical perceptrons are coupled map systems which generalize naturally the well studied Hopfield networks of graded response neurons [Marcus & Westervelt, 1989, Shiino & Fukai, 1990, Mertens, 1991].

Our main result is the verification that, in a well delimited region in parameter space, the response of this simple map to external inputs has striking similarity to the dynamical behavior of more complicated models with continuous time dynamics like the space-clamped FitzHugh-Nagumo system (sometimes called Bonhoeffer-van der Pol equations) and even strongly biologically motivated models like Hodgkin-Huxley equations [Tuckell, 1988].

Depending on the choice of its parameters, the map behaves as an *excitable element* or as an *autonomous oscillator*. By excitable element we refer to a dynamical system which relaxes to a fixed point following a short or a long trajectory depending on a natural threshold. Then, our map seems to be a good candidate for further studies within the coupled map paradigm, which is a recent and interesting research area by itself.

Our results, however, have interest beyond any neuron modeling task, since they also represent the possible attractors learnable by a two input single-layer perceptron used as a time series predictor. So, an interesting link with standard (backpropagation) feed-forward neural networks

(FNN) is established, the dynamical perceptron being the prototype of FNN modeling of dynamical systems (a neuron or neural assembly being particular instances of this type of application). The dynamical perceptron also has some links with traditional statistical tools like auto-regressive models [Froyland, 1992, Takens, 1993] which will be briefly discussed.

In this study we explore the behavior of a single dynamical perceptron under external input. In Sec. 2 we define the model and discuss its motivation. In Sec. 3 we present phase diagrams in parameter space for the stationary behavior of the map under constant applied inputs. The model transient response to an instantaneous current pulse is discussed in Sec. 4. Section 5 contains some considerations about networks of dynamical perceptrons and their relationship with standard neural networks models. Our conclusions are offered in Sec. 6.

## 2 The Model

Neuron models have to deal with two competing constraints: biological realism and mathematical tractability. Some models (for example, Hodgkin-Huxley neuron) stress the first one while others (formal neurons) achieve the second one at the cost of dramatic simplifications. Hodgkin-Huxley-like neurons present a varied repertoire of dynamical behaviors depending on its parameter values, but are not easy to study analytically or even numerically. On the other hand, formal neurons most considered in the literature are structurally simple but have no intrinsic dynamics.

According to the approach usual in physics, we study the *necessary* (in contrast with the *sufficient*) requisites for the appearance of some collective behavior in networks, the simplest elements with the simplest interactions being considered first. But we want to propose a formal neuron which, although structurally simple, presents complex dynamical behavior at least qualitatively similar to real neurons. However, unlike other proposals (e.g., phase oscillators), our model stays within the current neural network paradigm popularized by Hopfield [1984], since it is a simple generalization of a standard formal neuron widely used in the literature. This is interesting because knowledge accumulated in this field can be directly used in the analysis of our model.

The two most considered formal neurons are the *McCulloch-Pitts neuron* (a binary variable like an Ising spin) [Hertz *et al.*, 1991] and the *graded response neuron* [Hopfield, 1984, Marcus & Westervelt, 1989]. Usually, the state variable  $V(t)$  of the graded response neuron is interpreted as describing not the single action potential but an average frequency of these spikes [Abbott, 1990]. Here, however, the variable  $V(t)$  will represent the neuron membrane potential measured at discrete time steps. This will be done because we intend to make a comparison with more sophisticated neuron models like the space clamped FitzHugh-Nagumo and Hodgkin-Huxley equations [Tuckell, 1988].

Consider a time series of this membrane potential (how this time series can be obtained is not our concern now). Our task will be to find a simple model which describes such series. A general approach to this modeling problem, which we will follow here, is to use a feed-forward neural network (FNN) to emulate the system behavior [Hertz *et al.*, 1991, Albano *et al.*, 1992]. It is well known that FNNs with one layer of hidden units can approximate any continuous function. Then, we can *in principle* train a feed-forward net to reproduce the biological neuron time series (a somewhat self-referential application of neural nets!). Once we find such FNN (which will be a formal neuron model) we may couple many of them to form a large ensemble of formal neurons. At the end of this process, however, we will achieve a large, complicated and theoretically intractable

system.

So, it is worthwhile to consider a simpler task. We ask for the *simplest feedforward net* which qualitatively models the neuron time series. By *qualitatively* we mean a very weak requirement: we want a formal neuron which behaves, like biological neurons, as an excitable element with some type of oscillatory behavior (repetitive firing) under external input.

A single-layer perceptron (a feedforward net without hidden units) can do this and has the advantage of being a very well studied system (see Fig. 1a). The perceptron learns the time series  $\{S(t)\}$  by using *examples*, that is, input-output pairs  $(\mathbf{X}_t, Y_t)$ . The desired output is the value of the time series at time  $t$ ,  $Y_t \equiv S(t)$ . The input may be the previous  $n$  values of the time series  $\mathbf{X}_t \equiv \{S(t-1), \dots, S(t-n)\}$ . Then, the examples are generated simply by slipping a window of length  $n$  over the data, the so called tapped-delay method [Hertz *et al.*, 1991, Albano *et al.*, 1992].

The perceptron output will be given by

$$V(t) = g(\mathbf{W} \cdot \mathbf{X}_t + \theta) = g\left(\sum_{\tau=1}^n W_\tau S(t-\tau) + \theta\right), \quad (1)$$

where  $\mathbf{W} = \{W_1, \dots, W_n\}$  is the weight vector which defines the perceptron, the constant  $\theta$  is the so called *bias* term and  $g(x)$  is a non-linear continuous sigmoidal function.

After training over a time series, that is, after some set of weights  $\mathbf{W}$  is found by minimizing a cost function (say,  $E(\mathbf{W}) = \sum_t [V(t) - S(t)]^2$ ), we can create a dynamical model from the perceptron so obtained. To do this we simply send the perceptron output to the rightmost input node and transfer the value present at each input node to its left neighbor (the leftmost value is discarded, see Fig. 1b). That is, the network output will be given by the  $n^{\text{th}}$ -order recurrence equation

$$V(t) = g\left(\sum_{\tau=1}^n W_\tau V(t-\tau) + \theta\right). \quad (2)$$

We call this system a *dynamical perceptron of order  $n$* , or  $DP(n)$ . Here we will restrict the transfer functions  $g(x)$  to be considered to the family of sigmoidal functions composed of translations and scale changes of the hyperbolic tangent:

$$g(x) = c_1 + c_2 \tanh(\gamma x), \quad (3)$$

where  $c_1$ ,  $c_2$  and  $\gamma$  are constants ( $\gamma$  is usually called the *gain* of the transfer function). The very used logistic function  $g(x) = [1 + \exp(x)]^{-1}$  with image in the  $[0, 1]$  interval [Pasemann, 1993] is obtained when  $\gamma = c_1 = c_2 = 1/2$ . All these maps are topologically conjugated to the tanh one through a change of variables  $V' = (V - c_1)/c_2$ , giving

$$V'(t) = \tanh\left[\gamma' \left(\sum_{\tau=1}^n W_\tau V'(t-\tau) + \theta'\right)\right], \quad (4)$$

with the transformed variables

$$\gamma' = c_2 \gamma, \quad \theta' = \frac{\theta}{c_2} + \frac{c_1}{c_2} \sum_{\tau=1}^n W_\tau. \quad (5)$$

By the way, we note a connection between DP( $n$ ) models and standard auto-regressive models AR( $n$ ) (or 'linear predictors') used in time series analysis [Froyland, 1992, Takens, 1993] defined by

$$V(t) = \sum_{\tau=1}^n W_{\tau} V(t-\tau) + \theta + \eta(t), \quad (6)$$

which can be regarded as a linear perceptron ( $g(x) = x$ ) fed with white noise  $\eta$ . This class of statistical models are applied to oscillating time series by choosing the  $\mathbf{W}$  parameters so that some eigenvalues  $\lambda_i$  of the linear map are complex (with modulus  $|\lambda_i| < 1$ ). The model can be regarded as a dissipative oscillator subjected to random perturbations in order to prevent convergence to the fixed point.

In the AR( $n$ ) models it is not possible to use parameters  $\mathbf{W}$  such that some eigenvalues have modulus greater than one. This range of parameters, however, can be used in the DP( $n$ ) models since the bounded transfer function  $g(x)$  prevents any diverging behavior. This fact eliminates the necessity of noise to feed the system. Furthermore, the nonlinear nature of  $g(x)$  may give us the possibility of using chaotic attractors for fitting the data, which is not possible in the AR( $n$ ) models, where all aperiodicities must be regarded as originating from noise. Of course, we may construct *stochastic* DP( $n$ )s where, similarly to the AR( $n$ ) models, there is some noise  $\eta(t)$  added to the local field (this seems to be an interesting extension which deserves further exploration).

Then, like the AR( $n$ ) sequence of *linear stochastic* models, we have a natural hierarchy of elements to study, the set {DP( $n$ )} of *nonlinear deterministic* models. The DP(0) model corresponds to the standard graded response neuron which has no self-couplings. We have seen that it has no isolated dynamical behavior whatever. The DP(1) model has been recently studied as an oscillatory formal neuron by Pasemann [Pasemann, 1993]. However, the dynamical perceptron with one self-coupling has very poor behavior, exhibiting only fixed points or cycle-two as attractors. Networks of such neurons have already been considered by statistical physicists some time ago [Marcus & Westervelt, 1989].

We will focus our attention in the *simplest non-trivial* dynamical perceptron, that is, the DP(2) model. The low dimensionality of this system allows us to obtain phase diagrams representing the behavior of *all* dynamical perceptrons of this class (that is, all possible choices for  $\mathbf{W}$  and  $\theta$ ). Then, considerations about the learning process like the sketched above are unnecessary. Our task will be to determine if, for this very simple net, there is some region in parameter space where it gives an interesting neuron model.

The DP(2) system, indeed, presents a very rich behavior (fixed points, limit cycles, quasiperiodic and chaotic attractors, coexisting attractors, natural threshold like the FitzHugh-Nagumo system etc.) which can be used to mimic some well known behaviors of real neurons. It also allows the modeling of time-dependent neuron responses like *habituation*, *bursting* etc., since the internal parameters  $\mathbf{W}$  and  $\theta$  eventually can be made history dependent (this possibility will be explored in another work [Kinouchi, 1995]).

We may rewrite Eq. (4) for the DP(2) model as

$$V(t) = \tanh \left[ \frac{V(t-1) - \kappa V(t-2) + H}{T} \right], \quad (7)$$

with

$$\kappa = \frac{-W_2}{W_1}, \quad T = \frac{1}{c_2 \gamma W_1}, \quad H = \frac{I + \theta + c_1 (W_1 + W_2)}{c_2 W_1}, \quad (8)$$

where we have used Eq. (5) and an extra term  $I$  for the external input has been introduced. This is the simplest neural network model of a dynamical system and the full phase diagram in the variables  $(\kappa, T, H)$  gives all the possible time series implementable by this architecture.

The choice of these variables is motivated by convenience in the visualization of the phase diagram as well as to connect the  $n = 2$  dynamical perceptron with previous literature on the so called YOS map. This map (for the case where  $H = 0$ ) has been first studied in the context of statistical mechanical models of magnetically modulated materials by Yokoi, de Oliveira and Salinas [1985]. In that context the variable  $V(t)$  describes the magnetization on the  $t^{\text{th}}$  layer of an Ising model with competing interactions on a Bethe lattice. Recently, Yokoi and one of us (MHRT) have studied the map for constant and non-zero  $H$  [Tragtenberg & Yokoi, 1994].

