Neural nets with chemical markers and firing threshold fluctuations

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Abstract

We examine the behavior of probabilistic neural nets with the inclusion of chemical markers and with Gaussian fluctuations on the firing threshold. We use the known probabilistic theories and we perform Monte-Carlo computer calculations on a variety of neural nets with a wide range of parameters. We find that the two methods are in excellent agreement. Our results are both in qualitative and quantitative agreement with previous similar studies.

1. Introduction

Over the past twenty years neural nets have been a subject of intensive studies from several different points of view. An area with considerable importance is that of biological nets, i.e. models of nets that try to imitate the human (or other living) brain structure and functions in an effort to understand such vital processes as learning, memory, understanding, feeling, etc. Widely used models (not an exhaustive list) include the early pioneer work (McCulloch & Pitts, 1943) of assemblies of neurons as logical decision elements, the mathematical formalism (Caianiello, 1961) of "neuronic equations", and the probabilistic neural structures (Wilson & Cowan, 1971; Griffin,

1963; Harth et al., 1970; Anninos et al., 1970), that monitor the activity, i.e. the fraction of neurons that become active per unit time, and they have all been quite successful towards our understanding of the above mentioned functions. In these models a network is made of a large number of neurons (the elementary unit), which are interconnected according to some rules. As each unit has several connections, and there is a large number of units, it is quickly realised that the number of connections grows very fast, making the task of calculations quite difficult. But it should be realised that it is exactly this complicated connectivity structure that produces the collective properties that neural nets possess. An isolated unit (one single neuron) is incapable of producing any of the results described below, it is the sum of all units working together that produce these observations.

The probabilistic nets initially were quite simple (Harth et al., 1970; Anninos et al., 1970), but later got more involved (Anninos & Kokkinidis, 1984; Kokkinidis & Anninos, 1985; Anninos et al., 1984; Anninos & Kokkinidis, 1987; Adamopoulos & Anninos, 1989) and incorporate today several advanced characteristics met in neural networks. Their theoretical basis is the binomial distribution, as one tries to attribute some specific properties to a fraction of units out of the total population.

The mathematical formalism may be quite involved, but it is straihgtforward (Anninos et al., 1970). Alternatively, we can construct a computer simulation model and apply standard Monte Carlo techniques in our search for the net properties. The two methods are used interchangeably, and in all cases where direct comparision can be made the agreement is satisfactory.

In section 2 we describe the details of our model, giving emphasis to two features: (a) the chemical markers, and (b) noise with chemical markers. In section 3 we present our results, and in section 4 the conclusions of the present work.

2. Description of the model

Each netlet is made of a collection of neurons with a total number A. Each neuron at some instance may carry an electrical potential, which it passes on to the neurons that it is connected to. This potential is of the order of a few mV and it is characterized as excitatory (inhibitory) if it increases (decreases) the neural overall potential due to its connections with other neurons. The average number of neurons receiving excitatory postsynaptic potential (EPSP) is μ^+, while that receiving inhibitory postsynaptic potential (IPSP) is μ^-. The fraction of neurons that are inhibitory, out of the total is h ($0<h<1$). All potentials are instantly summed up and compared to a threshold value θ. If the sum is greater or equal to θ then the neuron will fire in the next time sequence. If it is smaller than θ then it will be idle. Time is measured in units called synaptic delays, τ, and a neuron that is firing at a particular instance cannot fire immediately after for a period called refractory period, which is usually assumed to be one (1) synaptic delay. The size of the PSP produced by an excitatory (inhibitory) unit is K^+ (K^-). The dynamics of a netlet is monitored by inputting a certain initial signal at time t=0 to some units in the netlet, and observing its propagation throughout the netlet and the results it produces.

