



## Contributed article

## On the piecewise analysis of networks of linear threshold neurons

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**Abstract**

The computational abilities of recurrent networks of neurons with a linear activation function above threshold are analyzed. These networks selectively realise a linear mapping of their input. Using this property, the dynamics as well as the number and the stability of stationary states can be investigated. The important property of the boundedness of neural activities can be guaranteed by global inhibition. If used together with self-excitation, the global inhibition gives rise to a multi stable winner-take-all (WTA) mechanism. A condition for a neuron to be a potential winner of the competing dynamics is derived. The network becomes a largest input selector when the self-excitation is marginal.

Slowing down the global inhibition produces oscillations. The study of oscillations of random networks suggests that all cyclic trajectories of linear threshold networks are a result of the existence of partitions with undamped linear oscillations. Chaotic dynamics were never encountered in computer simulations and perhaps do not exist at all in small networks. © 1998 Elsevier Science Ltd. All rights reserved.

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**Nomenclature**

$N$	Number of neurons
$N^+$	Number of active neurons (at time $t$ )
$\mathbf{I} = (I_i)$	Neural states ( $i = 1, \dots, N$ )
$\mathbf{F} = (F_i)$	Neural activities ( $i = 1, \dots, N$ )
$\mathbf{J} = (J_i)$	Input currents
$J^+$	Sum of inputs to active neurons only
$P^+$ and $P^-$	Set of active and inactive neurons respectively
$F^t = I^+$	Total network activity (sum of positive neural states)
$W = (w_{ij})$	Synaptic weights
$\Theta = (\theta_i)$	Firing thresholds
$\tau, L$	Time constant of inhibitory neuron $L$
$\delta_{ij}$	Kronecker–Delta ( $\delta_{ij} = 1$ if $i = j$ and 0 otherwise)
$\underline{X}$	Steady state of variable $X$

**1. Introduction**

Linear threshold (LT) neurons have a non-saturating activation function. Their output, which is a rate-coded firing

frequency, is confined to the positive real axis. One of the first neural network models using linear threshold neurons was the model of the Limulus eye (Hartline and Ratliff, 1958) based on the concept of lateral inhibition. More recently, the modelling of cortical microcircuits has shown to be a well suited domain of application for LT-networks as the growing literature illustrates (Malsburg, 1973; Douglas et al., 1994; Ben-Yishai et al., 1995; Salinas and Abbott, 1996). The structure and some behavior of these networks have been investigated since (Hadel, 1974) and one of the major results is the derivation of a necessary and sufficient condition for a LT-network to possess a unique stationary state (Kuhn and Rainer, 1987; Feng and Hadel, 1996). The condition is that all determinants of the linear pieces the entire system is made of must be nonzero and have the same sign. An intuitive understanding of this fact is that the determinant of a linear mapping is related to its orientation. If the orientation is preserved at partition boundaries, then these boundaries divide the image space into disjoint domains where each point is uniquely represented. However, monostable networks are computationally restricted: they cannot deal with important neural computations such as decision making. Therefore, the main focus of this paper is on important properties of multistable networks.

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The non-saturating activation function implies that the firing rate of some recurrently connected neurons might be unbounded. We interpret this undesired range of operation as being equivalent to the firing rate of real nerve cells saturating due to the absolute refractory period. Linear threshold neurons have to be kept from diverging by wiring a suitable inhibitory pathway. This is consistent with cortical cells rarely operating close to saturation, despite the strong recurrent excitation (Douglas et al., 1995). The nonlinear dynamics can be studied in detail by virtue of the switching patterns between different linear pieces which are characterized by an effective recurrence matrix. Using this method we are able to describe the qualitative behavior of the dynamics and the stationary states expressed by synaptic weights and input values.