### 3 Asymptotic Behavior for Constant Input

Classical measurements on the electrophysiology of neurons have been done mainly under two experimental situations [Tuckell, 1988]. In the first one, a constant current input is injected during some time interval, enabling the study of the neuron stationary response. In the second one the neuron response to a single 'delta' pulse of current is observed. In this section we study the stationary response for the case of a constant current. Transient responses to current pulses are discussed in the next section.

#### 3.1 Diagram $T$ versus $\kappa$

The diagrams shown in Figs. 2-3 refer to the dynamical behavior in the  $T$  vs  $\kappa$  plane for a DP(2) with  $g(x) = \tanh(\gamma x)$  when  $H = 0$  (the meaning of the region labels is discussed below). In region (0/1) there are only trivial fixed points (this corresponds to a paramagnetic phase in the magnetic model). In region (0/2) two fixed points coexist for all values of  $T$  and  $\kappa$ , and these states are found to be the solutions of  $V = \tanh[(1 - \kappa)V/T]$  (corresponding to the ferromagnetic phases in the magnetic model). The convergence to each fixed point depends on the initial conditions  $V(t=0)$  and  $V(t=1)$ . In the region labeled (1/2) there is a two-cycle (antiferromagnetic phase).

The so called *modulated phases* in the statistical mechanics model correspond to oscillating behavior in the time series model. For the periodic oscillations (*commensurate phases* — gray regions) the so called winding numbers  $q/2\pi = P/Q$  are defined in terms of the attractor period  $Q$  (the number of steps after which the series *exactly* repeats) and the number of complete oscillations  $P$  within a period ( $q$  is the modulated phase 'average wave number' in the *spatial* magnetic model, and an 'average frequency' in our *temporal* neuron model — see Fig. 4). Quasiperiodic phases have  $q/2\pi$  irrational. Probably infinitely many quasiperiodic and periodic attractors lie between the gray regions. Details concerning the numerical methods for the determination of the phase boundaries are given in [Tragtenberg & Yokoi, 1994]. We will use the word *modulated phases* to refer generically to the periodic, quasiperiodic and chaotic attractors of the map, although in the associated statistical mechanics magnetic model not all attractors correspond to true phases in the thermodynamics sense.

In the regions (0/2 + 1/2) two fixed points and a two-cycle coexist. More interesting is the modulated-fixed point coexistence region (0/2 + MOD) where periodic, quasiperiodic and chaotic attractors may be attained depending on the initial conditions [Yokoi *et al.*, 1985,

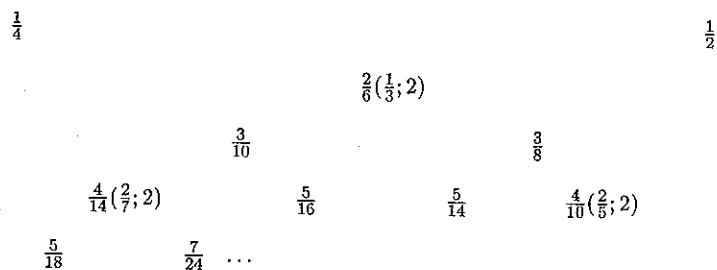
Prado & Fiedler-Ferrari, 1989]. The same occurs at the modulated-two-cycle coexistence region ( $1/2 + \text{MOD}$ ).

The periodic phases can be ordered in a systematic way following a so called *nonstandard Farey construction* [Perez et.al, 1993]. A Farey construction is an ordination of the rational numbers according the following rule. Given two rationals  $F'/G'$  and  $F''/G''$ , the next Farey number between them is given by

$$\frac{F}{G} = \frac{F' + F''}{G' + G''}. \quad (9)$$

In the standard Farey tree the first two rationals are such that in all the subsequent Farey numbers the numerator  $F$  and the denominator  $G$  are relative primes. In nonstandard Farey trees [Perez et.al, 1993] it is possible that  $F$  and  $G$  have some common factor, say  $F = mP$  and  $G = mQ$ . It is found that the winding numbers of the Arnol'd tongues are given by  $P/Q$  and that  $m$  gives the number of coexistent attractors with such winding number. Thus, the Farey number give us more information than simply the winding number.

To see how this Farey construction appears in our system, consider first the third quadrant ( $T, \kappa < 0$ ) in our phase diagram. The dominant phases are the cycle-2 and the cycle-4. Then, if we start the Farey construction from the extrema  $1/2$  and  $1/4$  we obtain the following tree:



The corresponding winding number  $P/Q$  and the number of coexisting attractors  $m$  are show between parenthesis when  $m > 1$ .

By symmetry, it must be possible to do a similar construction for the first quadrant. In fact, this occurs if we start from the extrema  $0/2$  and  $1/4$  which means to assign the Farey label  $(0/2)$  to the 'ferromagnetic' phase. This Farey number indicates that there are two attractors with winding number  $0/1$  (that is, two fixed points) in this region, what indeed is the case. We also have observed the multiple attractors in the Arnol'd tongues with  $m \neq 1$ .

We have found that the label  $(0/m)$  is relevant for various systems presenting Arnol'd tongues and that most authors are not aware of the need of using this label for obtaining a correct Farey ordination:

- For example, Mettin *et al.* [1993] present a phase diagram for the driven van der Pol oscillator (Fig. 2) where the Arnol'd tongues can be obtained in the correct order if we use a Farey tree with extremes  $1/1$  and  $0/2$ . In Fig. 15 of the same article a Farey tree with extremes  $1/3$  and  $1/5$  is made simplifying the fractions at each level, the next tongue being written as  $1/4$  instead of  $2/8$ , which leads to an incorrect ordination of the subsequent tongues.

- The phase diagram presented by Yokoi & Oliveira [1985] of a chiral-Potts model on the Cayley tree is related to a Farey tree with extrema  $1/3$  and  $0/3$  (the ordered phase has tree fixed points).

- The Arnol'd tongues which appear in a phase diagram for an asymmetric Hopfield model [Laughton & Coolen, 1994] are given by a Farey tree with extrema  $1/4$  and  $0/4$  (the fixed point phase has four fixed points).

In all these systems there are Arnol'd tongues with multiple attractors. So, nonstandard Farey trees seem to be very common although somewhat unnoticed in the literature. We are not aware of a theoretical justification for such universal vality of nonstandard Farey trees, but we also do not know any counterexample.

### 3.2 Diagrams $T$ versus $H$

In Figs. 5, 6 and 7 we show diagrams in the plane  $T$  vs  $H$ , which are the most interesting for our neuron modeling purpose since they give the asymptotic neuron response to external (constant) input  $I$ . These diagrams, unlike the previous ones, are valid for the entire family of transfer functions defined by Eq. (3) if the proper parameter transformations given by Eq. (8) are done.

The phase diagrams for  $\kappa \leq 0.5$  are qualitatively similar to that presented in Fig. 5a. For completeness, Fig. 5b shows the same diagram in the variables  $\omega = W_1$  and  $\theta$  used by Pasemann [Pasemann, 1993], and related to ours by Eq. (8) with  $\gamma = c_1 = c_2 = 1/2$ , that is,  $\omega = 4/T$  and  $\theta = 2(H - 1)/T$ .

The stability boundaries for the  $(0/2)$  and  $(1/2)$  phases coincide with the stability line for the  $(0/1)$  phase, which can be obtained from a linear stability analysis. Their analytic form are simple, given by

$$H_c^\pm = (\kappa - 1)V_c^\pm + T \tanh^{-1}(V_c^\pm), \quad (10)$$

where the  $(\pm)$  signs refer to different signs of the fixed points correspondent to the  $(0/1)$  phase. The functions  $V_c^\pm$ , for the  $(0/2)$  phase and  $T > 0$ , are

$$V_c^\pm = \pm \sqrt{1 - \frac{T}{1 - \kappa}}, \quad (\kappa < 0.5), \quad (11)$$

or

$$V_c^\pm = \pm \sqrt{1 - \frac{T}{\kappa}}, \quad (0.5 < \kappa < 1). \quad (12)$$

On the other hand, the  $(1/2)$  phase boundaries at  $T < 0$  are given by

$$V_c^\pm = \pm \sqrt{1 + \frac{T}{1 + \kappa}}, \quad (\kappa > -0.5), \quad (13)$$

or

$$V_c^\pm = \pm \sqrt{1 - \frac{T}{\kappa}}, \quad (-0.5 < \kappa < -1). \quad (14)$$

In this paper we will focus our attention on the  $\kappa, T > 0$  behavior of the DP(2) map, which is more relevant to our neuron modeling purposes. The  $T < 0$  case, which is related to another statistical mechanics system, is the subject of a forthcoming publication [Tragtenberg, 1995]

In the interval  $\kappa = [0.5, 1.0]$  the diagrams are similar to the one for  $\kappa = 0.6$  plotted with more details in Fig. 7, where we depict some periodic phases.

The stability line for the modulated attractors was numerically determined by a careful iteration of the map (dashed line) and does not coincide with the (0/1) line for lower  $T$  (corresponding to a first order phase transition in the magnetic model). The coexistence regions (0/1 + MOD) lie between this line and the  $H_c^\pm$  lines, disappearing above the *tricritical* points TCP [Tragtenberg & Yokoi, 1994]. In the region (0/2 + MOD) there is a coexistence of two different fixed points and one (or more than one) modulated attractor. Chaotic attractors are observed inside these coexistence regions.

Each set of parameters  $(\kappa, T, H_0)$ , where  $H_0 = H(I = 0)$ , defines a neuron model. Five general types of behavior are found in this type of diagram (to obtain the neuron response for increasing current, we must start from the point considered and follow to the right along an horizontal line since  $H$  is proportional to  $\theta + I$ ):

- If the parameters locate the model at point A, we have an element with a low potential resting state. Under constant external input, it relaxes to a somewhat higher resting state (corresponding to a new fixed point) after a transient damped oscillation. The system never crosses a bifurcation point.
- Model B has its natural threshold  $H_0$  situated inside the modulated phases bubble. It represents a natural oscillator with periodic or quasiperiodic behavior even without external input. Spontaneously firing neurons (*pacemaker neurons*) are well known in biological systems [Llinas, 1988, Pinsker & Ayers, 1983].
- Model C has  $H_0$  outside the bubble and corresponds to an excitable element. This means that, if there are no external inputs, it presents a low resting state. With a step current input  $I$  of small amplitude we observe subthreshold damped oscillations. For higher input amplitudes (which means increasing  $H$  in the diagram, but before penetrating the bubble) a single or many suprathreshold responses ('action potentials') can be elicited before the element returns to the resting state. On some input interval  $[I_1, I_2]$ , which corresponds to an interval  $[H_1, H_2]$  defined by the intersection of the dashed lines with an horizontal line through C (see Fig. 7), the model presents stable oscillatory behavior to be interpreted as repetitive firing. If  $T$  is below the level of the TCP point, there are intervals  $[H_1, H_c^-]$  and  $[H_c^+, H_2]$  where a stable fixed point coexists with the oscillatory solution.
- Model D has a stable resting potential for  $I = 0$ , but presents bistable behavior in the interval  $[H_c^+, H_c^-]$ . In this region it has two coexisting attractors (fixed points), one with a low potential and other with a high potential (plateau).
- Model E is bistable even without external input. A current step or even an instantaneous perturbation  $I(t) = I_0\delta(t - t_0)$  can put the neuron in the high state and vice versa.