(a) Neural Networks with Chemical Markers

In earlier studies on probabilistic neural nets consisting of discrete popula-
tions of formal neurons, it has been assumed that all neurons have the same probability of connection with any other neuron in the net (Harth et al., 1970; Anninos et al., 1970). This is not the case under consideration. Here, it is assumed that the nerve connections are set up by means of chemical markers carried by the individual cells, according to the theory of neural specificity (Sperry, 1943, 1963; Prestige, 1975). According to this theory each neuron makes synaptic connections only with those neurons in the network which carry markers with the highest chemical affinity to its own. Thus, the whole network is divided to neural subpopulations, each of them characterized by its own marker.

The basic assumptions and definitions of the model are similar to those of previous work (Harth et al., 1970; Anninos et al., 1970). The elementary unit in this model is again the *neuron*, which is a bistable element. It can be either in the resting or in the active (firing) state. The transition from the resting to the firing state of the neuron occurs when the sum of *postsynaptic potentials* (PSPs) arriving at the cell exceeds a certain critical value, the threshold θ of the neuron. PSPs may be either excitatory (EPSP) or inhibitory (IPSP), shifting the membrane potential closer to or further away from θ, respectively. A neuron may be either excitatory with all of its axon branches generating EPSPs or inhibitory with all of its axon branches generating IPSPs.

If a neuron fires at time t, it produces the appropriate PSPs after a fixed time interval τ, the *synaptic delay*. PSPs arriving at a neuron are summed instantly, and if this sum exceeds θ, it will cause the neuron to fire immediately. Firing is momentary and causes the neuron to be insensitive to further stimulation for a time interval called the *refractory period*. Postsynaptic potentials, if below θ, will persist with or without decrement for a period of time called the *summation time*, which is assumed to be less than the synaptic delay. It was also been assumed here that the refractory period is greater than the synaptic delay, but less than twice the synaptic delay. If a number of neurons fire simultaneously at time t, then all neural activity resulting from this initial activity will be restricted to times t+τ, t+2τ,..., etc.

The dynamic variable that is usually monitored in the model under consideration is the level of activity a_n, i.e. the fraction of neurons that are active in the netlet at $t=n\tau$, which is a scalar quantity and does not specify which particular neurons are firing in the netlet. The activity a_n at time $t=n\tau$ will depend exclusively on the firing record of the netlet at $t=(n-1)\tau$. The expectation value $<a_{n+1}>$ of the activity at time $t=(n+1)\tau$, is the average value of a_{n+1} generated by a collection of netlets with identical structural parameters and the same a_n. It is also assumed that all subsystems in a netlet with different markers are assigned the same fraction of active neurons a_n.

In this model the important constraint of markers, gives rise to ordered patterns of nerve connections. The interconnections between the neurons are assumed to made up at random, just as in the previous model. However active connections are considered to be only these that belong to cells which carry the same type of marker. Thus, the total number of A neurons is divided into several subpopulations. Neural connection exist at random with no restriction among all cells, but the EPSP (and IPSP) are carried only to the connections that belong to the same marker. Connection between neurons of different marker are inactive, i.e. they carry no signal. If m_1, m_2,...., m_N are the fractions of neurons in a network of N markers corresponding to each subpopulation, then $m_1+m_2+......+m_N=1$.

The quantity $<a_{n+1}>$ is calculated similarly to previous studies (Harth et al., 1970; Anninos et al., 1970). Let a_nA be the active neurons at time t in a netlet with A neurons and N markers. Let also m_j, h_j, (j=1,2,3,...,N) be the fractions of neurons and the fractions of inhibitory neurons, respectively, carrying the jth marker in the netlet. Then, it follows that at $t=(n+1)\tau$ will appear $Aa_n\mu_j^+(1-h_j)m_j$ EPSPs and $Aa_n\mu_j^-h_jm_j$ IPSPs in the subnet with j marker.