## 2. A general network of LT-neurons

The equations for  $N$  recurrently connected LT-neurons are:

$$\tau_i \dot{I}_i(t) = -I_i(t) + \sum_j w_{ij} F_j(t) + J_i, \quad F_j(t) = \max(I_j(t) - \theta_j, 0) \quad (1)$$

The dot denotes temporal differentiation.  $W = (w_{ij})$  is the recurrent synaptic matrix,  $\mathbf{I}(I_1, \dots, I_N)$  the neural states (dissipated currents),  $\mathbf{F}$  the activities (firing rates) and  $\tau = (\tau_1, \dots, \tau_N)$  are positive time constants. The  $\mathbf{J} = (J_1, \dots, J_M)$  are excitatory inputs, which for example originate from the LGN if  $\mathbf{I}(t)$  represents states of neurons in primary visual cortex.  $\Theta = (\theta_1, \dots, \theta_N)$  are individual firing thresholds. The feedforward, feedback and dissipated currents are summed to yield the net current that causes the firing rate to change. The dissipative current  $-\mathbf{I}(t)$  tries to dynamically annihilate the net current and bring the neuron back towards its resting state. A large time constant indicates that a neuron presents a large inertia to the net current and makes it respond slowly. The nature of the distinct nonlinearity in the LT activation function is well suited to interpreting the output as a firing rate, much better for example than a smooth activation function.

For the following, we put  $\theta_j = 0$  ( $j = 1, \dots, N$ ). This does not change the computations of the network, since it is equivalent to interpreting the inputs and the neural states being shifted by  $\theta_j$  and  $-\theta_j$ , respectively. Experimentally, it is common to subtract the spontaneous background activity before onset of a visual, somesthetic or other stimulus. This operation thus resembles the shifting of the input, since the absence of inputs turns off the activities in LT-networks<sup>1</sup>.

A possible computation of LT-networks is the input–output

relation of  $\mathbf{J}$  and the steady state  $\mathbf{I} = \mathbf{I}(\infty)$ , provided that such a state is reached after transient dynamics.

## 3. The effective recurrence matrix

At any fixed time  $t$ , each LT-neuron is either firing or silent. We can, therefore, divide the whole ensemble of neurons into a partition  $P^+(t)$  of neurons with positive states:  $I_i(t) \geq 0$  for  $i \in P^+(t)$ , and a partition  $P^-(t)$  of neurons with negative states:  $I_i(t) < 0$  for  $i \in P^-(t)$ . Clearly we have that  $P^+(t) \cup P^-(t) = [1, \dots, N]$  and that there are in total  $2^N$  different possible partitions for  $\mathbf{I}$ .  $P^+$  and  $P^-$  are constant most of the time except at discrete times when a neuron starts or stops firing.

Suppose now that we look at the dynamics at a particular time interval, for which  $P^+$  and  $P^-$  are fixed. It is then possible to define a matrix  $W^+$  such that:

$$W^+ \mathbf{I}(t) = W \mathbf{F}(t) \quad (2)$$

This relation holds for all  $\mathbf{I}(t)$  constrained to this partition. The matrix  $W^+$  is called the *effective recurrence matrix*. It is simply constructed out of  $W$  by substituting all the columns with an index belonging to  $P^-$  by the null vector. Thus  $w_{ij}^+ = w_{ij}$  for  $j \in P^+$  and  $w_{ij}^+ = 0$  for  $j \in P^-$ . It is straightforward that  $W^+$  satisfies the microscopic relations:  $w_{ij}^+ I_j = w_{ij} F_j$ . Drawing lines to neurobiology, the recurrence matrix describes the connectivity of the anatomical network; whereas the effective recurrence matrix describes the connectivity of the operating network, taking into account only active neurons. Silent neurons are not dynamically relevant; this is why their effective output weights are zero.

We find that for any partition, the dynamics of the LT-neural network are accurately described by the following linear differential equations:

$$\tau_i \dot{I}_i(t) = \sum_j (w_{ij}^+ - \delta_{ij}) I_j(t) + J_i \quad (3)$$

where  $\delta_{ij}$  denotes the Kronecker delta. These equations are easy to study by virtue of their linearity. The whole complexity of the entire dynamics now resides in the switching between different partitions. It is this switching that gives rise to effects like dynamic amplification and nonlinear decisions. A simple illustrative analogy is the situation where a car driver is confronted by a green traffic light shining at the same time as the red light. If he was only capable of linear reactions, he would press the accelerator and brake pedals at the same time, yielding at best a little traffic jam. But no reasonable person would react like this. On the contrary, the driver might reduce the sensorimotor mapping dynamically to one where the effective recurrence matrix neglects the neural code of either the red or the green light. His appropriate reaction would thus be either to press on the accelerator or the brake pedal, the latter of which might cause a nervous honking from behind.