Behaviors of type A, D and E are found in the Hodgkin-Huxley-like models for certain ranges of parameters and in some experimental preparations with real neurons [Tasaki & Hagiwara, 1957,

FitzHugh, 1960, Morris & Lecar, 1981]. It seems, however, that the interesting parameters to model standard physiological responses correspond to those presenting behavior of type B and specially of type C.

We may call C1 a neuron with  $T < T_{TCP}$  (first order transition in the statistical mechanics jargon) and C2 a neuron with  $T > T_{TCP}$  (second order transition). If a C1 neuron is put in the coexistence region  $[H_1, H_c^-]$ , a proper instantaneous perturbation can switch its behavior between the oscillating and resting state. This type of response has been found in FitzHugh-Nagumo and Hodgkin-Huxley equations [Tuckell, 1988, Troy, 1976, Troy, 1978] and confirmed in experimental settings [Best, 1979], being called *annihilation of pacemaker activity*. The disappearance of oscillations for high inputs ( $H > H_2$ ) is also a well known behavior called *nerve blocking effect* in the literature. This effect is illustrated in Fig. 8.

For small  $T$  (C1 type element) the threshold behavior is more sharp and the oscillations are more peaked. The excitable type dynamics appears only for neurons not very far from the bifurcation surface. It is also known that biological neurons seem to adjust their internal parameters so that they become sensible to small inputs. Translating this fact to our model corresponds to supposing that some slow dynamics produces a drift of the internal parameters to values near the bifurcation surface, that is, models with (quasi) critical behavior (large transients etc.). The corresponding spin system on the Bethe lattice would be at the border of a phase transition. From these considerations we suggest that:

**For neuron modeling purposes, the most interesting model is a C1 type element situated near the critical region. The corresponding parameter range in the  $(\kappa, T, H_0)$  space is  $0.5 < \kappa < 0.8$ ,  $H_0$  near the transition region (0/1 + MOD), and  $T < T_{TCP}$ .**

This parameter volume will be referred as the *near critical* region. We observe that some experimental results thought as unexplainable by certain models probably represent side effects of this critical behavior. For example, Morris & Lecar [1981] comment that some experimentally observed cell oscillations which grows with time (Fig. 4cii in [Morris & Lecar, 1981]) are not described well by their model. This type of transient oscillation, however, has been observed in our simple system (our Fig. 8 for  $I = 0.03$ , which refer to a cell behavior in the transition region (0/1 + MOD), has striking similarity with their data). We suppose that the much more complex Morris-Lecar model should present the same behavior near the critical region if a careful adjustment of parameters is done.

The view that neurons are somewhat near a self-organized critical state due to some slow adaptive dynamics seems to be a very interesting idea to be explored in another work. By now we only suggest a simple mechanism to implement this idea in the DP(2) model. We only need to assume  $H_0$  as being a slow changing variable (having the same character of the *adaptive current* usual in other neuron models [Rose & Hindmarsh, 1995]):

$$H_0(t+1) = (1 - \lambda_1)H_0(t) - \lambda_2[V(t) - V(t-1)]^2, \quad (15)$$

where  $\lambda_1, \lambda_2$  are small parameters. Then, the decay factor  $\lambda_1$  induces the system to enter the modulated phases bubble, but oscillations increase the importance of the second factor, leading to a change of  $H_0$  back to the near critical region.

This *adaptive* DP(2) neuron (or better, its associated Bethe lattice spin system) presents an explicit 'self-organized criticality' of the type described by Sornette [1992] which originates from

a coupling between a control parameter (in our case,  $H$ ) and an order parameter ( $V$ ). But this is not an *ad hoc* change in our model, since new biologically realistic characteristics appear: one observes fatigue under constant input and bursting phenomena, which are not possessed by the simpler model with constant  $H_0$  [Kinouchi, 1995].

This bursting dynamics involves a new time scale (controlled by  $\lambda_1$  and  $\lambda_2$ ). In this large time scale the neuron behaves as an relaxation oscillator: bursting cycles correspond to successive approximations of  $H_0$  to the threshold  $H_c^-$  followed by oscillatory discharges and a reset of  $H_0$ . In the fast time scale, however, the neuron continues behaving as an excitable element.

A network of such bursting neurons (adaptive DP(2) neurons) corresponds to a slip-stick model [Olami, Feder & Christensen, 1992], so we expect that standard SOC (not Sornette-type SOC) appear at this collective level. This two level SOC model and its connection with collective synchronization phenomena is developed in another work [Kinouchi, 1995].

Returning to the standard (non-adaptive) DP(2) model, we present other diagrams for values of  $\kappa$  in the range 0.5 – 1.0 in Fig. 9. Note that for increasing  $\kappa$  the periodic phases (Arnol'd tongues) have larger areas, which is not a good property for our purposes (biological neurons without external forcing do not present self-entrainment). These tongues must be regarded as an artifact due to the discrete nature of our oscillator. This fact motivates our suggestion of using the map for neuron modeling only up  $\kappa = 0.8$  where these tongues are relatively small. Of course, for other time-series modeling purposes, the presence of these Arnol'd tongues may be a positive and interesting feature.

A more elaborated discussion and detailed diagrams for higher values of  $\kappa$  are given in [Tragtenberg & Yokoi, 1994]. As an example of the complex nature of these regions we show the diagrams for  $\kappa = 1.0$  and  $\kappa = 1.5$  (Fig. 10). Although there are no coexistence regions (0/1+MOD) in these diagrams (the TCP point disappears at  $\kappa = 1.0$ ), there are coexistence regions of modulated attractors with different frequencies near the inferior boundary of the bubble (in the center of the onion-like regions). Chaotic attractors, as presented in Fig. 11, can be found in these coexistence regions.

## 4 Transient Response to Instantaneous Pulses

Now we will show interesting similarities between the behavior of continuous time models (FitzHugh-Nagumo, Hodgkin-Huxley) and the transient response of our model after an instantaneous current pulse  $I(t) = I_0\delta(t - t_0)$ . We focus our attention in the dynamical perceptron with parameters corresponding to a type C1 element.

By a change of variables,  $x(t) \equiv V(t)$  and  $y(t) \equiv V(t - 1)$  the second order recurrence Eq. (7) can be written as the two dimensional YOS map

$$\begin{aligned} x_t &= \tanh\left(\frac{x_{t-1} - \kappa y_{t-1} + H}{T}\right), \\ y_t &= x_{t-1}. \end{aligned} \quad (16)$$

In the near critical region determined in the last section this map has a natural threshold behavior, as can be seen in a phase-plane analysis (Fig. 12). The solid curve is the null isocline where  $\Delta x_t = x_t - x_{t-1} = 0$ , given by

$$y = \frac{1}{\kappa} (x - T \tanh^{-1} x + H). \quad (17)$$

Above this line we have  $x_t > x_{t-1}$  (the membrane potential grows), and below it,  $x_t < x_{t-1}$ . The dashed line is the null isocline for the variable  $y$  which we may call the *recovery* variable. The point where the two lines cross defines the resting state P. We see that if  $I_0$  produces a perturbed value  $x < x_c$ , the potential  $x$  will monotonically decrease. However, if  $x(I_0) > x_c$  then  $x$  initially increases, with the possibility of a large displacement until the system returns to the resting state. Indeed, we can find a *separatrix* line in the  $x$  vs  $y$  plane (not showed) which passes at some distance to the right of  $x_c$  (say, at the point  $x_s$ ) delimiting the region of initial conditions in the phase plane where large displacements (which are interpreted as *action potentials*) occur.

This phase plane is very similar to the one presented by the FitzHugh-Nagumo (or Bonhoeffer-van der Pol) equations [Tuckell, 1988, Wallenstein, 1993, Kurrer *et al.*, 1991] and other reductions of Hodgkin-Huxley equations to 2-dimensional systems. A common factor in all these systems is the null isocline with an N-like shape [Abbott, 1990].

Examples of transient responses to delta pulse currents  $I = I_0\delta(t - t_0)$  are shown in Fig. 13a for a neuron with  $T = 0.35$ ,  $\kappa = 0.6$  and  $H_0 = -0.04$ . In a bottom — up sequence we have  $I_0 = 0.04, 0.05, \dots, 0.18$ . Note the quasithreshold behavior near  $I_0 = 0.13$ . Compare also the structure of the action potentials with that of biological neurons (Fig. 13b).

Another known effect in real neurons is the *rebound* response which occurs when a negative (inhibitory) pulse current is applied. We found that this rebound effect only occurs if the neuron parameters are really near the transition region. In Fig. 14 we plot the responses of a neuron with  $T = 0.35$ ,  $\kappa = 0.6$ ,  $H_0 = -0.028$  for increasing *negative* delta pulses. Note that there is also a threshold for the rebound effect near  $I_0 = -0.7$ . Then, this effect is another indication (independent of the considerations of the last section) that the ‘good’ models need to be near the transition region. A similar response (sometimes called *anode break*) occurs when the injected current is a *negative* step instead a delta pulse.

We have found another interesting effect when the neuron is even closer to the transition region. In Fig. 15 we show transient responses to delta currents applied at time  $t_0 = 0$  to a neuron with  $T = 0.35$ ,  $\kappa = 0.6$  and  $H_0 = -0.025$ . The currents are negative so we are seeing rebound responses (however, the same effect appears for positive currents). For small inputs there are only subthreshold responses. For greater inputs we have the generation of one or various action potentials before the system returns to the resting state. The number of these action potentials is *not monotonically related* to the amplitude of the perturbation. The transients are very long and have large dependence on the initial conditions, being an instance of *transient chaos* [Suzuki & Kaneko, 1994]. We are at the ‘border of chaos’ (or better, near a first-order transition region where chaos appears), which reminds us Langton ideas on implementing computation in excitable systems near phase transitions [Langton, 1986]. We will show in the next section that not only the single neuron but also a network of such neurons indeed can be described as excitable media near a phase transition.

## 5 Relation to Standard Neural Networks Models

We think that these preliminary findings justify our claim that the YOS map or DP(2) neuron, as a simple extension of graded response neurons, is a very interesting element of the excitable kind presenting a much more realistic biological behavior than, say, the logistic map or phase oscillators. Its behavior remembers very strongly the FitzHugh-Nagumo system.

The amplitude coupling (instead of phase coupling as in the phase oscillators models) between the elements is a desirable feature [van Hemmen & Wreszinski, 1993, Abbott & van Vreeswijk, 1993]. Of course, this property can also be found in the (continuous time) traditional neuron models (but not in the integrate-and-fire model since it has no natural threshold! [Tuckell, 1988]). Large simulations with DPs, however, are computationally very cheap compared with these continuous time models (there is no need of numerical integrations). Since lattices of 2-dimensional maps are not a well explored subject, we suggest that the YOS map may be a good candidate for further studies in this area.

## 5.1 Attractor networks of DP(2) neurons

How does a network of DPs relate to the attractor (Hopfield-like) networks studied by the statistical physicists? The most considered network [Marcus & Westervelt, 1989, Shiino & Fukai, 1990] is a fully connected set of  $N$  formal neurons without self-couplings and bias terms ( $J_{ii} = 0, \theta = 0$ ), with the (parallel) discrete neuron dynamics given by

$$V_i(t) = \tanh \left[ \gamma \sum_{j=1, j \neq i}^N J_{ij} V_j(t-1) \right]. \quad (18)$$

A phase diagram showing the retrieval (content-addressable memory), paramagnetic and spin glass phases has been obtained by Shiino and Fukai [1990] using the replica method. This phase diagram is very similar to the one obtained by Amit *et al.* [Hertz *et al.*, 1991] for the Hopfield network composed of McCulloch-Pitts neurons. The network presents only fixed points to be identified with stored memories.

