



## Modeling neural spatiotemporal behavior

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### Abstract

We study some aspects of the dynamic neural filter (DNF), a recurrent network that produces spatiotemporal sequences in reaction to sets of constant inputs. The biological motivation for this study came from the observation of spatiotemporal patterns in the locust antennal lobe. Some of the aspects of these results can be reformulated and characterized by the DNF. Studying deterministic dynamics we find differences between low and high numbers of neurons. For low numbers there exists clear correlation between distances in input space and edit distances of spatiotemporal sequences. For large numbers of neurons we observe divergence between close-by spatiotemporal sequences. Nonetheless neuronal correlations survive for small changes in input space.

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### 1. Introduction

An interesting issue in neuroscience is the question of spatiotemporal coding. Its existence has been demonstrated [7] in the locust olfactory system, where the spatiotemporal behavior of projection neurons encodes the odor presented to its receptor neurons. This transformation from odor-input to spatiotemporal activity occurs in the antennal lobe, that is the first module of the olfactory system. This system may therefore be regarded as a dynamic neural filter that turns spatial information distributed over its many glomeruli, that are fed by the receptor neurons, to specific spatiotemporal outputs. It is interesting to point out that, although this is a complicated biological

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system, it has an important simplifying feature that allows it to be represented by a simplified model of mathematical neurons, i.e. the fact that the activity of the projection neurons is limited to temporal bins defined by an oscillatory local field potential. Hence a model with binary neurons obeying Hopfield–Little dynamics [4] can provide a valid first-order approximation of the spatiotemporal behavior of the system. We have presented this model in a previous work [6] and demonstrated how it can be used to generate the spatiotemporal behavior of projection neurons observed by Wehr and Laurent [7]. An extensive study of the model was presented in [5]. Here we wish to expand on several aspects of the model that can be of particular interest to computational neuroscience.

## 2. The dynamic neural filter

The dynamics of the model has the following structure:

$$n_i(t+1) = H(h_i(t+1)) = H\left(\sum_j w_{ij}n_j(t) + R_i - \theta_i\right), \quad (1)$$

where  $w_{ij}$  is the synaptic coupling matrix,  $R_i$  is the external constant input (specifying odor activation) and  $\theta_i$  is the threshold.  $H$  is the Heaviside step function taking the values 0 for negative arguments and 1 for positive ones. For simplicity we choose  $w_{ij}$  and  $R_i$  as integers, fixing  $\theta_i = \frac{1}{2}$ .

Consider the problem presented by Table 1, where we observe  $K = 6$  series, representing the results of six inputs (e.g. odors), over  $T = 4$  time steps in a problem of  $N = 5$  neurons. The first two neurons correspond to the observed ones of Wehr and Laurent.

The modeler is challenged to find a matrix  $\mathbf{w}$  and six input vectors  $R$  that solve this problem. We have presented a solution to this problem in [5] based on the perceptron algorithm. The principle is to generalize the  $N$ -dimensional neural space to an  $N + K$  dimensional one, such that each one of the  $K$  series is presented by one 1 and  $K - 1$  null entries in these new axes. In this new space we define for each neuron  $i$ , a vector of perceptron weights  $\vec{w}^i$

$$(\vec{w}^i)_j = w_{ij} \quad \text{for } j = 1, \dots, N, \quad (\vec{w}^i)_{N+k} = R_i^k - \theta_i \quad \text{for } k = 1, \dots, K. \quad (2)$$

Table 1  
Six spatiotemporal sequences defined for four time-steps in a system with five neurons

Time/code	1	2	3	4	5	6
1	1 1 0 0 0	1 0 0 0 0	1 1 1 0 0	1 0 0 0 0	1 0 1 1 0	1 0 0 0 0
2	1 1 0 0 1	1 1 0 0 1	1 1 1 1 0	1 0 1 0 0	1 0 0 0 0	1 1 1 0 0
3	1 1 0 1 1	1 1 0 1 1	0 1 1 1 0	0 1 1 0 0	1 1 1 0 0	0 1 1 1 1
4	0 0 0 1 0	0 0 0 1 0	0 0 1 1 0	0 1 1 1 0	1 1 1 1 1	0 0 0 1 0

We assume that the  $K$  series start from an initial null state, and we use the perceptron algorithm to construct these vectors  $\bar{w}^i$ , whose  $(N+k)$ th component includes the information about  $R_i^k$ .

