

# Threshold Drift in Stochastic Neural Networks: An Ising-Spin Model<sup>1</sup>

U. Mortensen

FB Psychologie und Sportwissenschaften, Institut II  
Westfälische Wilhelms-Universität,  
Fliegerstr. 21,  
48149 Münster

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## **Abstract**

Threshold drifts are a very disturbing phenomenon when doing detection experiments in visual psychophysics. Here, a model is presented describing these drifts as a result of transitions between different fixpoints for the dynamics of individual neurons. These transitions result from noise within the neurons as well as from interactions among the neurons. To model these interactions the Ising-model of ferromagnetism is employed.

# 1 Introduction

A number of problems in visual psychophysics may be approached by determining thresholds of detection for various stimulus patterns. Here, a very disturbing problem for the visual psychophysicist is the sudden change of the range of values of stimulus contrast or intensity. While a slow drift of threshold may be due to fatigue, fluctuations of attention or adaptation, the observed sudden changes appear to call for an explanation of a different sort.

A possible approach to the problem starts from the observation that neurons are fairly nonlinear devices. Consider the case that the visual system has, as a whole, adapted to a certain luminance. This means that the neurons, say of the retina, are in a certain state of activity. If the neurons were linear, there would only be a single equilibrium or fixpoint, and the firing rate of the neurons would fluctuate around this fixpoint. However, the nonlinearity of the neurons allows for more than a single fixpoint. Even simplified versions of the well known Hodgkin-Huxley model of neuronal activity like the FitzHugh-Nagumo model allow for three fixpoints, one instable and two stable ones (c.g. Murray (1989), Sect. 6.5). Hoffmann and Benson (1986) argued that neuronal activity may be discussed from a more macroscopic view in terms of substrate inhibition models (Murray (1989), p. 126), here, also three possible fixpoints are considered. Corresponding to the two stable fixpoints the neuron may be in a state of reduced ( $\sigma_-$  or increased  $\sigma_+$  activity; these states are of course to be taken as relative to the general state of adaptation. In the state  $\sigma_+$  of increased activity the neuron will be *less* sensitive to a weak stimulus (i.e. one with contrast or intensity in threshold range) than in the state  $\sigma_-$  of reduced activity; this may be deduced from Weber's and related laws: the higher the activity of a neuronal system, the higher the increment threshold has to be. So the overall sensitivity of the neuronal field will – for a given adaptational state – depend upon the proportion of neurons being in the  $\sigma_+$ -state (or, equivalently, in the  $\sigma_-$ -state).

A neuron is a "noisy" mechanism. This may imply the occurrence of noise-induced transitions from  $\sigma_-$  to  $\sigma_+$  and vice versa. Since the neurons are interconnected with each other they do not act independent of each other. Via lateral connections a neuron receives inputs from other neurons, and these inputs may be seen as influencing the state of the neuron. So if a neuron is in state  $\sigma_+$  and at the same time is surrounded by neurons in state  $\sigma_-$  the neuron receives a "reduced" input which increases the probability for a shift into the state  $\sigma_-$ . The reverse may of course also occur: the neuron in state  $\sigma_+$  may cause a neighbouring neuron to change from  $\sigma_-$  into  $\sigma_+$ . Now there are two neurons in state  $\sigma_+$  and so there is an increased activity acting upon the neurons in state  $\sigma_-$ , so that even more neurons may change into  $\sigma_+$ . Since a change from  $\sigma_-$  to  $\sigma_+$  or vice versa does not only depend upon the input from other neurons, but also upon complicated processes within an individual neuron a change  $\sigma_- \rightarrow \sigma_+$  or  $\sigma_+ \rightarrow \sigma_-$  will be a random event. This means that even under stationary conditions the proportion  $p$  of neurons in the  $\sigma_-$  state will vary randomly over time, and consequently the overall sensitivity of the visual system will vary randomly over time. If certain macroscopic variables like fatigue, adaptation and attention are practically constant during an experimental session the sensitivity will vary within some definite range. If there are  $N$  neurons and each of them may be in one of two possible stable states the system may altogether be in one of  $N_s := 2^N$  states, and each of them corresponds to a certain sensitivity of the system as whole; thus the maximum number of sensitivity states is given by  $N_s$ . However, since many of these macrostates are equivalent with respect to a certain overall sensitivity the value of  $N_s$  is more of an upper bound.