Networks of neurons with self-couplings  $J_{ii} = W_{i1}$  have also been considered, the neuron dynamics being given by

$$V_i(t) = \tanh \left\{ \gamma \left[ \sum_{j=1, j \neq i}^N J_{ij} V_j(t-1) + W_{i1} V_i(t-1) \right] \right\}. \quad (19)$$

A condition of stability for the fixed point phase was determined by Marcus and Westervelt [1989]. If this condition is not satisfied a limit cycle of period two appears.

A network of second order dynamical perceptrons (YOS maps) with no external input ( $I = 0$ ) will have a dynamical evolution given by

$$V_i(t) = \tanh \left\{ \gamma \left[ \sum_{j=1, j \neq i}^N J_{ij} V_j(t-1) + W_{i1} V_i(t-1) + W_{i2} V_i(t-2) + \theta_i \right] \right\}. \quad (20)$$

This network, being a non Hamiltonian system, cannot be analysed by the usual statistical mechanical approach. It is a globally coupled map system which must be studied with the tools developed by the dynamical systems community. The simpler homogeneous case where all  $J_{ij}$  are equal should be studied first, and synchronization phenomena are expected to appear.

## 5.2 Homogeneous networks

Although we have not yet performed simulations of a large number of coupled DPs, we can make some simple theoretical considerations for a homogeneous network. Supposing the existence of a stable collective synchronized state  $V_i(t) = V^*(t)$  (for all  $i$ ) in the case of a network with identical neurons ( $W_{i\tau} = W_{\tau}$ ) and identical couplings  $J_{ij} = J/(N-1), i \neq j$ , the evolution of this state will be given by

$$V^*(t) = \tanh \{ \gamma [(J + W_1)V^*(t-1) + W_2V^*(t-2) + \theta] \}, \quad (21)$$

which is equivalent to the behavior of one isolated DP(2) with rescaled parameters

$$\tilde{\kappa} = \frac{-W_2}{J + W_1} = \rho\kappa, \quad \tilde{T} = \frac{1}{\gamma(J + W_1)} = \rho T, \quad \tilde{H} = \frac{\theta}{(J + W_1)} = \rho H, \quad (22)$$

where

$$\rho = W_1/(J + W_1) \quad (23)$$

is a rescaling factor (note that it may be greater or smaller than one depending on the signs of  $J$  and  $W_1$ ). **This means that diagrams as given in this work allows us to predict the character of the synchronized collective state of such networks (supposing it is stable).**

From the phase diagrams ( $\kappa, T, H$ ) presented in Sec. 3 it is easy to see that a network of elements which, when isolated, are all non-oscillating, can present a transition to an *emergent collective* oscillating state for some value of  $J$ . This can be found by locating in the tridimensional parameter space a type C neuron with fixed values ( $\kappa, T, H_0$ ) and drawing a line from the origin through this point, that is, the line ( $\rho\kappa, \rho T, \rho H_0$ ). The system can enter in the modulated phases bubble only if  $\rho > 1$ , that is, for *inhibitory* couplings  $J < 0$  (see Eq. 23).

To see this more formally, suppose that the system is initially situated over the  $H_c^-$  line. We want to determine if the transformation ( $\kappa, T, H$ )  $\rightarrow$  ( $\rho\kappa, \rho T, \rho H$ ) leads the system to penetrate the bubble or not. From Eq. (10) we obtain a relation between the new system parameter  $H(\rho)$  and the new line  $H_c(\rho)$

$$|H(\rho)| = |H_c^\pm(\rho)| + (1 - \rho) |V_c^\pm| \quad (24)$$

where we have used the fact that  $V_c^\pm$  is unchanged by the transformation of variables (cf. Eq. (12)). Then, the collective state will be inside the bubble ( $|H(\rho)| < |H_c(\rho)|$ ) only for  $\rho > 1$ . This is a very non-intuitive result which, surprisingly, is totally in agreement with recent simulations with realistic neurons in the modeling of thalamic spontaneous oscillations [Golomb & Rinzel, 1993]. On the other hand, a network of type B neurons (autonomous oscillators) when connected with *excitatory* synapses will show a transition to a non-oscillating state for increasing coupling  $J$  (often called *oscillator death effect*).

By adjusting the interaction strength  $J$  (or, perhaps, by the self-organized drift of  $H_0$  described earlier) we can put the whole network of neurons at the border of the critical region. Then, we will obtain the very long transients characteristic of this transition. We will get an extended excitable critical media. The 'edge of chaos' ideas of complex adaptive systems studies is that information processing is somewhat enhanced in this critical region due to the strong sensibility to signals, spatio-temporal long range correlations and the presence of super transients [Langton, 1986, Suzuki & Kaneko, 1994].

However, we accord with Suzuki and Kaneko [1994] observation that the location of the system at the 'edge of chaos' is not a *necessary* feature for this goal but only its location at the 'edge of



something' (that is, at a phase transition or bifurcating point). For the spin system associated to our map the relevant transition is a first-order paramagnetic-modulated transition (where incidentally chaotic attractors and transient chaos appears). We have noticed in Sec. 3 that SOC is expected to occur in a network of adaptive DP(2) neurons. It is very surprising that these edge of chaos and SOC concepts appear *naturally* and *simultaneously* in our DP(2) model since our primary concern were only to construct a simple but biologically realistic formal neuron.

We think that, although not being by now a fully developed idea, this sort of 'computation on excitable critical media' seems to be a more promising paradigm for neural information processing than the standard 'computation by fixed points attractors' view. The central purpose of this paper is to show that these two paradigms are not unrelated and can be connected (through the DP( $n$ ) hierarchy of computing elements) so that knowledge developed in one area can be transferred to the other.

### 5.3 Heterogeneous coupling

It also seems interesting to study a system with well chosen couplings (instead of homogeneous couplings  $J$ ) designed to store various dynamical attractors. The analysis of such systems is also a future enterprise. However, we can make a very interesting link with multi-layer perceptrons (which to our knowledge has not been done before):

**A multilayer perceptron with  $n$  input neurons,  $N$  hidden non-linear neurons and a single linear output neuron (a device often used in time series modeling) is equivalent to a network of  $N$  coupled DP( $n$ )s with  $n$  time-delayed synaptic couplings  $J_{ij}^T$ .**

To see this, consider the network of Fig. 16 (used by Albano *et al.* [1992] to learn chaotic attractors):

- the input layer has a window with  $n$  entries which receives the time series signal;
- the hidden layer has  $N$  *nonlinear* neurons with state  $V_i(t)$  ( $i = 1, \dots, N$ ) given by

$$V_i(t) = \tanh \left( \sum_{\tau=1}^n \omega_{i\tau} S(t-\tau) + \theta_i \right), \quad (25)$$

- the output is given by a *linear* neuron with state  $S(t)$  which is a weighted sum of the hidden neurons,

$$S(t) = \sum_{k=1}^N C_k V_k(t). \quad (26)$$

Substituting Eq. (26) into Eq. (25) we obtain

$$V_i(t) = \tanh \left( \sum_{k=1, k \neq i}^N \sum_{\tau} J_{ik}^T V_k(t-\tau) + \sum_{\tau} W_{i\tau} V_i(t-\tau) + \theta_i \right), \quad (27)$$

with

$$\begin{aligned} J_{ik}^T &\equiv \omega_{i\tau} C_k, & (k \neq i), \\ W_{i\tau} &\equiv \omega_{i\tau} C_i, \end{aligned} \quad (28)$$

which has the form of a network of  $n$ -order DPs including synapses with time delays. Networks with time delayed synapses have been studied in the literature, but always without self-couplings [Herz *et al.*, 1991, Gopalsamy & He, 1994].

But this seems to be very important since **we know how to train a feedforward network to implement an attractor** (say, by using the backpropagation learning algorithm [Albano *et al.*, 1992]). Then, we have a simple prescription to implement attractors in networks of DPs with transmission time delays: train the equivalent feedforward net and set the synaptic parameters  $J_{ik}^T$  and  $W_{i\tau}$  according to Eq. (28). So, we have a starting point to study the computational power of such networks and its possible applications, for example, storing memories as modulated attractors [Skarda & Freeman, 1987, Gelperin & Tank, 1990, Laurent & Davidowitz, 1994].

## 6 Conclusions

We have found that a single-layer perceptron with only two inputs used in tapped delay mode (a DP(2) model) has sufficient richness to implement an element of the FitzHugh-Nagumo type. We have delimited the region in parameter space which leads to biological neuron-like behavior. In this region, the model presents a natural threshold for action potentials, subthreshold oscillations, repetitive firing, nerve blocking effect, rebound response, coexistence of oscillatory and steady state behavior etc.

Our phase diagrams in the  $(\kappa, T, H)$ -space also have interest independently of this neuron modeling context. They represent the time series learnable by a two input single-layer perceptron. To our knowledge, these are the first set of phase diagrams in coupling space for the behavior of a feedforward neural network turned into a dynamical system. We think that the richness of the dynamical behaviors reported in this paper has pedagogical value since it gives some feeling about the variety of time series implementable by more complex networks. Perhaps the phase diagrams also have a pedagogical value for those in the neural network community who think that the single-layer perceptron is a trivial and completely understood device.

It is very interesting that the neuron-like behavior appears only in a well delimited parameter volume (which we have called the *near critical* region), which lies at the border of a *phase transition surface* for the equivalent Bethe lattice spin system. An homogeneous network of such neurons behaves as an excitable medium near a critical state. The statistical mechanics spin system associated to our model allows us to use the terms "phase transition", "criticality" etc. in a proper sense and not only metaphorically as is done frequently in the adaptive complex systems literature. The possibility of slip-stick type SOC in a network of *adaptive* DP(2) neurons is also a surprising result which will be fully explored in [Kinouchi, 1995].

The DP( $n$ ) models, as a nonlinear generalization of AR( $n$ ) models, can be applied to the description of any dynamical system (excitable elements, animal populations, economic time series etc.). Lattices of coupled dynamical perceptrons seem to be a very interesting class of systems with the potential of promoting real cross-fertilization between coupled map lattices, excitable media, self-organized criticality and standard neural network studies.

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**Note:** After the completion of this work we have found a very recent work where a 2-D map is proposed as a excitable neuron model [Chialvo, 1995]. To our knowledge, this is the unique instance in the literature with some similarity to our approach. Chialvo map, however, has not any of the dynamical perceptron deep connections with standard neural network studies.

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## Figure Captions

**Fig.1:** a) single-layer perceptron; b) dynamical perceptron with  $n = 2$ .

**Fig.2:** Global phase diagram in the  $(\kappa, T, H = 0)$  plane, showing regions with unique fixed point (0/1), two fixed points (0/2), cycle-two (1/2), oscillatory (MOD) solutions.

**Fig.3:** Main periodic phases in the first and third quadrants. The diagrams are symmetric, with a periodic attractor  $(V_1^*, V_2^*, \dots, V_Q^*)$  being changed to  $(V_1^*, -V_2^*, \dots, (-1)^{Q+1}V_Q^*)$ . The periodic phases can be ordered following a Farey construction (see text). Note the small coexistence region  $(0/2 + \text{MOD})$  where complex behavior appears.

**Fig.4:** Example of a 2/9 cycle. The series exactly repeats after an interval of nine points, but there are two oscillations in this interval. The 'average wavelength' is  $\lambda = 9/2$ .