Still based on the multiple linear Eq. (3), we want to

<sup>1</sup> As we will see, in some marginal cases, the activities can get latched at non-zero values for zero input. This latching is then given the role of a memory activity.

address now the question of the boundedness of such a network. This property has to be guaranteed for all inputs  $\mathbf{J}$ . A sufficient criterion is that the  $N$  eigenvalues  $\lambda_i$  ( $i = 1, \dots, N$ ) of all the  $2^N$  matrices  $(W^+ - \mathbf{1})$  have a negative real part ( $\mathbf{1}$  denotes the identity matrix). Then every partition is asymptotically stable; all the system can do is switch between different point attractors. However, since the determinant of a matrix equals the product of its eigenvalues, all the determinants of the effective linear systems have the same sign  $(-1)^N$  in that case. As a consequence of the theorem cited in the introduction, there is only a single stable fixed point in this network, which is not what we are interested in.

To build a network with more interesting properties, namely competition, it is much better to rely on a weaker condition, which allows for positive eigenvalues under some circumstances. A necessary condition for boundedness is that every partition with positive eigenvalues will eventually be quit by the dynamical system. A system can still be bounded but not converge to a fixed point if it switches endlessly between a stable and an unstable partition, as will be illustrated by a relaxed winner-take-all network. The eigenvector corresponding to the most unstable mode must be made of components of different signs, in this case at least one neuron dives into the sub-threshold region where a new linear system might prevent explosion. Unfortunately, conditions based on eigenvalues and eigenvectors are very exhaustive to verify and even more difficult to respect when designing a network. Thus for practical considerations, we have to rely on another argument.

We assume for the moment that the states are bounded and that they become stationary. What can be said about the set of fixed points of the network? If  $(W^+ - \mathbf{1})$  is invertible, then the explicit expression for the fixed point  $\underline{\mathbf{I}}$  of Eq. (3) is:

$$\underline{\mathbf{I}} = (\mathbf{1} - W^+)^{-1} \mathbf{J} \quad (4)$$

This is a true fixed point provided that  $\underline{\mathbf{I}}$  comes to lie in the partition dictated by  $W^+$ , e.g.  $\underline{I}_i < 0$  for  $i \in P^-$  and  $\underline{I}_j > 0$  for  $j \in P^+$ . The solution is unique for a given partition. If the steady state  $\underline{\mathbf{I}}$  is considered to be the output of the system, then a LT-neural network is characterized to be a selective linear mapper. Which linear mapping it actually realizes is determined by the effective synapses and depends strongly on the inputs and the initial conditions  $\mathbf{I}(0)$ . If  $(\mathbf{1} - W^+)$  is not invertible, then some neurons can get latched at a non-zero activity for zero input  $\mathbf{J} = 0$  and there are an infinite number of fixed points.

The operation of thresholding is conceptually one of the simplest ways to introduce a nonlinearity to a computational model, which is required to realize brain-like behavior. This is also a feature of the brain-state-in-a-box model (Anderson et al., 1977; Anderson, 1983), which is more suited to imitate psychophysical performances, notably categorical perception. The perception is coded as equilibrium points located at the corners of a high-dimensional box. However, unlike a LT-network, the BSB-model is not capable of a

highly sensitive response to variations in the input  $\mathbf{J}$ . On the contrary, LT-networks can categorize the input by the discrete set of active neurons in steady state.

By means of Eq. (4), it is possible to derive a simple algorithm that seeks for the fixed points of the network. It consists of three steps:

1. Choose a partition  $P^+$ .
2. Construct the effective recurrence matrix  $W^+$  according to Eq. (2) and solve the fixed point Eq. (4) for  $\underline{\mathbf{I}}$ .
3. If  $\underline{\mathbf{I}}$  is consistent with  $P^+$ , then it is a fixed point, if not, then there is none for this partition.

The search for fixed points runs through all the  $2^N$  partitions and is, therefore, very exhaustive, practically it works only for small  $N$ .

In order to learn something about the stability of the fixed points, the eigenvalues of the effective linear systems have to be computed, again a very time consuming task.

We focus now on more concrete examples. As a compromise for boundedness, we can show that by using global inhibition, the total network activity is always bounded, from which it follows that the activity of every single neuron is bounded. This requirement is still weak enough to allow for unstable modes and interesting computations, as we will see. The biological evidence of intracortical global inhibition seems to be weak. Long range competition has been modelled in a more elaborate model by means of subcortical regions (Taylor and Farrukh, 1996). But to keep the model simple and compact, global inhibition will be adequate.