Now one may try to arrive at an estimate of the probability that the proportion  $p$  of neurons in  $\sigma_+$ -state has a certain value, in particular one would like to know the

probability of a transition to higher or lower values of  $p$ , since these transitions would imply changes of the threshold range. If changes of state, i.e.  $\sigma_- \rightarrow \sigma_+$  or  $\sigma_+ \rightarrow \sigma_-$  for stochastically independent neurons would be assumed,  $p$  would, in a given time interval  $\Delta t$ , be binomially distributed, provided the probability of an individual change has constant probability  $p_o$ ; additional postulates assumptions would have to be set up for the change of the distribution from one time interval to the next. Certainly there would be only a single maximum of the distribution, and in the long run the value of  $p$  would be in the neighbourhood of  $Np_o$ . Thus one would observe slight drifts of the threshold, but no change into a different range of values with a subsequent longer stay in that range. To model such an effect the probability distribution for  $p$  should have at least two maxima; a change of threshold range would then correspond to a change from the range around one maximum to the range around the other maximum. In principle it is conceivable that there are more than two such maxima; however, in the following we propose a model allowing for just two such "attractors".

The idea is to arrive at a distribution for  $p$  via a simplified description of the neural net. The simplification is brought about

- assuming that all neurons are in a state such that their dynamics have two stable states (fixpoints)
- by internal and external noise as well as a result of the interactions with other neurons the activity of a neuron may shift from one stable state to the other
- assuming that each neuron  $C_i$  can be thus be characterised by its "spin"  $S_i$ ;  $S_i = 1$  if the neuron is in state  $\sigma_+$  and  $S_i = -1$  if the neuron is in state  $\sigma_-$

The dynamics of the net may then be described in by a master equation. The master equation does not yet provide an explicit characterisation of the distribution of  $p$ . However, the master equation may be approximated by a Fokker-Planck-equation, defining the dynamics in terms of a one-dimensional diffusion process. The stationary distribution of this process reflects the distribution of  $p$ , i.e. of the number of neurons in  $\sigma_+$ , say. An explicit expression for this distribution follows once the transition probabilities  $P(S_i \rightarrow -S_i)$  are specified. These probabilities may be chosen following the line of Hopfield (1981), who demonstrated that the dynamics of a neural net may be viewed as being similar to that of a ferromagnet once an appropriate "energy"-function has been specified. Then a reasonable choice of the transition probabilities follows from the Boltzmann-Gibbs distribution. It turns out that then bimodal probability distributions for  $p$  – or for a linear transformation of  $p$  – may be observed.

It may be of interest that the mathematical structure of the foregoing approach is not only of interest with respect to neuronal nets. Weidlich (1972) made use of the Ising-model to model the spread of opinions in a society; here, a spin  $S_i = 1$  reflects the fact that the  $i$ -th person adopts a certain opinion, while  $S_i = -1$  indicates that he does not. A person may change his opinion "spontaneously"; however, since people interact with each other the process of adopting an opinion proceeds like a contagious disease: other persons who do not yet accept the the opinion, may at a certain stage accept it. The reverse, however, may also hold, a person who shares the opinion may drop it. Sharing or rejecting the opinion is a probabilistic matter, one may change one's opinion by own thought with a certain probability, but also through interaction with others. This may lead to changes of the proportion of people who share the opinion, even to a probabilistic sort of an oscillation.

## 2 The Spin-model of neuronal activity

### 2.1 Basic assumptions and the master equation

The Ising-spin model for a neural net is characterised as follows (c.f. Hertz, Krogh and Palmer (1991)):

1. For each neuron  $\rho_i$  there exists a field

$$h_i = \sum_j v_{ij} S_j + h^{ext} \quad (1)$$

characterising its interaction with other neurons;  $v_{ij}$  reflects the strength of the synaptic connection between  $\rho_i$  and  $\rho_j$ , and  $h^{ext}$  defines some possible external influence acting upon the neurons. Further,

$$v_{ij} = v_{ji} = v \quad (2)$$

will be assumed for reasons of simplicity.