**Fig.5:** a) Stability limits for the (0/1) phase for  $\kappa = 0$ . In region (0/2) a fixed point parallel to  $H$  coexists with other of smaller amplitude antiparallel to  $H$ . In the region (1/2) there is a cycle-two; b) the same phase diagram in the variables used by Pasemann.

**Fig.6:** a) Stability limits for the (0/1) phase: a)  $\kappa = 0.7$ ; b)  $\kappa = 1.5$ : There is no phase (0/2) for  $\kappa > 1$ . Modulated phases appear mainly inside the bubble, although they can appear also outside forming a phase coexistence region (see next figure).

**Fig.7:** Phase diagram for  $\kappa = 0.6$ . Some periodic phases are shown. Limits of stability for the (0/1) phase are given by the  $H_c^\pm$  curves. The limits of stability for modulated phases are given by the dashed line. The coexistence region terminates at TCP (a tricritical point in the statistical mechanical model).

**Fig.8:** Response of a type C neuron ( $\kappa = 0.6; T = 0.4; \theta = -0.06$ ) to a step current  $I$  applied in the interval  $100 < t < 200$ . In this interval the asymptotic behavior is given by points in the diagram  $T$  vs  $H$  with  $H = I + \theta$ . Note that both the points with  $I = 0.02$  and  $I = 0.10$  lie in the  $0/1 + \text{MOD}$  coexistence region, and that, due to different initial conditions, the observed response is a fixed point or a modulated behavior.

**Fig.9:**  $T$  vs  $H$  phase diagrams for  $\kappa = 0.55$  (a), 0.7 (b), 0.8 (c), 0.9 (d) and 0.95 (e).

**Fig.10:**  $T$  vs  $H$  phase diagrams for  $\kappa = 1.0$  and  $\kappa = 1.5$ .

**Fig.11:** Strange attractor with largest Lyapunov exponent  $\lambda = 0.12$  found at the point ( $T = 0.15, \kappa = 1, H = 0.235$ ) situated in a  $(\text{MOD} + \text{MOD})$  coexistence region.

**Fig.12:** Phase plane analysis for the YOS map with  $T = 0.35$  and  $\kappa = 0.6$  and  $H = -0.15$  showing the null isocline for the variable  $x$  (bold solid line) and the null isocline for the variable  $y$  (dashed line). The thin solid lines are qualitative 'trajectories' from initial conditions  $x(I_0)$  drawn only for illustration (the true 'trajectories' are made of a few discrete points). The resting state P is asymptotically stable.

**Fig.13:** a) Transient responses of a tanh neuron with parameters  $T = 0.35, \kappa = 0.6$  and  $H = -0.04$ . Current pulses are applied at time  $t_0 = 1$  with amplitudes varying (bottom-up) from  $I_0 = 0.04$  to  $I_0 = 0.18$  by amounts of 0.01. Note the change of structure from the subthreshold to the suprathreshold oscillations near  $I_0 = 0.13$ ; b) Details of the action potential of a motoneuron (adapted from [Tuckell, 1988]): DD = delayed depolarization, AH = after hyperpolarization, LAD = late after depolarization.

**Fig.14:** Transient responses to inhibitory inputs of a tanh neuron with parameters  $T = 0.35, \kappa = 0.6$  and  $H = -0.028$ .  $V(t)$  initially decreases, then increases eventually producing an action potential for large negative currents. Current pulses are applied at time  $t_0 = 1$  with amplitudes varying from  $I_0 = -0.072$  to  $I_0 = -0.972$  by amounts of  $-0.1$ . Note the change of structure from the subthreshold to the suprathreshold oscillations near  $I_0 = -0.7$ .

**Fig.15:** Transient responses to inhibitory inputs of a tanh neuron with parameters  $T = 0.35, \kappa = 0.6$  and  $H = -0.025$ . Current pulses are applied at time  $t_0 = 0$ . We see a threshold for a rebound action potential near  $I_0 = -0.375$ . Note that the number of action potentials generated is strongly dependent on the input perturbation  $I_0$  and is not monotonically related to it.

**Fig.16:** a) A multilayer feedforward network used for modeling and forecasting: the hidden layer units are nonlinear neurons and the output unit is a linear neuron; b) a Hopfield-like neural network with two self-couplings and two transmission synaptic delays which has the same dynamical behavior (see text).

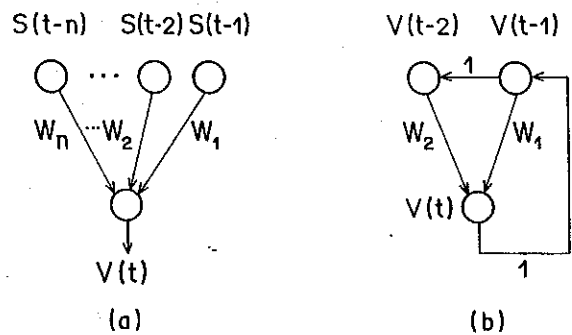


Fig. 1

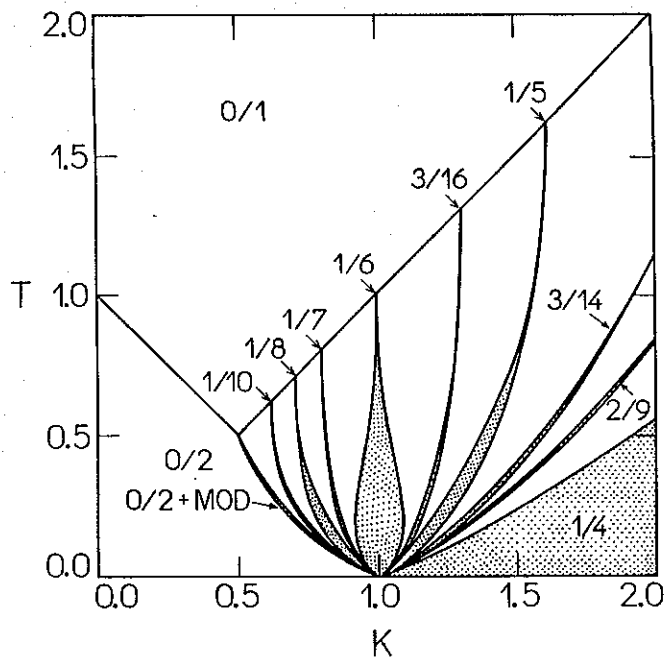


Fig. 3

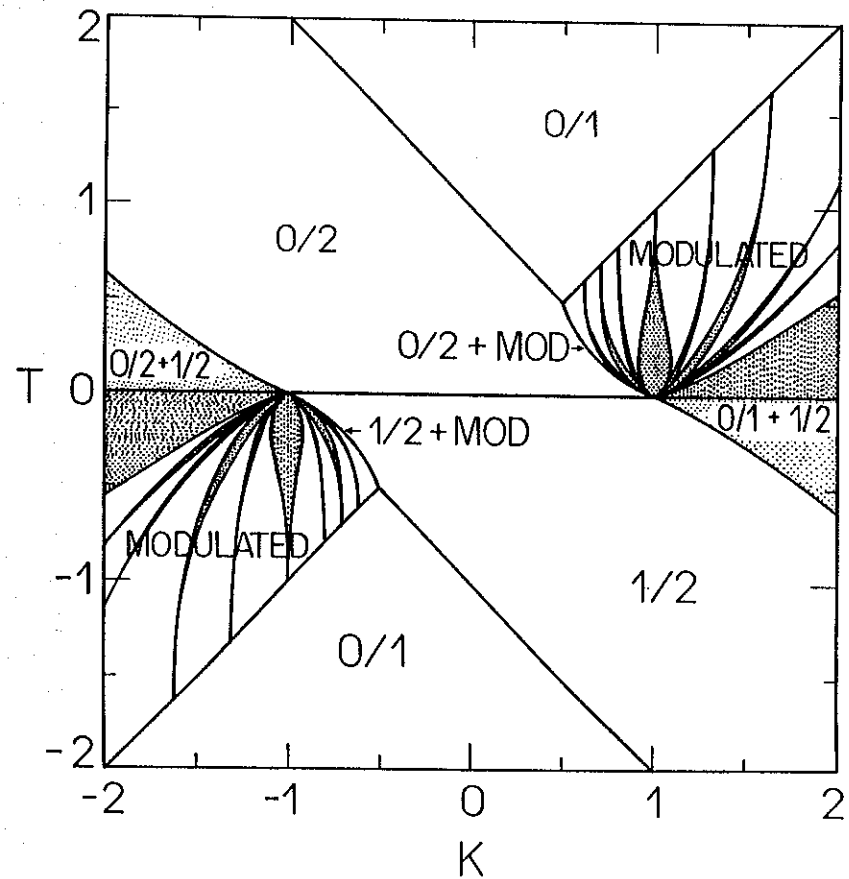
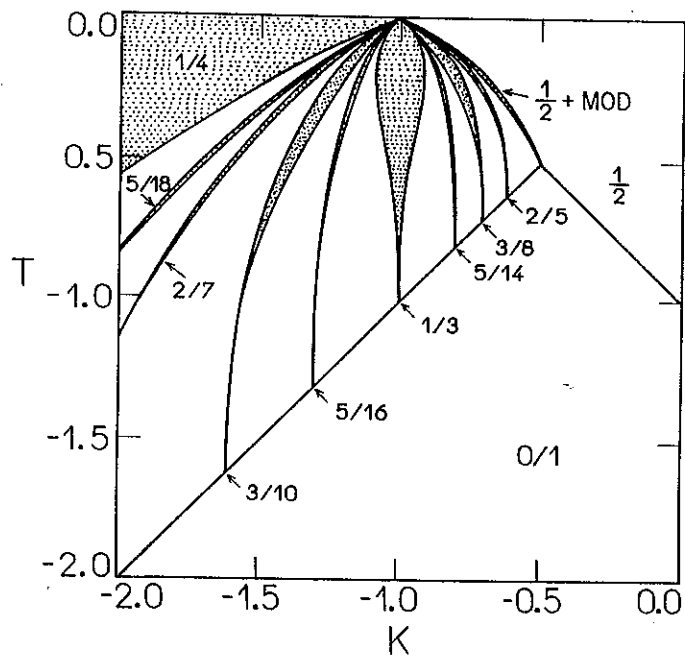


Fig. 2



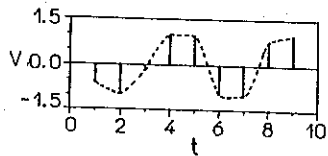


Fig. 4

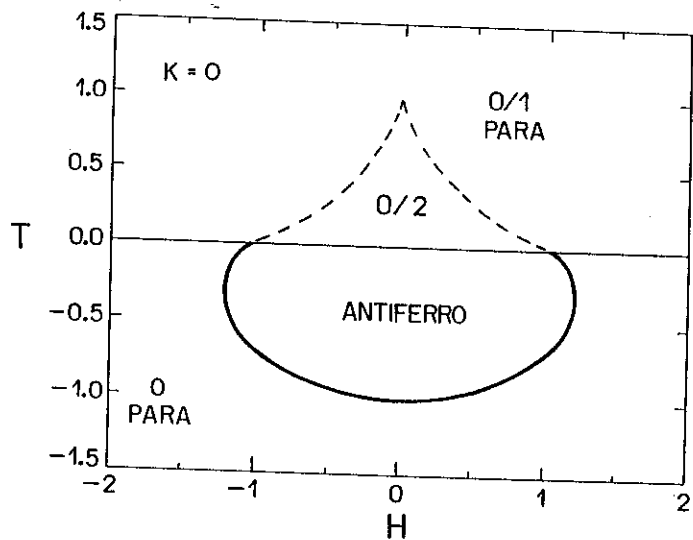


Fig. 5 a)