The expectation value of the activity $<a_{n+1}>$ for the netlet at time $t=(n+1)\tau$ is given by (Anninos & Kokkinidis, 1984):

$$<a_{n+1}> = (1-a_n) \sum_{j=1}^{N} m_j \sum_{I=0}^{I_{max,j}} (1 - \sum_{L=0}^{\eta_j-1} P_{L,j})Q_{I,j} \quad (1)$$

This equation results by adding all probabilities for all combinations of thresholds and PSPs that produce firing. $P_{L,j}$, $Q_{I,j}$, are the probabilities that a neuron of the jth marker will receive L-EPSPs and I-IPSPs at time $t=(n+1)\tau$, and they are given by:

$$P_{L,j} = \exp[-a_n\mu_j^+(1-h_j)m_j] \, [a_n\mu_j^+(1-h_j)m_j]^L/L!$$
$$Q_{I,j} = \exp(-a_n\mu_j^-h_jm_j)(a_n\mu_j^-h_jm_j)^I/I! \quad (2)$$

The upper limit $I_{max,j}$ in the sum is the total number of active inhibitory connections of the netlet in the subsystem of the jth marker, and is given by:

$$I_{max,j} = Aa_n\mu_j^-h_jm_j \quad (3)$$

The η_j in the upper limit in the inner sum is the minimum number of excitatory inputs necessary to trigger a neuron which has received I inhibitory inputs and carries marker j. It is given by:

$$\eta_j = u[(\theta_j+IK_j^-)/K_j^+] \quad (4)$$

The function u[x] is defined as the smallest integer which is equal to or greater than x. With the same considerations as in previous studies (Harth et al., 1970; Anninos et al., 1970) we may study the dynamics of a netlet with N markers which is attached to a cable of afferent fibers receiving sustained inputs. It is assumed that these fibers may be axons of A_0 neurons in another netlet with the same structure, and for simplicity $A=A_0$. We define μ_0^+ (μ_0^-) as the number of neurons (same for each subsystem), with which an external excitatory (inhibitory) neuron makes its synaptic contacts in the netlet if it carries the same marker; σ is the fraction of external active fibers, carring action potentials at a particular instance. The expectation value of the activity $<a_{n+1}>$ at time $t=(n+1)\tau$ is given by (Anninos & Kokkinidis, 1984):

$$<a_{n+1}> =$$
$$(1-a_n) \sum_{j=1}^{N} m_j \sum_{M=0}^{M_{max,j}} \sum_{I=0}^{I_{max,j}} (1 - \sum_{L=0}^{\eta_j-1} P_{L,j})Q_{I,j}R_{M,j} \quad (5)$$

Here $R_{M,j}$ is the probability that a neuron of the jth marker will receive M-PSPs from external neurons and is given by:

$$R_{M,j} = \exp(-\sigma\mu_0^{\mp} m_j)(\sigma\mu_0^{\mp} m_j)^M/M! \quad (6)$$

The uper limit $M_{max,j}$ is given by:

$$M_{max,j} = A_0\sigma\mu_0^{\mp} m_j \quad (7)$$

and η_j is given by:

$$\eta_j = u[(\theta_j+IK_j^- \mp MK_0^{\pm})/K_j^+] \quad (8)$$

(b) Noisy Neural Nets with Chemical Markers

Consider a probabilistic netlet similar to the one previously discussed which may be isolated or attached to a cable of afferent fibers. It has been shown in the past that such a netlet may exhibit sustained steady-state activity even if it is isolated. This activity is sometimes referred to as endogenous or spontaneous activity. Here, the term "spontaneous activity" is used to describe the firing of neurons occuring independently of the activity of other neurons, i.e. without triggering by the activity of other neurons. It is clear now that in an isolated netlet exhibiting spontaneous activity there are generally two components in its steady-state activity: the spontaneous activity or "noise", and the activity of neurons triggered by the preceding activity of the netlet.

The model for the origin of such spontaneous activity is mathematically simple. The PSPs which in the previous model were assumed to be zero in the absence of presynaptic activity, are now allowed to undergo spontaneous random fluctuations, somewhat similar to the random end plate potentials originating from the spontaneous release of synaptic transmitter substance in motorneurons (Katz, 1966). PSPs generated by presynaptic activity will be added linearly to these fluctuations, the total PSP determining again whether or not a neuron will fire. The random PSPs are functionally equivalent to fluctuations in the threshold of the neuron. Furthermore, it is assumed that these fluctuations of the neural firing thresholds may be positive or negative, and they have a Gaussian distribution. The spontaneous activity of the netlet is then described by a single parameter, the standard deviation δ of the Gaussian distribution.