2. The net as a whole is characterised by the "energy" or "Hamiltonian"

$$\begin{aligned} H &= -\frac{1}{2} \sum_i \sum_j v_{ij} S_i S_j - h^{ext} \sum_i S_i \\ &= -\frac{1}{2} \sum_i h_i S_i \end{aligned} \quad (3)$$

3. The *microstate*  $\alpha = \langle S_1, S_2, \dots, S_N \rangle$ , i.e. a particular distribution of spin values, differs from the microstate  $\alpha'$ , if  $\alpha$  and  $\alpha'$  differ with respect to at least one spin value; the energy corresponding to  $\alpha$  is given by  $H(\alpha)$  with  $H$  defined as in (3). In equilibrium the probability of a microstate  $\alpha$  is given by

$$p(\alpha) = c \exp(-\beta H(\alpha)), \quad \beta = 1/k_B T \quad (4)$$

$c$  a constant such that  $\sum_\alpha p(\alpha) = 1$ ,  $k_B$  the Boltzmann-constant and  $T$  the temperature.

**Comments:** The general characterisation of the the Ising-model with regard to its temporal dynamics was given by Glauber (1963), where also the justification for (4) may be found. Peretto (1984) provides a general justification for the thermodynamic approach to neural nets without the restriction  $v_{ij} = v$  for all  $(i, j)$ ; again a justification for (4) is given. Hopfield (1982) seems to have been the first to adopt the notion of a Hamiltonian (3) in order to characterise a neural net.

In equilibrium the condition

$$p(\alpha \rightarrow \alpha') p(\alpha) = p(\alpha' \rightarrow \alpha) p(\alpha') \quad (5)$$

has to hold, so that, taking (4) into account,

$$\frac{p(\alpha \rightarrow \alpha')}{p(\alpha' \rightarrow \alpha)} = \frac{p(\alpha')}{p(\alpha)} = \exp(-\beta \Delta H) \quad (6)$$

where

$$\Delta H = H(\alpha') - H(\alpha). \quad (7)$$

We make the following

**Assumptions:**

1. Each neuron can be in one of two possible stable states  $\sigma = \sigma_-$  or  $\sigma = \sigma_+$ . The states are represented as spins; for the  $i$ -th neuron  $\rho_i$ ,  $i = 1, \dots, N$ , we have  $S_i = -1$  if  $\sigma = \sigma_-$  or  $S_i = +1$  if  $\sigma = \sigma_+$ .
2. The sensitivity of the net decreases with increasing number of neurons that are in state  $\sigma_+$ .
3. For the transition  $\alpha \rightarrow \alpha'$  the probability

$$p(\alpha \rightarrow \alpha') = \nu \exp(-\beta\Delta H) \quad (8)$$

is adopted, with  $\nu$  a free parameter.

**Comments:** Obviously, (8) is compatible with (5) and (6). If  $\alpha$  and  $\alpha'$  differ only with respect to a single spin one has in particular

$$p(\alpha \rightarrow \alpha') = p(S_i \rightarrow -S_i)$$

Glauber (1963) discusses in detail possible choices for  $P(S_i \rightarrow -S_i)$ ; (8) is a special case adopted in particular by Weidlich (1972) in his attempt to describe the spread of opinions in a society in terms of the Ising-model and greatly simplifies the approximation of the net's dynamic in terms of a diffusion process. This is also the reason why it is adopted here.

Let us now turn to the derivation of a diffusion approximation for the proportion (or, equivalently, of some linear transformation of this proportion) of the number of neurons being in the  $\sigma_+$ -state. To this end it is no longer necessary to refer to the microstates  $\alpha$  since the individual spins are no longer of interest. Instead, a "state" of the net will taken to be defined by the pair  $(n_-, n_+)$ , where  $n_-$  is the number of neurons in state  $\sigma_-$  and  $n_+$  is the number of neurons in state  $\sigma_+$ . If the total number of neurons in the net is fixed a single number like  $n_-$  is of course sufficient to define the state. However, the formal structure is simplified if one refers to the state in terms of a single number  $n$  defined by  $n_-$  and  $n_+$  as follows (c.f. Weidlich (1972)): let the total number of neurons in the net be given by  $2N$ ; the restriction to even numbers simplifies the calculations and is, of course, of no importance for sufficiently large value of  $N$  when it comes to consider the proportion of neurons in state  $\sigma_-$ , say. Then  $n_- + n_+ = 2N$ . Define