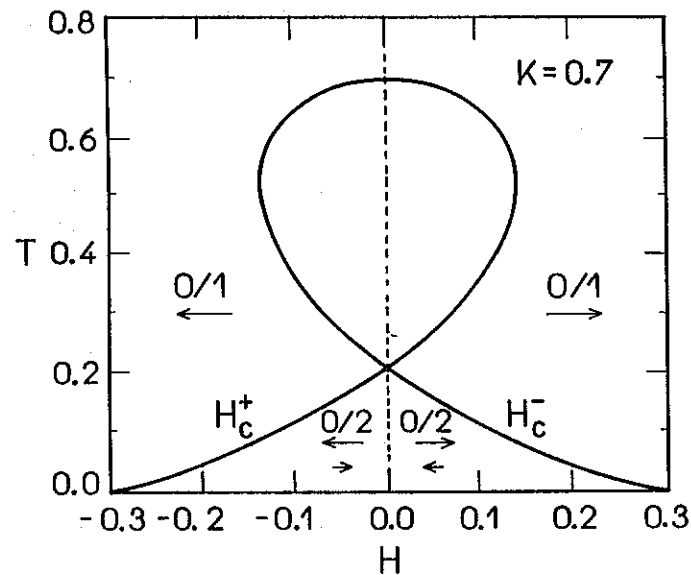


Fig. 6 a)

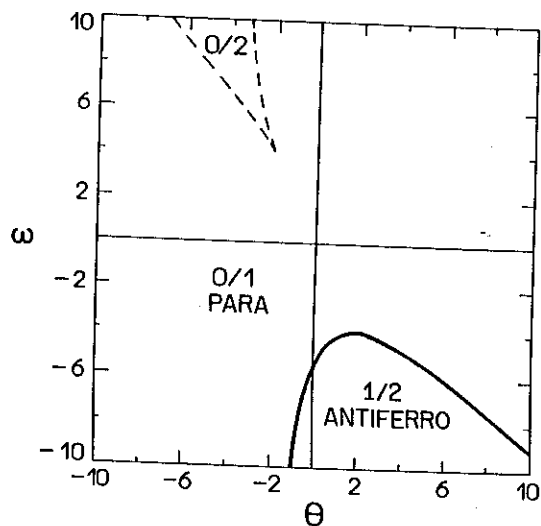


Fig. 5 b)

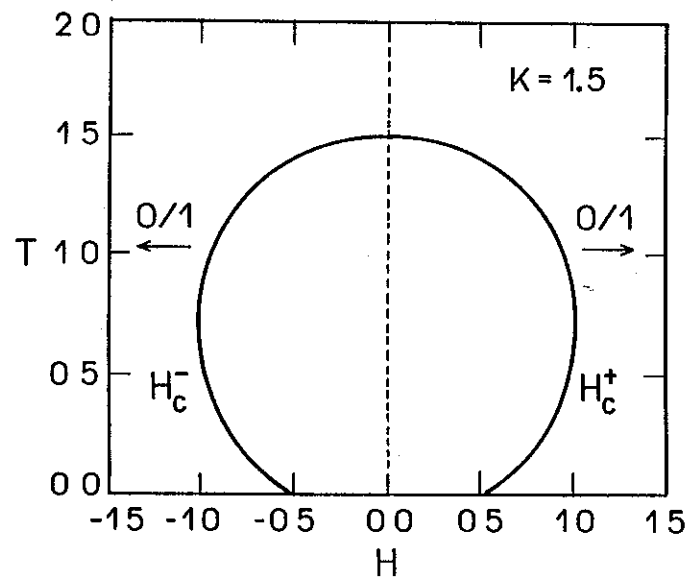


Fig. 6 b)