The network we introduce has arbitrary connections  $w_{ij} > 0$  between  $N$  excitatory neurons. The inhibition is assumed to be instantaneous, its subtractive influence is included directly in the equations of excitatory neurons:

$$\dot{I}_i = -I_i + \sum_j (w_{ij} - \bar{w}_j) F_j + J_i \quad (5)$$

where  $\bar{w}_j = \sum_i w_{ij}$ . We compute the total activity by summing over all active neurons in Eq. (5). We define the total positive state  $I^+ = \sum_{P^+} I_i$ , the corresponding input  $J^+ = \sum_{P^+} J_i$  and the total activity  $F^+ = \sum_i F_i$ . By construction we have that  $F_i = I^+$  and that  $I^+$  is a continuous function in time as opposed to the total effective input  $J^+$ . Because we do not sum over all the neurons but only over the active ones,  $\dot{I}^+$  is bounded by:

$$\dot{I}^+ \leq -I^+ + J^+ \quad (6)$$

Inequality (6) for  $I^+$  with an equality sign is bounded. If two different differential equations of the first order in time for  $x$  and  $y$  satisfy  $\dot{x} \leq \dot{y}$  and  $x(0) = y(0)$ , then the solutions are ordered,  $x(t) \leq y(t)$  for  $t > 0$ . Thus the original network, Eq. (5) is bounded.

Unfortunately this analysis does not lead to the conclusion that the dynamics always converge to an equilibrium point, because it does not eliminate the possibility of the system switching endlessly between different partitions. In

principle, the dissipation in one partition might counterbalance the dissipation in another one, such that the system oscillates between the two. However, such a case was not encountered in computer simulations with a random excitatory matrix  $W$ ; networks with strong and instantaneous inhibition seem to produce global point attractors only.

#### 4. Winner-take-all network

An interesting LT-network to be studied for its dynamics, fixed points and stability is a winner-take-all network. Such a network is constructed by restricting the excitatory connections of Eq. (5) to pure self-excitation of strength  $w \geq 1$ . Again a remark should be made about the biological plausibility. Autapses do exist, but they are quite rare, in fact they are too seldom for justifying exclusive self-excitation on the single neuron level. Therefore every equation of the coupled system is interpreted as the mean activity of disjoint groups of strongly connected neurons. This is reasonable, because strongly connected neurons are likely to fire simultaneously. Thus their activities might also be described by a common activation function. Every such group of excitatory neurons is inhibited by a global and recurrent inhibitory neuron. For a different biologically motivated WTA-model using global inhibition, and also additional references, see (Coultrip et al., 1992). The equations studied are:

$$\dot{I}_i = -I_i + wF_i - L + J_i \quad (7)$$

$$\tau \dot{L} = -L + w \sum_{j=1}^N F_j \quad (8)$$

Unlike in the general network, the global inhibition is now mediated by an additional neuron  $L$ . Its output does not need to be rectified, because due to the purely excitatory stimulation of strength  $w$  (corresponding to  $\bar{w}$  in Eq. (5)), it cannot go below the threshold. The fixed points are the same for instantaneous and delayed inhibition, but not the dynamics. These are strongly dictated by  $\tau$ , reflecting the delay of inhibition. The only inhomogeneities among excitatory neurons  $I_i$  in this network are the individual external inputs:  $J_i > 0$ .

The idea is to analyse the dynamics in each partition. By virtue of the simplicity of the network, it is possible to perform a single analysis for all partitions. Without loss of generality we choose a partition consisting of  $N^+ \geq 1$  active excitatory neurons ( $N^+ = 0$  leads to at least one firing neuron  $i$  because  $L \rightarrow 0$  in this case and because  $J_i > 0$ ). By summing over the active neurons in this partition, we find:

$$i^+ = -I^+ + wI^+ - N^+L + J^+ \quad (9)$$

$$\tau \dot{L} = -L + wI^+ \quad (10)$$

The behavior of  $I^+$  is described by the two eigenvalues of

the linear Eqs. (9) and (10):

$$\lambda_{1,2} = p \pm \sqrt{p^2 - q} \quad (11)$$

where  $p = (w-1-\tau^{-1})/2$  and  $q = \tau^{-1}(wN^+ - w + 1)$ .