$$n = \frac{n_+ - n_-}{2}, \quad x = \frac{n}{N} \quad (9)$$

Obviously,  $x = -1$  when  $n_+ = 0$  and  $x = 1$  when  $n_- = 0$ ; thus

$$-1 \leq x \leq 1 \quad (10)$$

and  $x$  is a linear transformation of the proportion of neurons in  $\sigma_-$ -state (or, equivalently, in  $\sigma_+$ -state). We are interested in the probability  $p(n, t) = p(xN, t)$  that the net is in state  $n$  at time  $t$ .  $p(n, t)$  is a function of time and we assume that the derivative  $dp(n, t)/dt = \dot{p}(n, t)$  exists for all  $n$  and  $t$ . An expression for  $p(n, t)$  may be derived by setting up a Master equation for  $\dot{p}(n, t)$ . The corresponding diffusion approximation then catches all the relevant qualitative aspects of the dynamics of the net.

Recall that a diffusion process may be derived from a random walk where a variable  $n$  changes, within some time interval  $\Delta t$ , either to  $n + 1$  with probability  $\pi$  or to  $n - 1$  with probability  $1 - \pi$ . We may proceed in an analogous way here and restrict ourselves to state transitions  $n \rightarrow n'$  according to

$$n' = \begin{array}{l} n - 1, \\ n + 1 \end{array} \quad \text{or} \quad (11)$$

Further we have to introduce the transition probabilities  $w_{nn'} = w(n \rightarrow n')$ ; from (11) they are of the form  $w_{n,n+1} = w(n \rightarrow n+1)$ ,  $w_{n,n-1} = w(n \rightarrow n-1)$ ,  $w_{n-1,n} = w(n-1 \rightarrow n)$  and  $w_{n+1,n} = w(n+1 \rightarrow n)$ . Since according to (11) the value of  $n$  can change only by 1 during the time interval  $\Delta t$  the probabilities for events like  $n \rightarrow n \pm k$  with  $k > 1$  are zero. The Master equation takes then the following form

$$\begin{aligned} \frac{d}{dt}p(n, t) &= w_{n+1,n}p(n+1, t) - w_{n,n+1}p(n, t) \\ &+ w_{n-1,n}p(n-1, t) - w_{n,n-1}p(n, t) \end{aligned} \quad (12)$$

So  $\dot{p}(n, t)$  for the state  $n$  is determined by the "flow" from and into the neighbouring states  $n-1$  and  $n+1$ : the first difference reflects the flow from state  $n+1$  into the state  $n$  and back into  $n+1$ , and the second the corresponding flow from and into the state  $n-1$ .

## 2.2 The diffusion approximation

The diffusion approximation results if  $\dot{p}(t)$  is developed into a Taylor-series with respect to  $n$  up to and including terms of second order. The result is

$$\begin{aligned} \frac{d}{dt}p(n, t) &= -\frac{\partial}{\partial n}[(w_{n,n+1} - w_{n,n-1})p(n, t)] \\ &+ \frac{1}{2} \frac{\partial^2}{\partial n^2}[(w_{n,n+1} + w_{n,n-1})p(n, t)] \end{aligned} \quad (13)$$

To arrive at a standard representation for a diffusion process, i.e. a Fokker-Planck equation, the transition probabilities  $w_{nn'}$  have to be specified further. The transition  $n \rightarrow n+1$  comes about if any of the  $n_+$  neurons in state  $\sigma_+$  changes into the state  $\sigma_-$ . The probability of such a change given a certain value of  $n$  has the same value for all elements of the net; the probability of a change of spin depends upon  $n$  because it depends upon the strength of the field  $h_i$ , see (1). Thus we introduce the probabilities  $p_{-+}(n)$  and  $p_{+-}(n)$  for the change of an individual spin. Consequently (c.f. (9))

$$\begin{aligned} w_{n,n+1} &= n_+ p_{+-}(n) \\ w_{n,n-1} &= n_- p_{-+}(n) \end{aligned} \quad (14)$$