In this model the basic assumptions about the structure - including the concept of chemical markers - and the unit properties are similar to those in the previously discussed model. The dynamical variable of interest in the model is again the level of activity a_n. The activity of the netlet a_n at time $t=n\tau$ will depend now exclusively on the firing record of the netlet at time $t=(n-1)\tau$ and on the level of the spontaneous activity in the netlet. In the case of a neural netlet of N markers $m_1, m_2, m_3,...,m_N$, where m_j is the fraction of neurons with the jth marker, the neurons in each marker have Gaussian distributed thresholds with standard deviations δ_j ($j=1,2,3,...,N$). In such an isolated netlet which is completely quiescent at one instant, the activity in each subpopulation one synaptic delay later will be entirely due to spontaneous firing of these neurons. These spontaneous activities a_{0j}, ($j=1,2,3,...,N$), according to this model, will correspond to the fractions of neurons of each subsystem m_j,($j=1,2,3,...,N$) whose threshold at $t=0$ is less than zero. Thus, they are given by the equations:

$$a_{0j} = \frac{1}{\sqrt{2\pi}} \int_{\bar{\theta}_j/\delta_j}^{\infty} \exp(-x^2/2)dx, \quad (j=1,2,3,...,N) \quad (9)$$

where $\bar{\theta}_j$ is the average value of the threshold of the jth marker.

The expectation value of the activity of such a netlet at $t=(n+1)\tau$, is given by (Anninos, Kokkinidis & Skouras, 1984):

$$<a_{n+1}>=(1-a_n)\sum_{j=0}^{N} m_j \sum_{I=0}^{I_{max,j}} \sum_{L=0}^{L_{max,j}} P_{L,j}Q_{I,j}T_{\delta j}(\theta_j) \quad (10)$$

This equation results by adding all probabilities for all combinations of

thresholds and PSPs that produce firing. $P_{L,j}$, $Q_{I,j}$, are the probabilities that a given neuron of the jth marker will reseive L-EPSPs and I-IPSPs, respectively, at time $t=(n+1)\tau$. They are also given by equations (2): The upper limits in the sums $I_{max,j}$ are given by (3) and the $L_{max,j}$ by:

$$L_{max,j} = Aa_n\mu_j^+(1-h_j)m_j \quad (11)$$

The $T_{\theta j}(\theta_j)$ is defined as the probability that the instantaneous neural threshold is equal or less than the value θ_j in the subsystem of the jth marker:

$$T_{\theta j} = \frac{1}{\sqrt{2\pi}} \int_{(\bar{\theta}_j-\theta_j)/\delta_j}^{\infty} \exp(-x^2/2)dx \quad (12)$$

3. Results

The plot of $<a_{n+1}>$ vs a_n for a netlet with four markers, following equation (1), is given in figures 1 and 2 for a certain combination of the netlet parameters. The curves in figure 1 represent the total activity of the netlet. We include all three cases of activities, i.e. classes A, B and C. Class A refers to nets for which an activity equal to zero is not a stable state, but they produce sustained activity for any initial activity $a_n<1.0$. They exhibit one stable steady-state slightly below the value $a_n=0.5$. Class B includes nets that have a threshold activity $a_n>0$, for which any initial activity above it causes the nets to produce sustained activity. Except the quiescent - at zero activity - stable steady-state they include one unstable steady-state, and above this another stable state. Class C refers to nets which show monotonically decreasing activity for all initial activities. In this third case the whole curve in the $<a_{n+1}>$ vs a_n diagram is below the $45°$ line. The solution of equation 1 (solid lines) and the computer simulation data (crosses) are in excellent agreement, as expected. Figure 2 shows the activities for each marker and the total activity of the netlet for a net of class B.