First we are interested in the stable case. The two eigenvalues  $\lambda_1$ , and  $\lambda_2$  have a negative real part if  $p < 0$  and  $q > 0$ , which leads to:

$$\tau < \frac{1}{w-1} \quad (12)$$

This condition no longer depends on  $N^+$  and is thus valid for every partition  $P^+$ . Therefore, provided the time constant  $\tau$  is sufficiently small,  $I^+$  tracks an asymptotically stable fixed point. Thus we find again that the total activity  $F_t$  is bounded.

There are still unstable modes in those partitions for which  $N^+ \geq 2$ : Suppose that any two neurons  $I_i$  and  $I_j$  are firing. By defining the differential state  $d = I_i - I_j$ , we find that the differential equation for  $d$  is:  $\dot{d} = (w-1)d + J_i - J_j$ . It follows that  $d$  is locally unstable, because  $w \geq 1$ . Any two firing neurons separate exponentially<sup>2</sup>. However, we know that the sum of their activities is bounded: therefore, at least one of them has to have a decreasing activity and fall below the firing threshold. Similarly, all the stationary states corresponding to multiply firing neurons are unstable, because differential modes are unstable: the vector  $(0, \dots, 1, 0, \dots, -1, 0, \dots, 0)$  with nonzero components 1 and  $-1$  for any two firing neurons is an eigenvector of  $(W^+ - \mathbf{1})$  with positive eigenvalue  $(w-1)$ .

From our stability analysis of the total network activity in Eq. (12), we conclude<sup>3</sup> that the only stable stationary states lie in the partitions for which  $N^+ = 1$ . By labelling the winning neuron with the index  $k$ , we find the following stable steady-states:

$$I_k = J_k \quad (13)$$

$$L = wJ_k \quad (14)$$

$$I_i = J_i - wJ_k \leq 0, \quad i \neq k \quad (15)$$

The winner  $I_k$  is not always the neuron which receives the largest external input current  $J_k$ . But the potential winners can be inferred. These are the neurons for which Inequality (15) holds. Their input times  $w$  must be larger than any other input (see Fig. 1). Thus the closer the self-excitation  $w$  is to

<sup>2</sup> In the case  $w = 1$  the separation is linear:  $d(t) = (J_i - J_j)t + d(0)$ . Note that the direction in which the separation takes place only depends on the difference in the input currents  $J_i - J_j$ , and not on the initial condition  $d(0)$ . This is why  $w = 1$  produces an absolute WTA-network! The case  $w < 1$  leads to a network converging globally to a unique fixed point, because of the spectral radius of  $(W - \mathbf{1})$  being smaller than 1 (Feng and Haderler, 1996).

<sup>3</sup> Formally this does not prove that the network consists only of global fixed point attractors, although this was the case for all computer simulations. If the rectification in Eq. (7) is not applied to  $I_i$ , but to  $(wI_i - L + J_i)$ , then it is possible to derive a global Lyapunov function assuring convergence (S. Seung, personal communication).

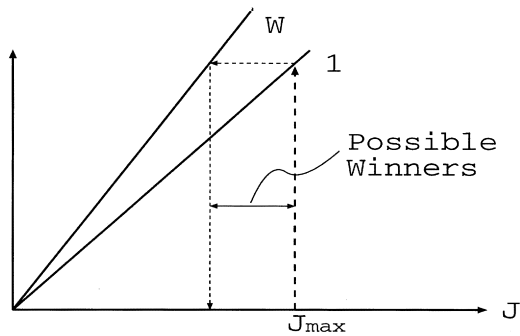


Fig. 1. The possible winners of the WTA-network as a function of the largest input  $J_{max}$  and the self-excitation  $w$ . The weakest neuron still able to win must have an input which multiplied by the self-excitation  $w$  is still larger than or equal  $J_{max}$ . For  $w = 1$ , this is only possible for the neuron with the largest input: the network is monostable.

1, the more selective is the WTA-mechanism and in the marginal case  $w = 1$  it is absolute. In this case the only stable fixed point consists of the winning neuron  $I_k$ , with largest external input  $J_k = \max_j(J_j)$ , if the maximum is unique. This concludes the analysis of the stable WTA-network.