Now, because of  $n_+ + n_- = 2N$  and of (9),  $n_+ = N + n$ ,  $n_- = N - n$ , or  $n_+/N = 1 + x$ ,  $n_-/N = 1 - x$ . Consequently,

$$\begin{aligned} w_{n,n+1} &= N(1+x)p_{+-}(Nx) \\ w_{n,n-1} &= N(1-x)p_{-+}(Nx) \end{aligned} \quad (15)$$

Defining the *drift*-coefficient

$$K(x) = \frac{w_{n,n+1} - w_{n,n-1}}{N} = (1+x)p_{+-}(xN) - (1-x)p_{-+}(xN) \quad (16)$$

and the *diffusion*-coefficient

$$Q(x) = \frac{w_{n,n+1} + w_{n,n-1}}{N} = (1+x)p_{+-}(xN) + (1-x)p_{-+}(xN) \quad (17)$$

equation (13) turns then into

$$\frac{\partial}{\partial t}P(x, t) = -\frac{\partial}{\partial x}[K(x)P(x, t)] + \frac{\epsilon}{2} \frac{\partial^2}{\partial x^2}[Q(x)P(x, t)] \quad (18)$$

This is the standard Fokker-Planck equation in one dimension. The equation has to satisfy the boundary conditions

$$K(-1)P(-1; t) - \frac{\epsilon}{2} \frac{\partial}{\partial x} Q(-1)P(-1; t) = 0 \quad (19)$$

$$K(1)P(1; t) - \frac{\epsilon}{2} \frac{\partial}{\partial x} Q(1)P(1; t) = 0 \quad (20)$$

We are particularly interested in the steady-state solution, in which case  $P(x, t)$  no longer depends upon  $t$ . Then  $\partial P/\partial t \equiv 0$  and (18) yields an expression for  $P_{st}(x)$ , describing the fluctuation of  $x$  in time according to a distribution with constant, i.e. not time varying parameters. The general form of  $P_{st}$  is well known (e.g. Gardiner (1990))

$$P_{st}(x) = P_{st}(x_0) \frac{Q(x_0)}{Q(x)} \exp\left(\frac{2}{\epsilon} \int_{x_0}^x \frac{K(\xi)}{Q(\xi)} d\xi\right), \quad \epsilon = 1/N \quad (21)$$

In order to evaluate  $P_{st}$ ,  $K(x)$  and  $Q(x)$  have to be specified further. It follows from (16), (17) and (15) that we need explicit expressions for  $p_{-+}(xN)$  and  $p_{+-}(xN)$ . To this end we may refer to (6). Let us assume that  $\alpha$  and  $\alpha'$  differ just with respect to the value of the spin  $S_i$ . Then  $\alpha \rightarrow \alpha'$  is equivalent to  $S_i \rightarrow -S_i$ ,  $\alpha' \rightarrow \alpha$  is equivalent to  $-S_i \rightarrow S_i$ , and from (6) and (8)

$$\begin{aligned} p(S_i \rightarrow -S_i) &= \nu \exp(-\beta\Delta H) \\ p(-S_i \rightarrow S_i) &= \nu \exp(\beta\Delta H) \end{aligned} \quad (22)$$

(Here the need for the parameter  $\nu$  becomes obvious: we have to make sure that  $0 \leq P(S_i \rightarrow -S_i), P(-S_i \rightarrow S_i) \leq 1$ ! Now  $\Delta H = H(\alpha) - H(\alpha')$ , and recall that  $\alpha$  and  $\alpha'$  differ only with respect to the sign of  $S_i$ ; so we have

$$\begin{aligned} H(\alpha) &= -\frac{v}{2} \sum_{k \neq i} S_k - \frac{v}{2} h_i S_i \\ H(\alpha') &= -\frac{v}{2} \sum_{k \neq i} S_k + \frac{v}{2} h_i S_i \end{aligned}$$