Thus we obtain a synaptic weight-matrix, that serves to define a dynamic neural filter (DNF), as well as  $K$  inputs that lead to the sequences of Table 1. But this can work only if each column in Table 1 does not include repetitive states, and if no xor-like contradictions of perceptron dynamics occur. If such situations occur we have to add hidden neurons. In fact this is the case with the Wehr–Laurent series, described by the first two neurons in Table 1. Since these sequences cannot be generated by an  $N=2$  DNF, we added three hidden neurons in the example of Table 1, leading to a system that can be generated by a DNF. In general, for any problem of  $K$  binary sequences with  $T$  time steps one can find hidden neurons that allow for a DNF representation. A solution is guaranteed for high values of  $T$  and  $K$  if the total number  $N$  of neurons (observed + hidden) obeys

$$N \geq \frac{1}{2} K(T-2), \quad (3)$$

which can be derived from the Cover limit [1].

### 3. Spatiotemporal distances

The DNF can be viewed as a generative tool for production of spatiotemporal sequences. Every such sequence can also be used to reconstruct a DNF that can serve as its generator. This relationship can be exploited to serve as a measure in the generalized space of all spatiotemporal sequences.

In [5] we have numerically studied an  $N=5$  model and observed that, for a fixed  $\mathbf{w}$ , distances in  $R$  correlate well with edit distances in the spatiotemporal sequence. This is easily demonstrated in Table 2, using a binary representation for every state of the sequence in the form  $1 + \sum_{i=1}^N n_i 2^{N-i}$ . These states are then represented by numbers ranging from 1 (the null state) to  $2^N$  when all neurons are active.

These sequences are generated by changing one  $R$  value. The initial state was always chosen to be the null state. Note that this set of sequences contains several 5-cycles. This is to be expected from a synaptic matrix that is asymmetric, i.e. far from being

Table 2

A list of six neighboring sequences in a system with five neurons, displayed over seven time steps

$t=0$	1	2	3	4	5	6	7
1	17	22	6	8	3	17	22
1	17	22	14	8	3	17	22
1	17	22	14	16	3	17	22
1	17	30	16	3	17	30	16
1	25	30	16	3	17	30	16
1	25	30	16	11	3	17	30

either symmetric or antisymmetric. Asymmetry may be defined by the parameter  $\alpha = \text{tr}(\mathbf{w} \cdot \mathbf{w}) / \text{tr}(\mathbf{w} \cdot \mathbf{w}^T)$  whose extreme values 1 and  $-1$  correspond to full symmetry or antisymmetry, respectively. The matrix that has generated Table 2 and, incidentally, provides a solution to the problem of Table 1, has  $\alpha = -0.41$ . Large cycles are to be expected when  $\alpha \approx 0$  [3].

So far we have discussed examples with small numbers of neurons. It is of interest to ask what happens if the number of neurons in our system is higher, e.g.  $N = 50$ . Investigating such a system with  $\alpha \approx 0$  we find that close-by  $R$  values can generate divergent spatiotemporal sequences. In one such example, we varied  $R_1$  and produced 27 different sequences that were tested over 1000 time steps. None of the sequences has shown any periodicity within this large range. Moreover, two sequences generated by neighbors in  $R$  space, coincided for several tens or hundreds of time steps until different states appeared. From this point onwards the states in the two sequences formed completely disjoint sets, i.e. complete divergence of the sequences occurred.

Obviously, there seems to be a large difference between small and large  $N$  values. This is due to the fact that the space of all available states increases exponentially as  $2^N$ . Hence, for large  $N$ , once a change occurs in some state in the sequence, it becomes almost impossible to return to the original sequence.