What happens if the inhibition is slow (for  $w > 1$ ):  $\tau > 1/(w-1)$ ? Then  $p > 0$  in Eq. (11) and at least one eigenvalue has a positive real part. A simple calculation shows that if the inhibition is not too slow  $1/(w-1) < \tau < w/[(w-1)^2]$ , then the eigenvalues are complex conjugates of each other for

all  $N^+$ . Physically this describes an undamped linear oscillation.  $I^+$  oscillates more and more around the fixed point and has to go negative sooner or later. Then the driving forces of Eqs. (7) and (8) vanish; all eigenvalues of the corresponding partition are real and negative. However, there is no stable fixed point of the equations for  $N^+ = 0$ . Thus, at least one neuron will start firing, the oscillations set in again and the cycle restarts. The ‘epileptic’ network switches endlessly between this stable and other unstable partitions such that its activity remains bounded. Further, computer simulations show that the state trajectory approaches a limit cycle, which is a periodic solution of the equations (Fig. 2).

On the other hand, for very slow inhibition,  $\tau \gg w$ , both eigenvalues in Eq. (11) are real and positive for all  $N^+$ . The solution for  $I^+$  is then purely exponential: the total activity diverges to infinity without crossing partition boundaries any more.

The appearance of periodic orbits in linear threshold networks seems to be related to the existence of complex conjugate eigenvalues with positive real parts. This questions is investigated in computer simulations in the following section.

### 5. A completely arbitrary network

Complex eigenvalues of real matrices appear always in

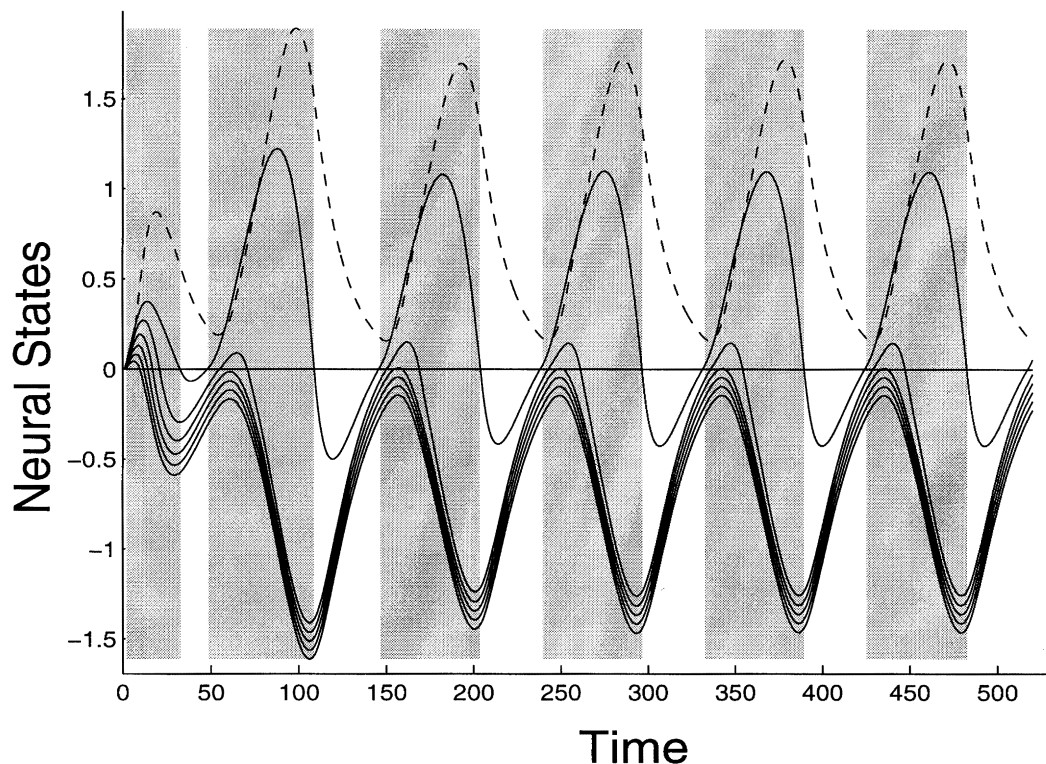


Fig. 2. Cyclic dynamics of the WTA-network of 6 neurons due to alterations between undamped oscillations marked by the shaded areas and exponential decaying dynamics.  $\mathbf{J} = (0.1, 0.15, 0.2, 0.25, 0.3, 0.35)$ ,  $\tau = 1.8$ ,  $w = 2$ . Note that  $\tau$  is in the region where undamped oscillations occur [ $(1 = 1/(w-1)) < \tau < w/[(w-1)^2] = 2$ ]. The undamped oscillations terminate as soon as the last excitatory neuron stops firing. The algorithm seeking for the fixed points isolated nine unstable fixed points. The labeling of the time-axis arises from the Forward–Euler method with stepsize  $\Delta t = 0.1$ . For the same network with  $\tau = 0.5$ , the four fixed points in the unitary partitions where  $N^+ = 1$  become stable while the other five remain unstable. These numbers depend strongly on the input  $\mathbf{J}$ .