Therefore

$$\Delta H = H(\alpha) - H(\alpha') = -v h_i S_i$$

But from (1)

$$h_i = v \sum_j S_j + h^{ext} = v(n_+ - n_-) + h^{ext}$$

since the  $S_j$  assume only the values  $+1$  or  $-1$ . Consequently

$$\Delta H = \pm(v(n_+ - n_-) + h^{ext}) = \pm(x2Nv + h^{ext}) \quad (23)$$

the actual sign depending upon that of  $S_i$ . So with

$$a := 2N\beta v, \quad b := \beta h^{ext} \quad (24)$$

we find for the drift

$$K(x) = (1+x)\nu \exp(-(ax+b)) - (1-x)\nu \exp(ax+b)$$

and for the diffusion-coefficient one finds

$$Q(x) = (1+x)\nu \exp(-(ax+b)) + (1-x)\nu \exp(ax+b).$$



Because  $(e^z - e^{-z})/2 = \sinh(z)$ ,  $(e^z + e^{-z})/2 = \cosh(z)$  these expressions simplify to

$$K(x) = \nu (\sinh(ax + b) - x \cosh(ax + b)) \quad (25)$$

$$Q(x) = \nu (\cosh(ax + b) - x \sinh(ax + b)) \quad (26)$$

In (18) the parameter  $\nu$  cancels out, so the distribution  $P_{st}(x)$  depends just upon the parameters  $a$  and  $b$ .

### 2.3 The meaning of the parameters

From (24) one sees that both depend upon  $\beta$ ; the *different* effects of  $a$  and  $b$  are due to  $v$  and  $h^{ext}$ . These effects will be considered first, so we assume a given, fixed value of  $\beta$ .

$h^{ext}$  is the strength of some external field, increasing the tendency of the neuron to assume the spin +1, if  $h^{ext} > 0$ , or the spin -1, if  $h^{ext} < 0$ . For  $h^{ext} = 0$  there is no such tendency, for a single neuron without influence from other neurons the probability of being in the  $\sigma_+$ -state or in the  $\sigma_-$ -state would be 1/2.  $h^{ext}$  may reflect certain properties of the "chemical" environment of the neurons implying a preference for one of the stable states, independent of the connections between the neurons and thus independent of the state  $n = n(n_-, n_+)$  occupied by the net at time  $t$ .

Since  $a = a(v)$ ,  $v$  the strength of the connections among the neurons, this parameter reflects the influence of the state  $n$  upon the probability of a transition  $S_i \rightarrow -S_i$ . Since  $P(S_i \rightarrow -S_i) = \nu \exp(-\beta\Delta H)$  this probability depends upon the field  $h_i$  of the neuron  $\rho_i$ , and from (1) it is clear that this field is the stronger the larger the number of spins with equal sign, and the larger the value of  $v$ . So  $a$  reflects the tendency of the neurons to assume that type of spin which dominates in the neighbourhood. However, due to some inbuilt random mechanism ("noise") there may be spontaneous changes of spin for individual neurons which again have, via  $v$ , a contagious effect upon their neighbours. Therefore the value of  $x$  does not remain fixed but varies over time.

Let us now consider the effect of  $\beta$ . According to (4),  $\beta \propto 1/T$ ,  $T$  the temperature; this is, of course, a metaphorical expression. Still, the effect of  $\beta$  corresponds indeed to that of the inverse of a temperature. To see this, consider (22), which may be rewritten in the form

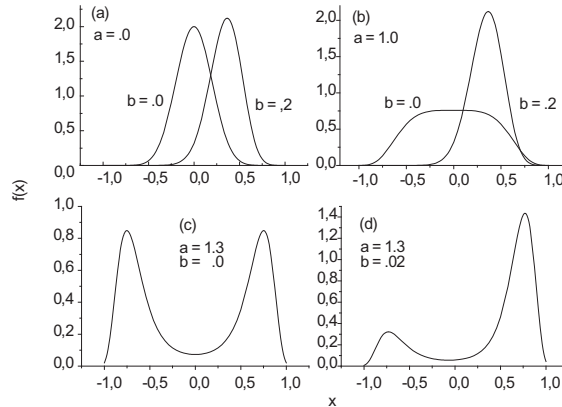
$$\frac{P(S_i \rightarrow -S_i)}{P(-S_i \rightarrow S_i)} = \exp(-2\beta\Delta H)$$

For increasing  $T$   $\beta \rightarrow 0$  and  $\exp(-2\beta\Delta H) \rightarrow 1$ , i.e.  $P(S_i \rightarrow -S_i) \rightarrow P(S_i \rightarrow S_i)$ . So an large value of  $T$  means that the probability of a "flipping"  $S_i \rightarrow -S_i$  or  $-S_i \rightarrow S_i$  is close to 1/2. This applies to all neurons  $\rho_i$ , and consequently we can expect that the distribution for  $x$  becomes symmetrical with respect to  $x = 0$ . In other words, the proportion of neurons being in the  $\sigma_-$ - or in the  $\sigma_+$ -state will fluctuate around 1/2, if  $T$  is large relative to the values of  $v$  and  $h^{ext}$ .