The expectation value $<a_{n+1}>$ vs a_n for the case of zero refractoriness is given in figure 3 for a netlet with two markers, in
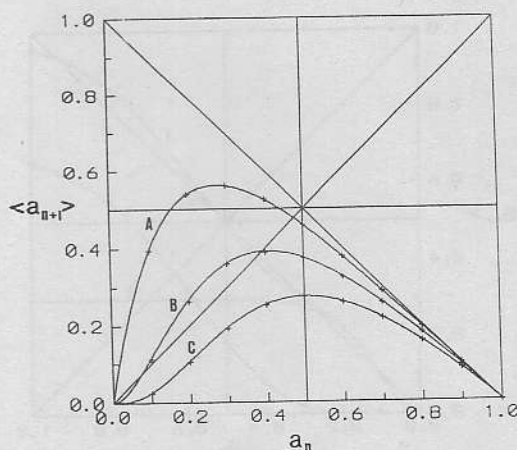

Figure 1. Expectation value of the total neural activity $<a_{n+1}>$ vs preceding activity a_n for isolated netlets with four markers, $m_a=0.1$, $m_b=0.2$, $m_c=0.3$, $m_d=0.4$, with $h_a=h_b=h_c=h_d=0$, $\mu_a^+=\mu_b^+=\mu_c^+=\mu_d^+=20$, $K^+=1$, refractory periods $r_a=r_b=r_c=r_d=1$. A, (A class), $\eta_a=\eta_b=\eta_c=\eta_d=1$; B, (B class), $\eta_a=\eta_b=\eta_c=\eta_d=2$; C, (C class), $\eta_a=\eta_b=\eta_c=\eta_d=3$. The solid lines are obtained by means of equation (1), whereas the crosses are results of computer simulation of a netlet of 1000 neurons.
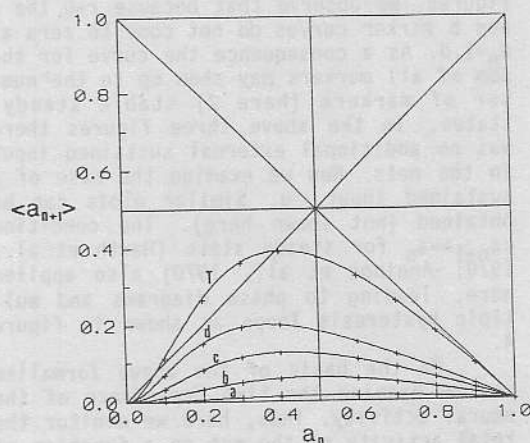

Figure 2: $<a_{n+1}>$ vs a_n for a class B ($\eta_a=\eta_b=\eta_c=\eta_d=2$)netlet with four markers a, b, c and d, with the same parameters as in the fig 1.The curves a-d represent the activities of each marker whereas T gives the total activity of the netlet. Solid lines are obtained by equation (1), while the crosses are results of computer simulation.
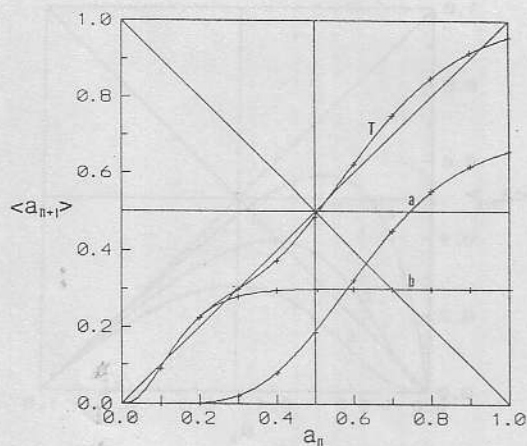
Figure 3: <a_{n+1}> vs a_n for netlets with two markers, m_a=0.7, m_b=0.3, with h_a=h_b=0, μ_a+=20, μ_b+=65, θ_a=9, θ_b=3, K*=1, refractory periods r_a=r_b=0, σ = 0. The curves a and b represent the activities of each marker whereas T the total activity of the netlet. Solid lines represent theoretical values, while the crosses are results of computer simulation of a netlet of 1000 neurons.