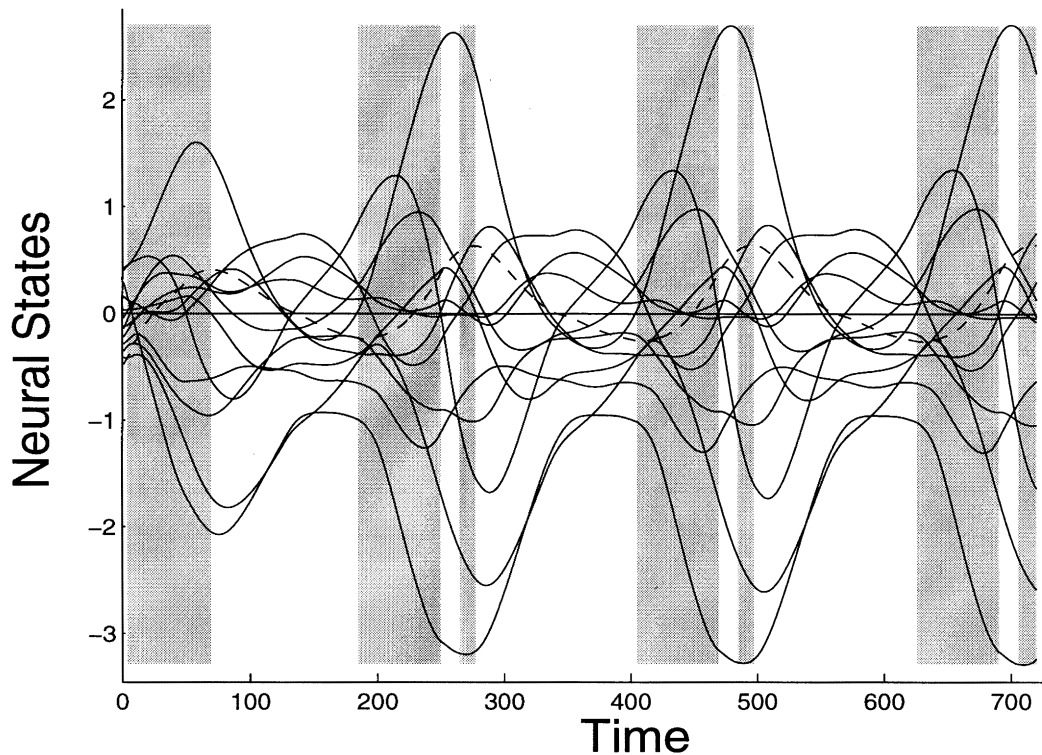


Fig. 3. Cyclic dynamics of a network consisting of 13 fully connected neurons with weights uniformly distributed in the range from  $-1.1$  to  $0.9$ . The eigenvalues used for detecting the regions of undamped oscillatory dynamics as marked by the shaded surfaces were computed with the software package Matlab.

conjugate pairs. The probability that an arbitrary matrix has two positive eigenvalues with conjugate imaginary parts is infinitely larger than the probability of two purely imaginary eigenvalues, because the imaginary axis has zero measure. If all oscillations in LT-networks are a result of unstable modes defined by pairs of eigenvalues with positive real parts, then oscillations should appear much more often than in purely linear systems. Computer simulations of an arbitrary LT-network of 16 neurons with random weights in the range from  $-1.1$  to  $0.9$  and uniform time constants  $\tau_i = 1$  were performed. If the dynamics approached a limit cycle, then the underlying mechanism was studied by splitting up the network trajectory in pieces of linear dynamics according to Eq. (3). This was done by computing all the zero crossings of the network state trajectory. The eigenvalues of all the effective linear systems were then computed and checked whether they fell in the right half of the complex plane excluding the positive real axis. The result of this analysis to a periodic trajectory is depicted in Fig. 3, the pieces of the dynamics which possess undamped oscillatory modes are shown by the shaded surfaces. Extensive studies revealed that for all periodic trajectories, it was possible to isolate a time interval smaller than the period with undamped oscillations<sup>4</sup>. This study suggests that periodic

oscillations are always due to the existence of undamped oscillatory modes. It might be interesting to pursue whether this can be undermined theoretically or whether on the contrary a periodic orbit can be constructed based only on damped and purely exponential modes.