In the following figures, different distributions  $P_{st}$  corresponding to different parameter combinations are shown. Fig. 1 shows distributions of activity for different parameter combinations. Distributions (a) and (b) are symmetrical and unimodal; for  $b = 0$  they are centered around 0, and for  $b = .2$  they are shifted to the right.

In (c) and (d), the value of  $a$  is identical and is more than twice the value of that in (a) and (b). Since  $a \propto v/T$  this may be taken as an increase of  $v$ , since  $b$  keeps its value. The effect is a polarisation of the activity: it fluctuates either around a low or around a higher level; for  $b > 0$  the higher level is more likely. The two peaks represent attractors, and the activity may shift from one attractor to the other just by the intrinsic

Figure 1: Activity distributions for different parameter values, I



stochasticity of the network, i.e. without any input pushing the activity towards one of the attractors.

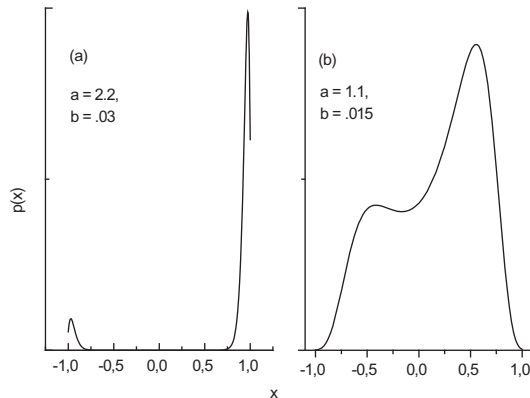
Fig. 2, the distribution (a) is generated by the parameters  $a = 2.2$ ,  $b = .03$ , while that in (b) is generated by parameter values  $a = 1.1$ ,  $b = .015$ . The values of  $a$  and  $b$  correspond to the quotients  $a \propto v/T$  and  $b \propto h^{ext}/T$ . Thus the difference between the two distributions may be explained in terms of doubling the temperature  $T$  in (b). The effect is a much higher rate of fluctuations of the proportions of neurons being in the higher (or, equivalently, in the lower) state of activity. For the lower value of  $T$ , i.e. for the case (a), one has a very pronounced bimodality. Once  $x$  has reached one of the "attractors"  $-1$  or  $+1$  it is likely to stay there; also the variation of  $x$  is very small near these extremes. The times  $x$  needs to creep over from  $-1$  to  $+1$  or vice versa will be very long; most likely such a change will not occur during an experimental session. This case seems to be the one usually referred to when detection of patterns in noise is discussed with respect to the noisy firing of individual neurons, in particular when counting models (at least  $k$  spikes within some time interval  $\Delta t$  for the neuron to signal a stimulus) or timing models (not more than  $\tau_0$  time units between two adjacent spikes) are discussed; here it is implicitly assumed that a neuron remains in a certain activity basin, i.e. domain of attraction of a fixpoint, during the experiment<sup>2</sup>. So we can characterise the case where fluctuations of  $x$  are small and where, correspondingly, only small drifts of the threshold can be expected: either the value of  $v$ , reflecting the coupling between neurons, has to be "high" with respect to that of  $T$ ; an example is provided by the distributions (b) and (c) in Fig. 1. Alternatively, the value of  $T$  has to be low, as in Fig. 2, (a). Larger drifts may occur in cases of a "small" value of  $v$  relative to the value of  $T$ .

### 3 Discussion

Let us first summarise our results. Starting from the notion that neurons are highly nonlinear units their spontaneous activity has most likely more than a single fixpoint. So the spontaneous activity is characterised either by a fixpoint with higher, or a fixpoint with a lower spontaneous activity. In case the activity fluctuates around the upper

<sup>2</sup>Parameter values have been chosen with reference to  $N = 25$ ; for a different value of  $N$ , a different range of values has to be determined. So  $N$  is actually another free parameter when a neural network is discussed.