Figure 4: Phase diagram and hysteresis curves for a netlet with two markes, a and b, with sustained inputs. Parameters: m_a=0.7, m_b=0.3, h_a=h_b=0, μ_a+=20, μ_b+=65, θ_a=9, θ_b=3, r_a=r_b=0, K*=1 (the same as in fig 3) K_0*=0.5, μ_0*=10. Solid lines represent stable steady states whereas dotted lines unstable ones.

the same method as the previous two figures. We observe that because r=0 the a and b marker curves do not come to zero at a_n=1.0. As a consequence the curve for the sum of all markers may show up to the number of markers (here 2) stable steady-states. In the above three figures there was no additional external sustained input in the nets. Now we examine the case of a sustained input, σ. Similar plots can be obtained (not shown · here). The condition <a_{n+1}>=a_n for steady state (Harth et al., 1970; Anninos et al., 1970) also applies here, leading to phase diagrams and multiple hysteresis loops as shown in figure 4.

On the basis of the above formalism we now examine the time dependence of the neural activity. Thus, here we monitor the total activity of the net as a function of time, for several time units (here t=15). At time t=0 the net is presented with some initial activity. Figures 5-7 show the results for nets belonging to class A, B, and C, respectively. Each net includes four markers, and the values of parameters are the same as in figure 1. In each figure we
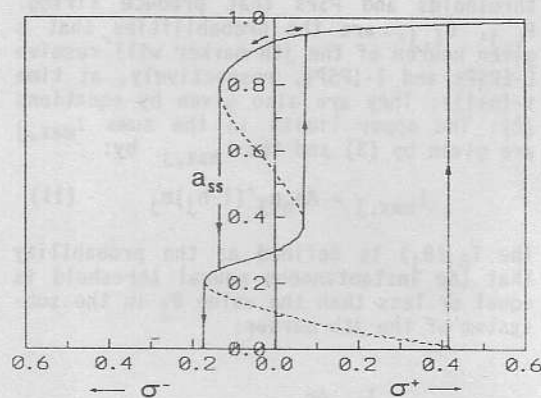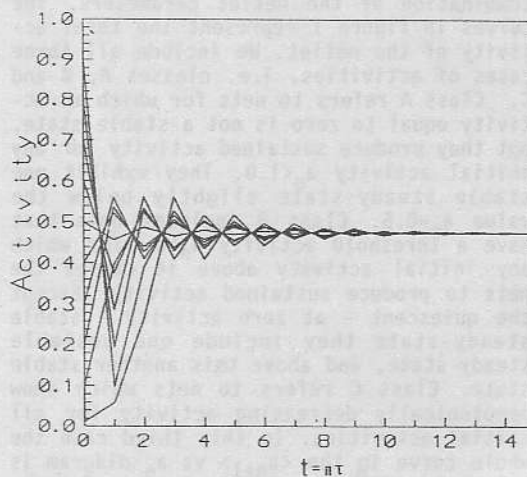

Figure 5: Time dependence of total activity a_n for the A class (θ=1) netlet with the four markers a,b,c and d of figure 1, for initial activities 0.01, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, and 0.9.