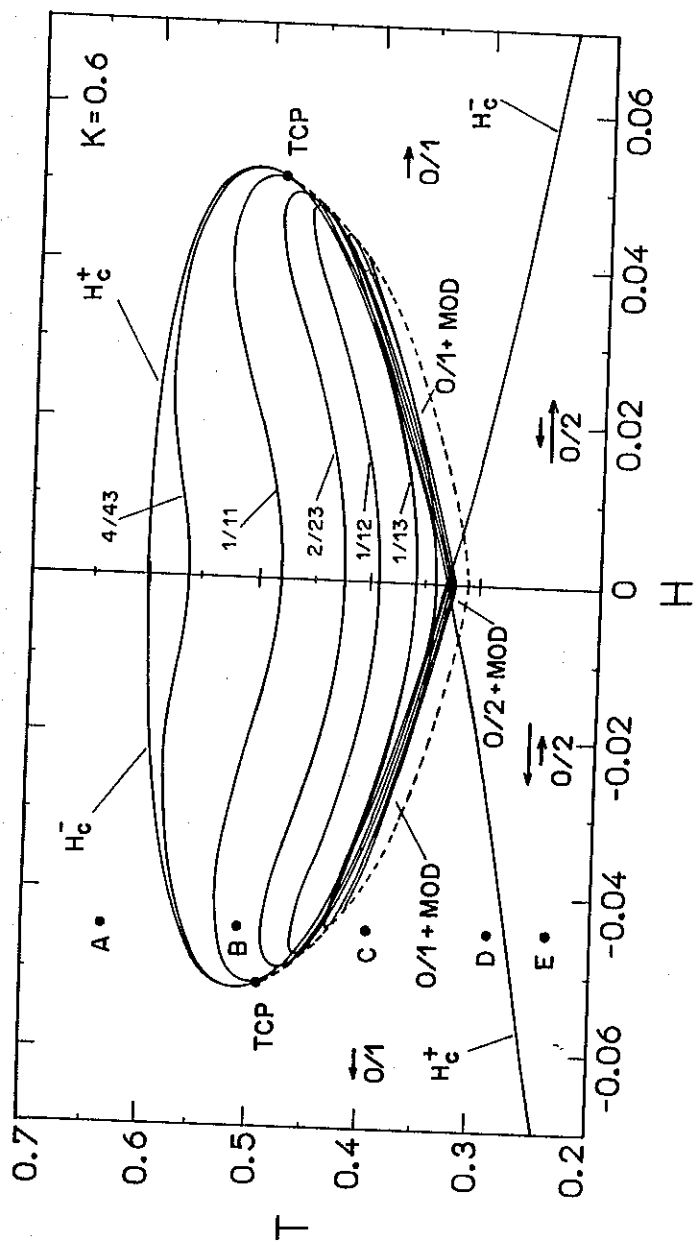


Fig. 7

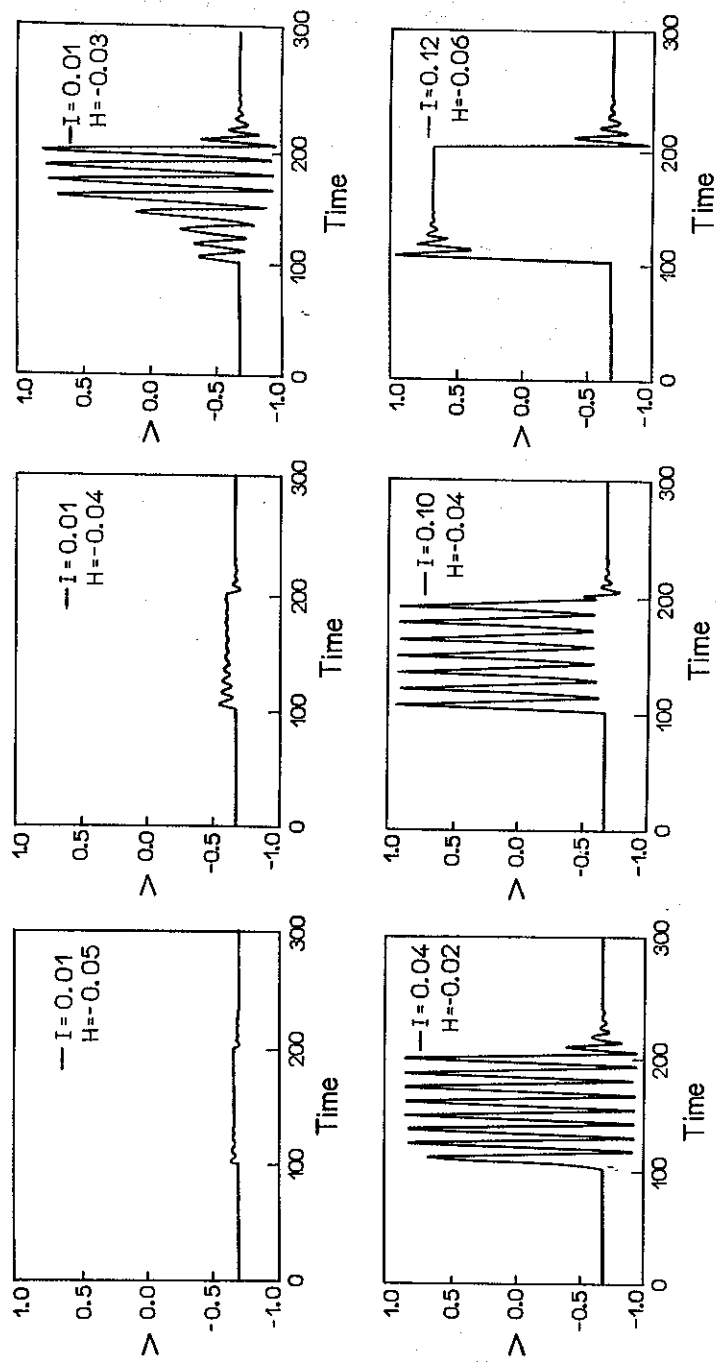


Fig. 8

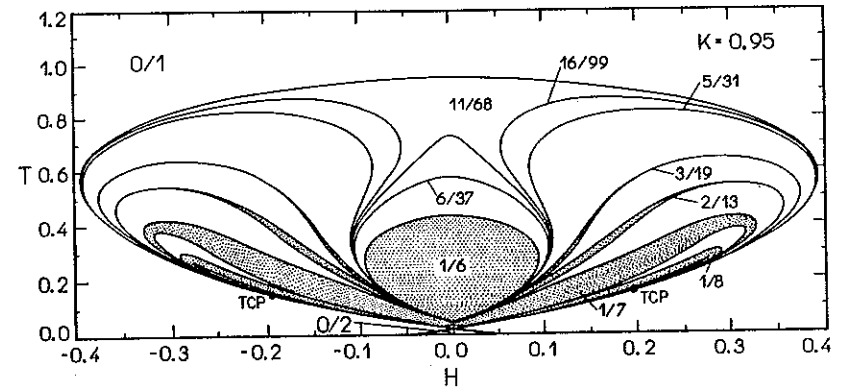
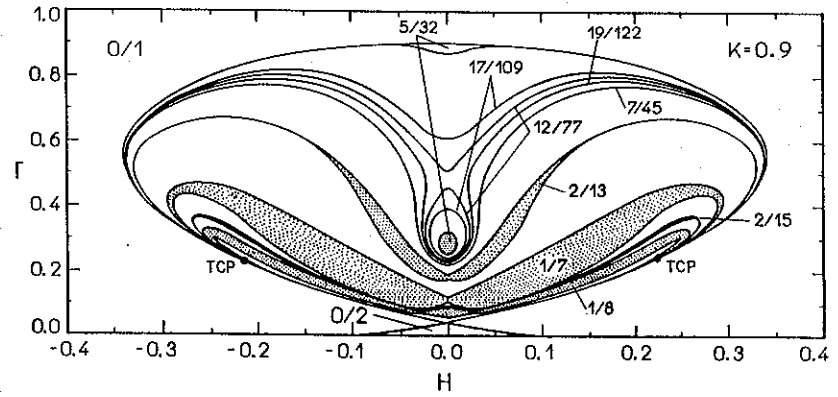
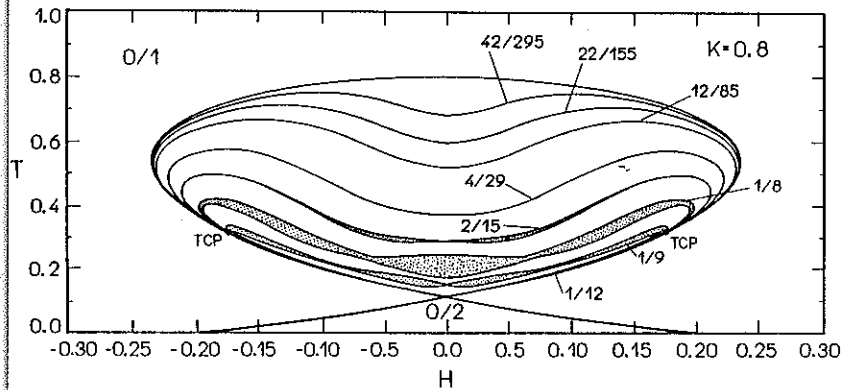
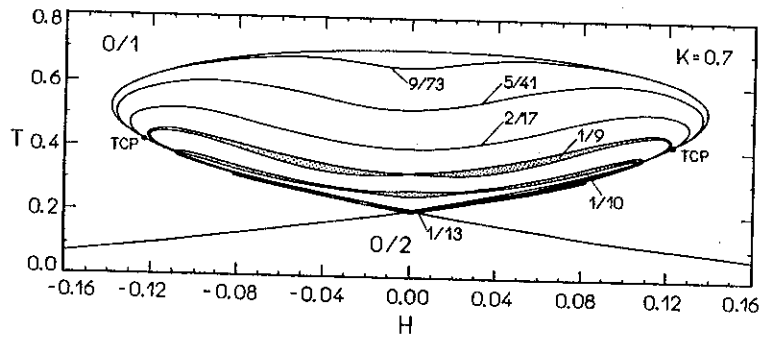
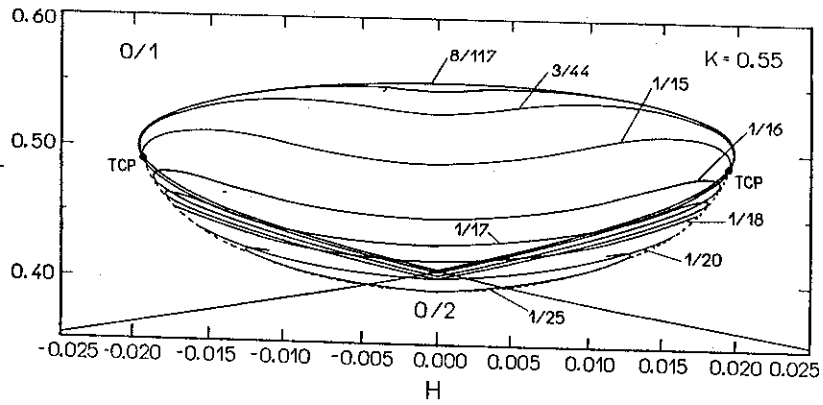


Fig 9.

Fig 1  
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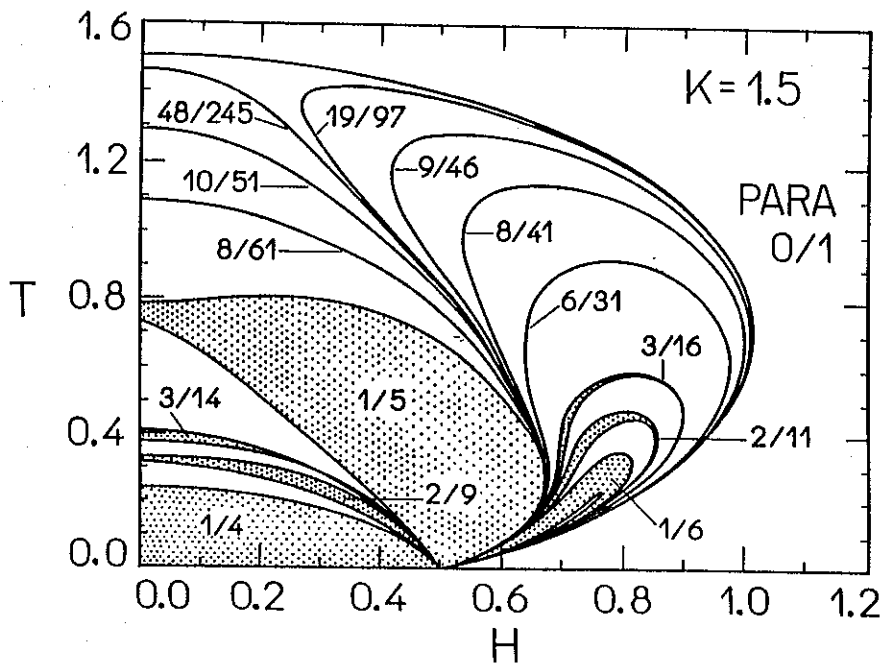
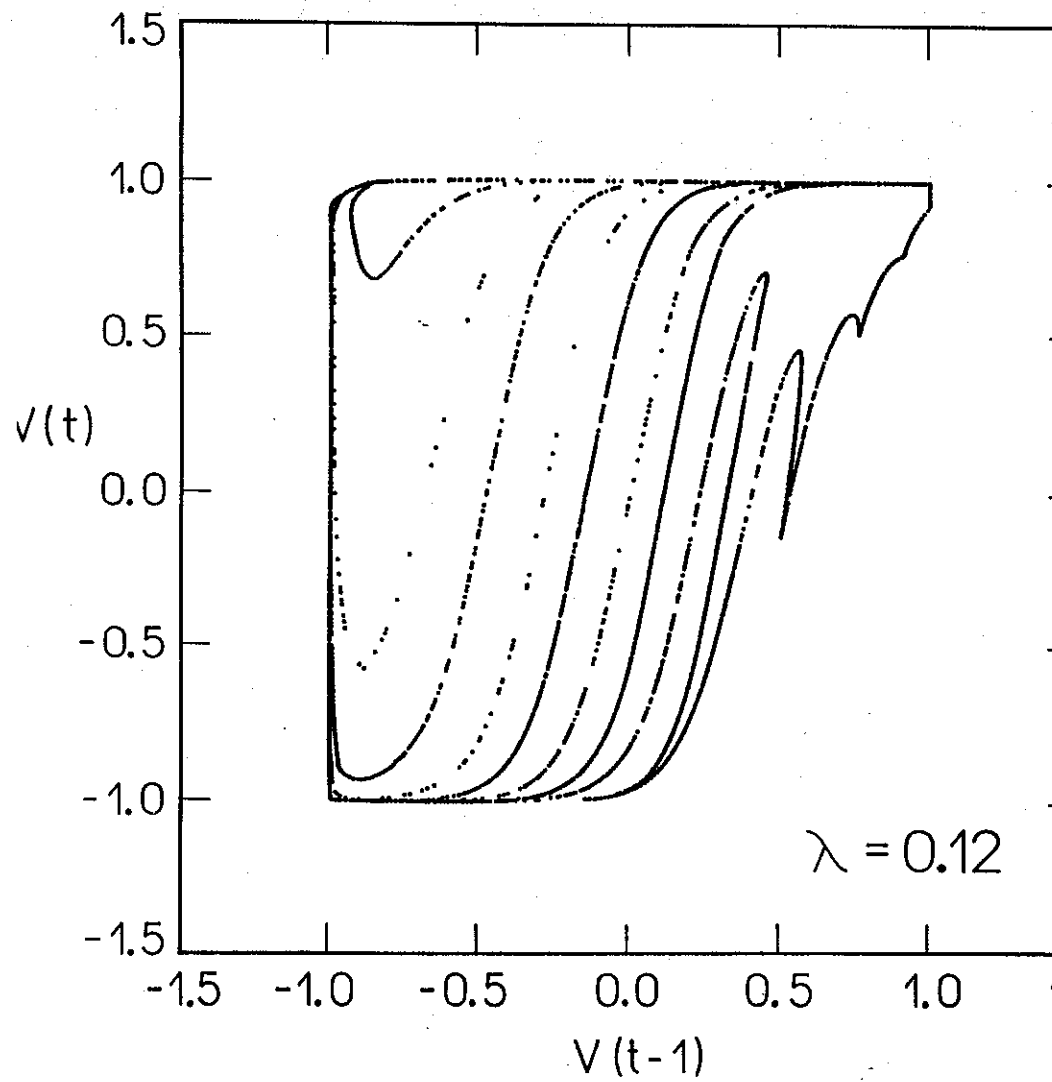
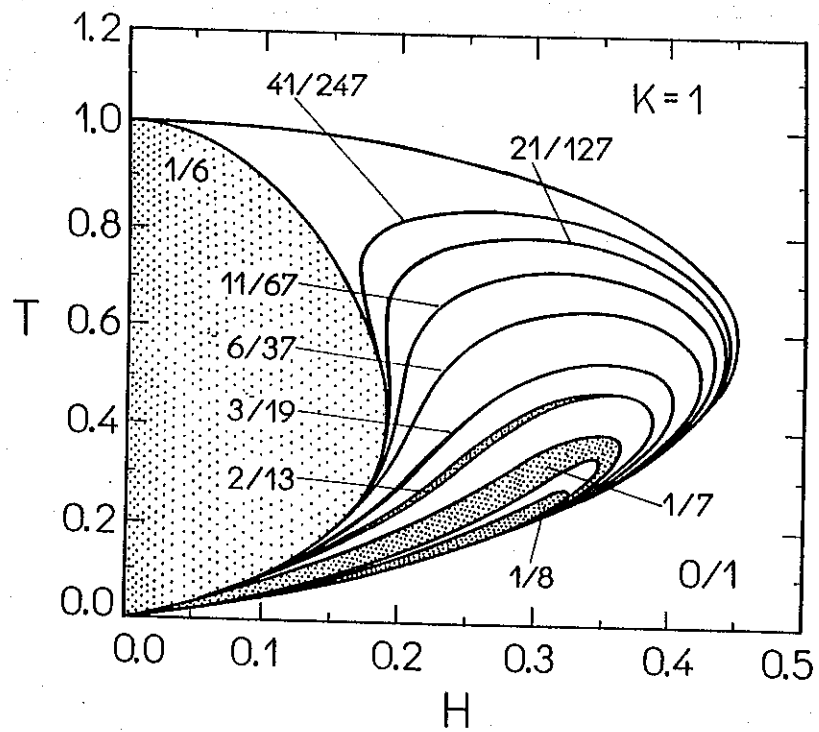