Figure 2: Activity distributions for different parameter values, II



fixpoint the neuron will be less sensitive than in the case when its activity fluctuates around the lower fixpoint. Because of noise and input from other neurons the activity of a neuron may shift from one fixpoint to the other. Depending upon the degree of coupling between the neurons and the general "temperature" (noise) of the network the proportion  $p$  of neurons in state  $\sigma_-$ , say, may fluctuate around a value near zero or near one, and transitions among attractor-values  $p_-$  or  $p_+$  may occur, so that the threshold may, from a certain time on, fluctuate in a different range. Instead of  $p$  the linear transformation  $x = 2p - 1$  was used, simplifying the expressions for the drift and diffusion coefficients entering the FPE for the movement of  $x$  (or  $p$ ).

The model is based on assumptions simplifying the true state of affairs rather drastically, like  $v_{ij} = v$  for all  $(i, j)$ , the neurons  $\rho_i$  have essentially the same characteristics, etc. it is one step closer to reality than models assuming that neuronal activity fluctuates around a single fixpoint only. An interesting feature of the approach is that the "noise" enters the model in terms of a single parameter,  $T$ . However, even if the parameters  $a$  and  $b$  of the model could be estimated from real data,  $v$  and  $T$  could not be separated, their effect is confounded in  $a$ . Still, a single peaked distribution  $P_{st}$  would point to a "high" value of  $T$  with respect to the coupling  $v$  (which may be taken as the average coupling). In spite of the simplifications some qualitative insight is, however, provided by the model: synergetic effects among the neurons are demonstrated to be responsible, at least in principle, to generate the well-known threshold drifts.

So far no explicit description has been given of the temporal behaviour of  $x$ . Of course,  $x$  is a random function of time, and in order to discuss the time course of threshold drifts, in particular the possibility of comparatively sudden drifts, the Langevin-equation

$$dx(t) = K(x)dt + q(x)\xi(t), \quad q^2(x) = \epsilon Q(x) \quad (27)$$

corresponding to the FPE (18) has to be discussed; here,  $\xi(t)$  represents  $\delta$ -correlated ("white") noise with zero-mean, i.e.

$$\langle \xi(t) \rangle = 0, \quad \langle \xi(t)\xi(t + \tau) \rangle = \delta(\tau).$$

Eq. (27) is equivalent to

$$x(t) = c + \int_{t_0}^t K(x)dt + \int_{t_0}^t q(x)dW_t \quad (28)$$

with  $c$  either some constant or some random variable, and the integral  $\int_{t_0}^t q(x)dW_t$  being the Ito-integral. The mean value function is known to be

$$\langle x(t) \rangle = \langle c \rangle + \int_{t_0}^t \langle K(x) \rangle dt \quad (29)$$

which unfortunately does not allow for a closed solution. Since  $q$  depends upon  $x$  we may also conclude that  $x(t)$  cannot be represented as some deterministic (= mean value) function plus some stationary random process. So the time dependency of  $x$  will not be pursued here any longer; a consequence of the foregoing considerations is, however, that the usual assumption of *additive noise* may not be correct. On the other hand, the analysis of detection data presented by Roufs (1974) and Roufs and Blommaert (1981) (Mortensen and Suhl (1991)) was (i) based precisely on this assumption, and was (ii) successful is so far as the data could be perfectly explained assuming (a) that detection occurs if the activity reaches some threshold  $S$ , (b) the activity consists of a deterministic response plus some stationary noise. The second spectral moment  $\lambda_2$  of the noise could be estimated from the data and indicated that the noise is white for all practical purposes. This result may indeed be compatible with our results concerning the process  $x(t)$ : the stimulus presentation in the experiments of Roufs (1974) may have been short with respect to the variation of  $x(t)$ ; it was certainly short in the work of Roufs and Blommaert (1981). So the results of Mortensen and Suhl (1991) could indicate that during the stimulus presentation  $x(t)$  is practically constant and the noise stems from the random movement of the activity of the neuron around a single fixpoint, i.e. no change of fixpoint occurs during this time. These changes occur on a slower time scale, developing during a session with a few hundred trials.

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