plot ten different initial activities a_0, in the whole interval a_0=0 to 1, resulting
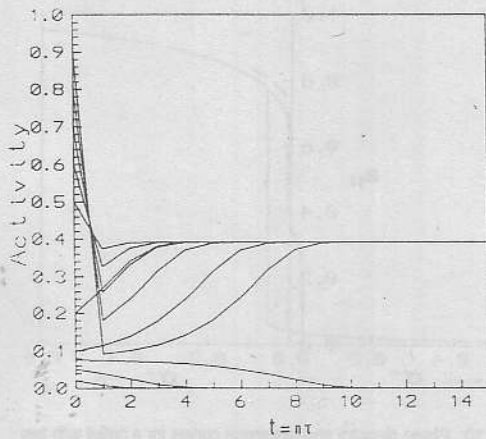
Figure 6: Time dependence of total activity a_n for the B class ($\theta=2$) netlet with the four markers a,b,c and d of figure 1, for initial activities 0.02, 0.05, 0.075, 0.1, 0.2, 0.5, 0.6, 0.7, 0.8, and 0.9.
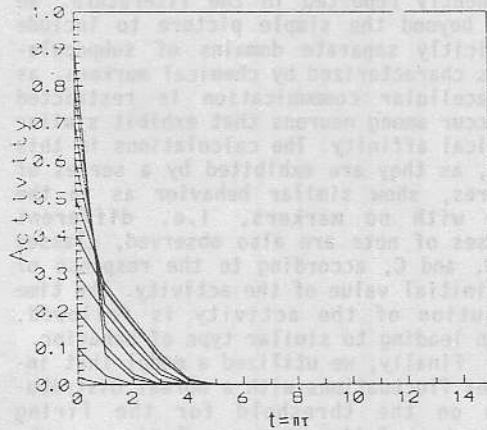

Figure 7: Time dependence of total activity a_n for the C class ($\theta=3$) netlet with the four markers a, b, c and d of figure 1, for initial activities 0.02, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8 and 0.9.

in ten different curves. We observe that in figure 5 all initial activities collapse to the same value, a=0.48, after approximately

t=10 synaptic delays. This is because this case (class A) corresponds to a stable steady-state. In figure 6 we notice that the first three initial activities after a few time steps become eventually zero, while the rest reach a stable steady-state. This is because the first three are below a threshold value, as this net belongs to class B. Finally in figure 7 we notice that all ten curves lead to a zero activity as this net belongs to class C.

We now treat the cases of neural nets with noise (fluctuations) in the value of the threshold. The behavior of a net with two markers and a Gaussian fluctuation with $\delta=1.77$ is shown in figure 8. A plot of the expectation value $\langle a_{n+1} \rangle$ vs a_n is given. We see that the results for the two markers are similar to those without noise, as in figure 3.

As in the previously discussed noiseless model, we may also study the dynamics of a noisy netlet with N markers which is attached to a cable of afferent fibers receiving through it sustained inputs from another netlet with the same structure. If σ is the fraction of external active fibers, i.e. those carrying action potentials at a particular instant, the expectation value of the activity $\langle a_{n+1} \rangle$ at $t=(n+1)\tau$ is given by (Anninos et al. 1984):

$$\langle a_{n+1} \rangle = (1-a_n)$$

$$\sum_{j=0}^{N} m_j \sum_{M=0}^{M_{max,j}} \sum_{I=0}^{I_{max,j}} \sum_{L=0}^{L_{max,j}} P_{L,j} Q_{I,j} R_{M,j} T \delta_j(\theta_j)$$

$$(13)$$

Here $R_{M,j}$ (the probability that a given neuron in the subsystem of the jth marker will receive M-PSPs from external neurons), is given by equation (6), and the upper limit in the sum $M_{max,j}$ by equation (7).

The condition $\langle a_{n+1} \rangle = a_n$ for steady-states of activity may also be applied here, leading to phase diagrams and hysteresis curves of the type shown in figures 9 and 10.