FIG. 11

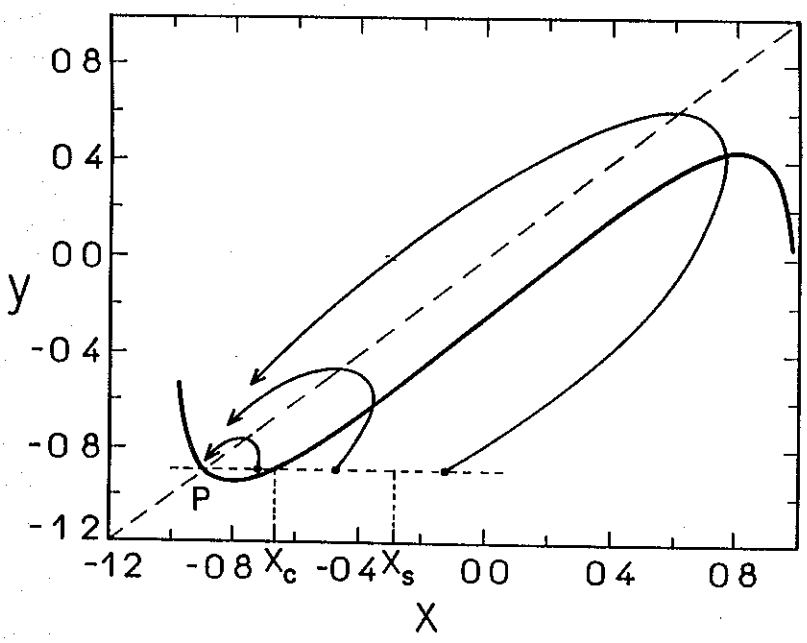


Fig. 12

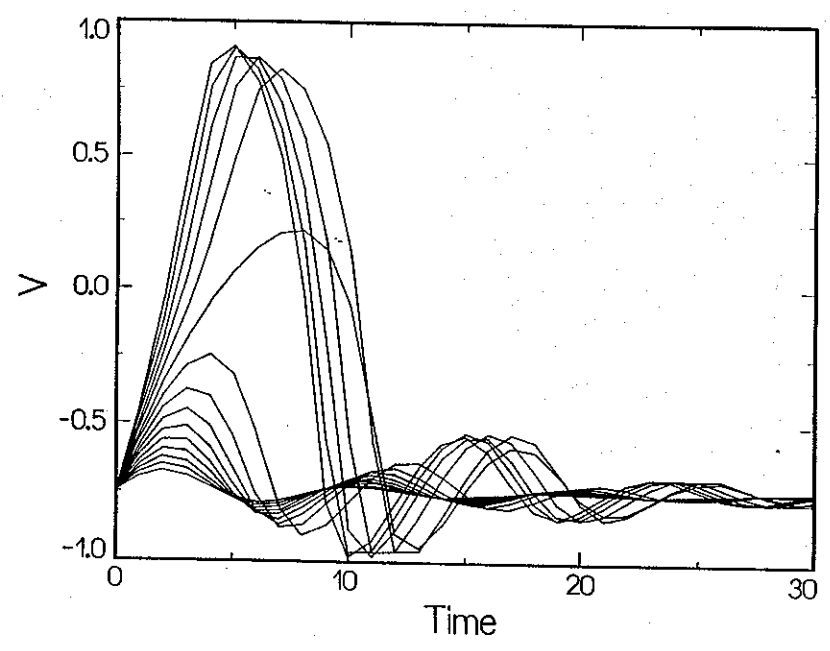


Fig 13

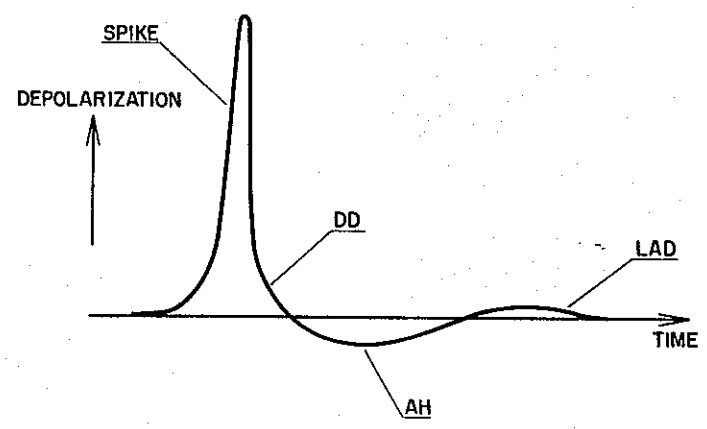


Fig 13 b

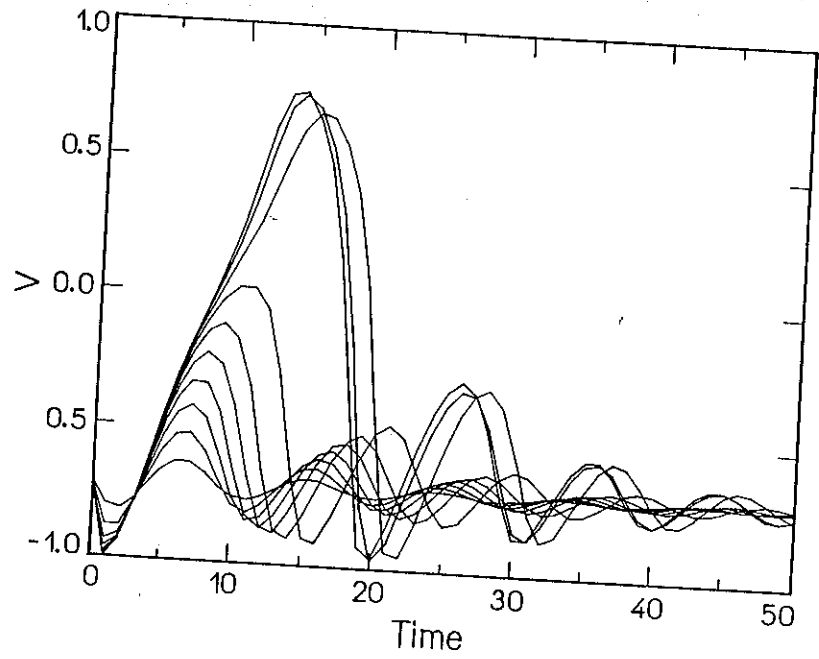


Fig. 14

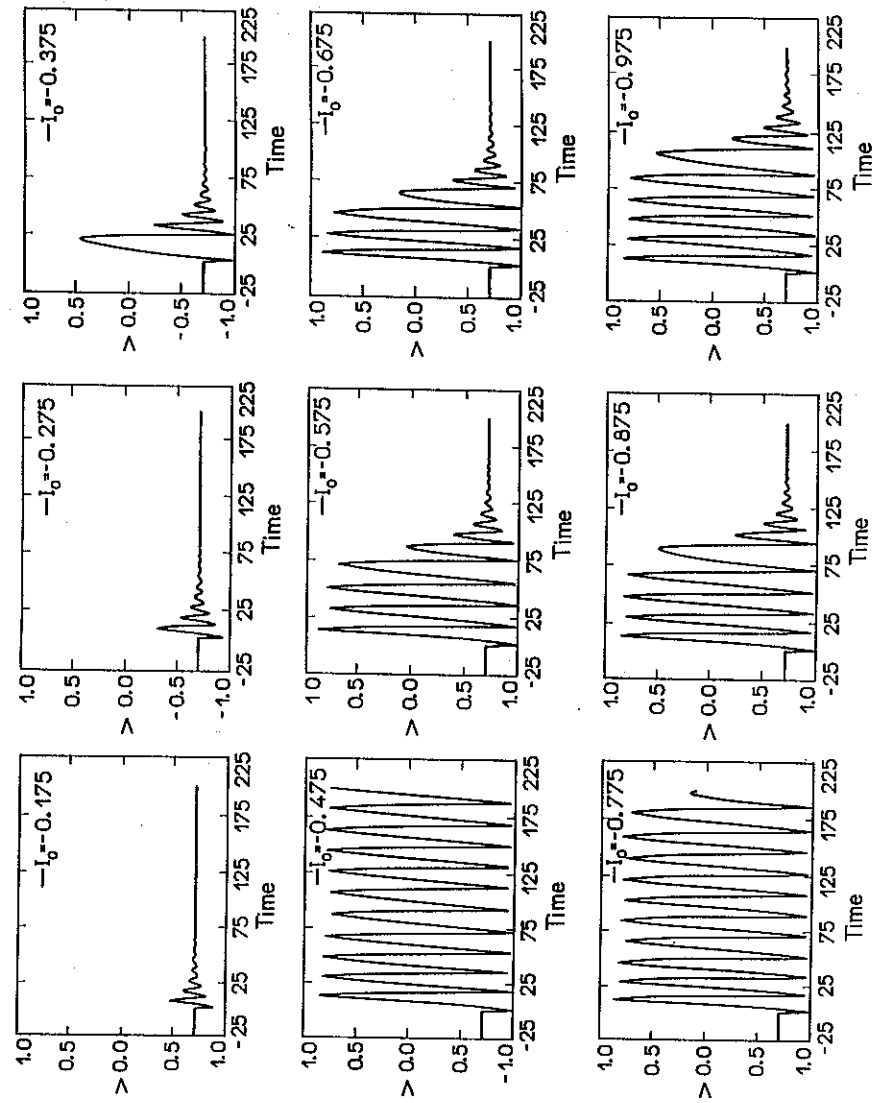


Fig. 15

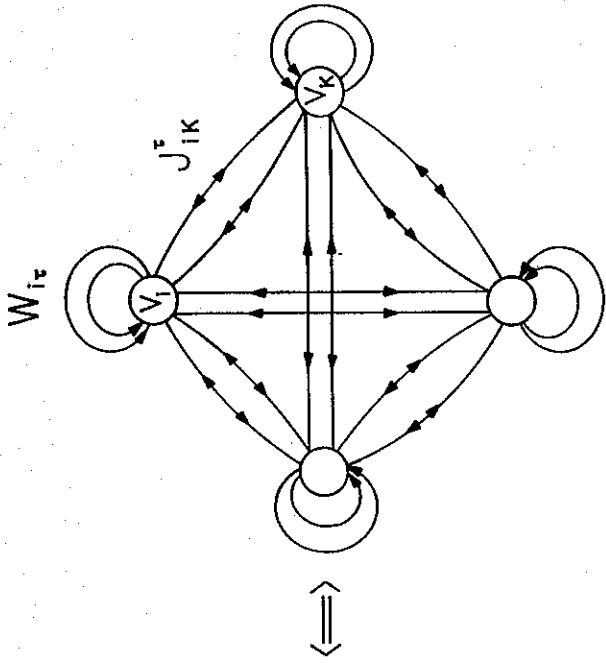


Fig 16. a)

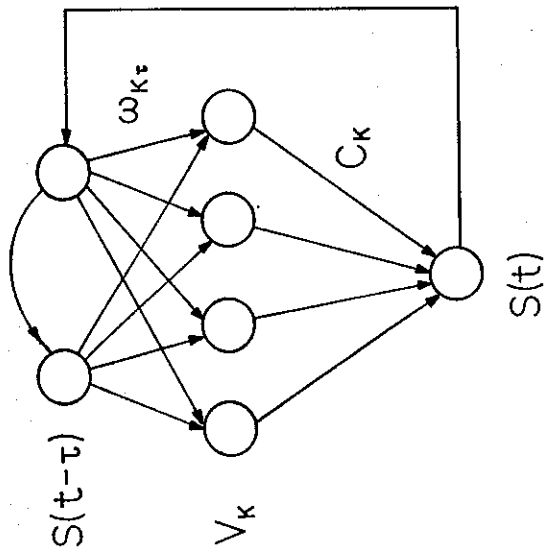


Fig 16 b)