## 6. Conclusions

The main goal of this article was to investigate the analytic approach to networks of linear threshold neurons. Here, a general excitatory network was shown to be bounded by using global inhibition. Lateral inhibition as proposed in the original model of Hartline–Ratliff has been shown elsewhere to be bounded (Hadel, 1974). In both these kinds of LT-networks, there is thus no need for a saturation in the activation function; the dynamics and the fixed points can be analyzed with reasonable effort. For piecewise linearity of higher than first the analyses would be more expensive and nearly impossible for smooth activation functions such as sigmoids. It might be possible that a combination of semi-global and lateral inhibition also produces bounded networks while revealing even more complex computations and behavior. The WTA-network is a paradigm for global inhibition. As a contrast to other recurrent WTA-networks in the literature, the network studied here includes the possibility of always selecting the neuron with largest input independently of the initial conditions.

<sup>4</sup> Interestingly, all trajectories that occurred in the simulations were divergent or convergent to either stationary states or limit cycles. There were no chaotic trajectories, not even in an arbitrary network of 50 neurons. This suggests that chaos is not possible at all in small LT-networks.

The study of complex dynamics in LT-networks showed that limit cycles were always a result of repetitive undamped oscillations. An illustrative example of these rhythmic activities is the ‘epileptic’ WTA-network. Although the analytic methods presented in this paper are elementary, they are well suited to revealing the basic properties of simple, as well as complex networks.

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### References

- Anderson J.A. (1983). Cognitive and psychological computation with neural models. *IEEE Transactions on Systems, Man and Cybernetics*, 13 (5), 799–815.
- Anderson J.A., Silverstein J.W., Ritz S.A., & Jones R.S. (1977). Distinctive features, categorical perception, and probability learning: some applications of a neural model. *Psychological Review*, 84, 413–451.
- Ben-Yishai R., Lev Bar-Or R., & Sompolinsky H. (1995). Theory of orientation tuning in visual cortex. *Proceedings of the National Academy of Sciences, USA*, 92, 3844–3848.
- Coultrip R., Granger R., & Lynch G. (1992). A cortical model of winner-take-all competition via lateral inhibition. *Neural Networks*, 5, 47–54.
- Douglas R., Koch C., Mahowald M., Martin K., & Suarez H. (1995). Recurrent excitation in neocortical circuits. *Science*, 269, 981–985.
- Douglas R., Mahowald M., & Martin K. (1994). Hybrid analog-digital architectures for neuromorphic systems. In *IEEE International Conference on Neural Networks*, volume 3, pages 1848–1853, Orlando.
- Feng J., & Hadel K. (1996). Qualitative behaviour of some simple networks. *J. Phys. A*, 29, 5019–5033.
- Hadel K. (1974). On the theory of lateral inhibition. *Kybernetik*, 14, 161–165.
- Hartline H.K., & Ratliff F. (1958). Spatial summation of inhibitory influence in the eye of limulus and the mutual interaction of receptor units. *Journal of General Physiology*, 41, 1049–1066.
- Kuhn D., & Loewen R. (1987). Piecewise affine bijections of  $R^n$ , and the equation  $Sx_+ - Tx_- = y$ . *Linear Algebra and its Applications*, 96, 109–129.
- Malsburg C.v.d. (1973). Self-organization of orientation sensitive cells in the striata cortex. *Kybernetik*, 14, 85–100.
- Salinas E., & Abbott L. (1996). A model of multiplicative neural responses in parietal cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, 93, 11956–11961.
- Taylor, J.G., Farrukh, N.A., 1996. A Basis for Long-Range Inhibition Across Cortex. Electronic Book. The UTCS Neural Networks Research Group, Austin, TX, <http://www.cs.utexas.edu/users/nn/web-pubs/htmlbook96>