#### 4. Neuronal correlations

It is interesting to note that divergence of spatiotemporal representations was observed experimentally by Friedrich and Laurent [2] in the olfactory bulb of zebrafish. The authors have studied the response of this system to similar odors, characterized by small changes in molecular structures of the relevant chemicals. One of their interesting results is that the correlation between temporal patterns of similar odors over the mitral cells reduces with time (between the first and second 500 ms after odor presentation). This leads us to wonder whether in our large  $N$  system we can find transitions in time from large to medium correlations, rather than abrupt transitions from equality of sequences to maximal inequality.

The answer is affirmative. To understand it we have to realize that the relevant volume of  $R$  space is limited by constraints [5]

$$-\sum_j w_{ij}H(w_{ij}) \leq R_i \leq -\sum_j w_{ij}H(-w_{ij}) + 1. \quad (4)$$

Outside this range the dynamics become trivial because the input determines directly the neuronal values. The center of  $R$  space is the region where the system leads to large cycles (provided  $\mathbf{w}$  is asymmetric) and where the chaotic-like phenomena of total divergence occur. As we move out of the center of this space, small changes in  $R$  may lead to a divergence, but finite correlations survive. An example of this behavior is shown in Fig. 1 which describes the Hamming distance between two neighboring sequences, that were generated by  $R$  values off the center, in an  $N = 40$  problem. Once divergence occurred, none of the states in one system appeared in the other, nonetheless

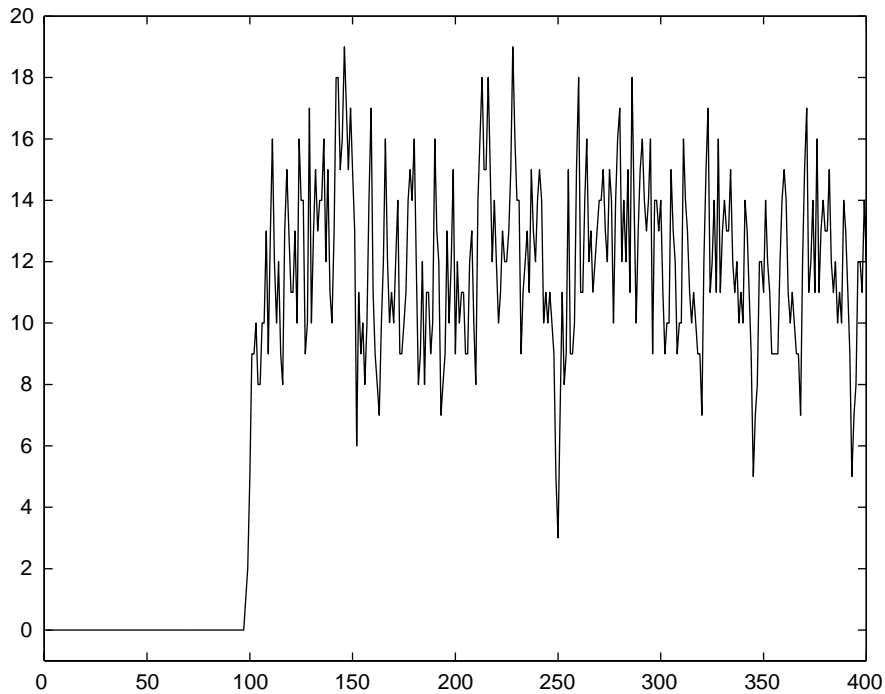


Fig. 1. Hamming distance between two neighboring sequences, in an  $N=40$  problem, plotted vs. the temporal evolution of the sequences.

a finite correlation survived as indicated by the fact that the mean Hamming distance is around 12 and not 20, the number expected if no correlation had survived. In the olfaction problem, small changes in  $R$  may be thought of as small changes in the type or concentration of odor. We may then expect the latter to be traceable through neuronal correlations even if their spatiotemporal patterns look quite different.

## 5. Summary

We saw that the DNF can serve several purposes. For low  $N$  values it serves as a simple model for generating a set of binary spatiotemporal sequences. Any given set can be accommodated by a DNF. The latter can be explicitly constructed using a generalized perceptron rule, but may necessitate invoking hidden neurons. For large  $N$ , the DNF can be used as a simple testbed for discussing experimental observations of neuronal correlations in an almost chaotic regime. Both cases were exemplified by results of spatiotemporal behavior observed in olfaction.

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