4. Conclusions

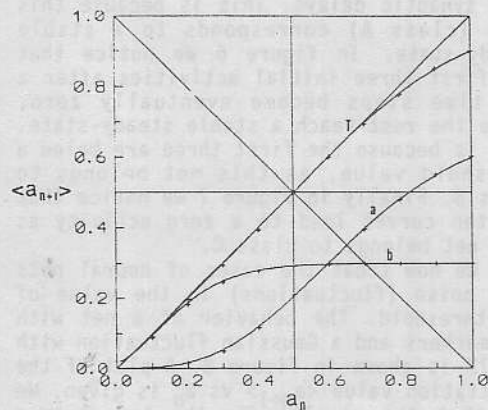In this paper we used neural nets in

Figure 8: $<a_{n+1}>$ vs a_n for netlets with two markers, $m_a = 0.7$, $m_b = 0.3$, with $h_a = 0.0105$, $h_b = 0$, $\mu_a^{\pm}=16$, $\mu_b^+=65$, $\theta_a=7$, $\theta_b=3$, $K^{\pm}=1$, refractory periods $r_a = r_b = 0$, $\sigma = 0$, $\delta = 1.77$. The curves a and b represent the activities of each marker, whereas T the total activity of the netlet. solid lines represent theoretical values, while the crosses are results of computer simulation of a netlet of 1000 neurons.
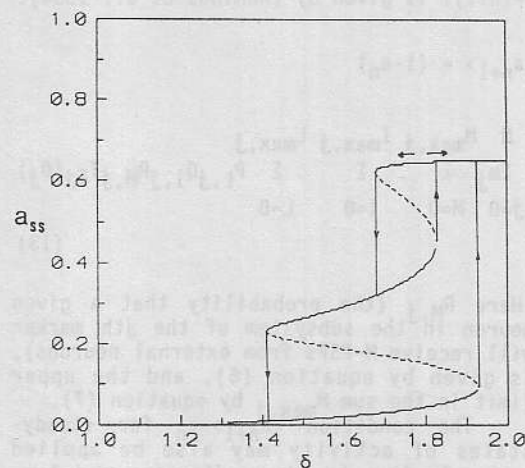

Figure 9: Phase diagram and hysteresis curves for a netlet with two markers a and b. The steady-states of activity a_{ss} have been plotted against δ. Parameters: $m_a = 0.7$, $m_b = 0.3$, $h_a = 0.0105$, $h_b = 0$, $\mu_a^+=16$, $\mu_b^+=65$, $\theta_a=7$, $\theta_b=3$, $K^{\pm}=1$, refractory periods $r_a = r_b = 0$, $\sigma = 0$, Solid lines represent stable steady - states whereas dotted lines unstable ones.
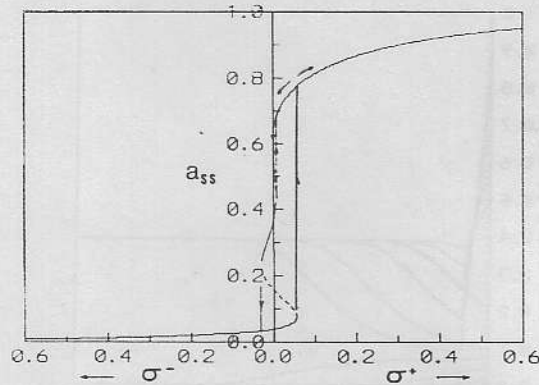

Figure 10: Phase diagram and hysteresis curves for a netlet with two markers a and b, receiving sustained inputs. The steady - states of activity a_{ss} have been plotted against σ. $m_a = 0.7$, $m_b = 0.3$, $h_a = 0.0105$, $h_b = 0$, $\mu_a^{\pm}=16$, $\mu_b^+=65$, $\theta_a=7$, $\theta_b=3$, $K^{\pm}=1$, $K_0^{\pm}=0.5$, $\mu_0^{\pm}=10$, refractory periods $r_a = r_b = 0$, $\delta = 1.77$. Solid lines represent stable steady - states whereas dotted lines unstable ones.

the spirit of mathematical models frequently reported in the literature. We went beyond the simple picture to include explicitly separate domains of subpopulations characterized by chemical markers, as intracellular communication is restricted to occur among neurons that exhibit similar chemical affinity. The calculations in this work, as they are exhibited by a series of figures, show similar behavior as in the case with no markers, i.e. different classes of nets are also observed, classes A, B, and C, according to the response of the initial value of the activity. The time evolution of the activity is followed, again leading to similar type of behavior.

Finally, we utilized a model that includes fluctuations with a normal distribution on the threshold for the firing mechanism of the neurons. Again, we observed similar behavior as with the cases of constant firing threshold.

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