

OSCILLATION AND CODING
IN A FORMAL NEURAL NETWORK CONSIDERED AS
A GUIDE FOR PLAUSIBLE SIMULATIONS
OF THE INSECT OLFACTORY SYSTEM

Ginette HORCHOLLE-BOSSAVIT*, Brigitte QUENET**,

Olivier FOUCART

**Equipe de Statistique Appliquée

* UMR CNRS 7084

Ecole Supérieure de Physique et de Chimie Industrielle de la Ville de Paris

10 rue Vauquelin, 75005 Paris, France

Ginette.Bossavit@espci.fr, brigitte.quenet@espci.fr,

Keywords: *Oscillations; Complex Dynamics; Neural coding; Spatiotemporal patterns;*
Hodgkin-Huxley model; Formal neural network.

Abstract

For the analysis of coding mechanisms in the insect olfactory system, a fully connected network of synchronously updated McCulloch and Pitts neurons (MC-P type) was developed (Quenet and Horn, 2003). Using an internal clock, this "Dynamic Neural Filter" (DNF) produces spatiotemporal patterns identical to synchronized activities recorded from the Projection Neurons (PN) in the locust antennal lobe (AL) in response to different odors.

Here, in a first step, we separate the populations of PN and Local inhibitory Neurons (LN) and use the DNF as a guide for simulations based on biological plausible neurons (Hodgkin-Huxley: H-H type). We show that a parsimonious network of 10 H-H neurons generates action potentials corresponding *exactly* to the olfactory codes.

In a second step, we construct a new type of DNF in order to study the population dynamics when different delays are taken into account. We find synaptic matrices which lead to *both the emergence of robust oscillations and spatio-temporal patterns*, using a formal criterion, based on a Normalized Euclidian Distance (*NED*), in order to measure the use of the temporal dimension as a coding dimension by the DNF. Similarly to biological PN, the activity of excitatory neurons in the model can be both phase-locked to different cycles of the oscillations corresponding to the local field potential (LFP), and nevertheless exhibit dynamic behavior complex enough to be the basis of spatio-temporal codes.

1. Introduction

Rhythmic activities of neuronal populations can be observed "in vivo" at various frequencies in numerous brain areas. They are associated with motor behaviors, perception of sensory inputs, memory or consciousness states both in normal and pathological conditions. In addition, oscillatory patterns are also generated in brain slices and neuron cultures.

Many experimental and theoretical results suggest that synchronization of neuron firings could be associated with 1) properties of single neurons 2) nature of synapses and connectivity of network. Regarding the emergent properties of neural networks, the mathematical analysis of recurrent networks with spiking neurons is highly non trivial since dynamic responses in neurons varies from type to type, according to their shape, the distribution and densities of ion currents and the mechanisms of synaptic transmission. In contrast, formal neurons are the simplest models of neuronal elements and networks of interconnected MC-P neurons can perform many formal computational tasks and show various types of dynamics with nonlinear behaviors (Nowotny, 2003). Thus they can be used as a starting point to understand how the activity patterns are generated in sparse recurrent networks and the respective roles of the input and the connectivity in driving the network towards chaotic behavior (Horn et al., 2004), oscillations (Gutfreund et al., 1988) or clusters of neurons firing synchronously. It is also possible to explore the effects of noise that generate stochastic behavior on the neuronal dynamics.

In the olfactory system, a large corpus of data gave evidence that oscillations at frequency of about 20 Hz play an important role in the coding of sensory information. There is a wealth of experimental evidence on the antennal lobe (AL) of the locust (Laurent and Davidowitz, 1994; MacLeod and Laurent, 1996 ; Laurent, 2002) showing that odors are represented by both specific activity sequences in PN and transient synchrony of PN clusters. The spatio-temporal patterns, which characterize the population activity, change under various conditions; however the connectivity structure and dynamical mechanisms underlying the information processing which provides the codes about the odorant are not well understood so far. As the AL comprising only hundreds of excitatory and inhibitory neurons is a very small set of neurons (Laurent, 1996), it is an attractive case study for modeling.

2. Inverse problem and Dale principle in the Dynamic Neural Filter

One of the neuronal models of this study is a fully connected network of MC-P units, updated synchronously according to equation 1.

$$s_i(t) = H\left(\sum_{j=1}^N w_{ij} \cdot s_j(t - \tau_{ij}) + R_i - \frac{1}{2}\right) \quad \text{Eq 1}$$

Here $s_i(t)$ is the binary state, 0 or 1, of neuron i at time t , w_{ij} is the synaptic weight from neuron j to neuron i , τ_{ij} is the delay from neuron j to neuron i , R_i is an external input to neuron i , and H is the Heaviside function, whose value is nil if its argument is non positive, and 1 if its argument is strictly positive. The typical dynamics of such a network, *for all delays equal to 1*, exhibits cyclic spatio-temporal patterns whose length depends on some characteristics of the synaptic matrix W and on input vector R (Elyada et al., 2005; Horn et al. 2004). The richness of the dynamics of this system is such that it is possible to use it in order to address the following question: can we find a family, or at least an example, of connection matrices and of inputs that can elicit a given sequence of binary activities of a given number of binary units? This is called an « inverse problem », which has been described and analyzed for the DNF in Quenet et al., 2002, Quenet and Horn, 2003 and Quenet et al., 2005. Given the matrix S of binary spatio-temporal patterns for N neurons and T time steps, its general term is $s_{ti} = s_i(t)$ the activity of neuron i at time t . The conditions on the general terms w_{ij} and R_i can be written as N sets of T inequalities, i.e. one set per neuron; moreover each set of inequalities refers to a corresponding subset of W and R : the set of inequalities for neuron i refers to the synaptic weights and input that are afferent to neuron i *only*, which can be seen in general equation 2¹.

¹ If the initial state of the network is included in the T times of the sequence, the number of inequalities is $(T-1)$.

$$(2s_{ti} - 1) \left(\sum_{j=1}^N w_{ij} \cdot s_{(t-1)j} + R_i \right) > 0 \quad \text{Eq 2}$$

We note that all the factors of one inequality have the same sign, which is given by $(2s_{ti} - 1)$.

When such a set of inequalities has a solution, *it has several solutions*. Because there is a separation of the variables, each set can be solved independently of the others, but the whole inverse problem which consists on the definition of a synaptic matrix and input vectors able to elicit some pre-defined spatio-temporal sequences implies that there is a solution for each set of inequalities.

It may happen that one of the sets has no solution, which means that for the corresponding neuron, there is no way to define a vector of its inputs which can be compatible with both the activities of the pre-synaptic neurons and its own pre-defined activity. In such a case, it is necessary to add extra (or hidden) units. The new problem consists of building the activity of such hidden units that allows for finding a solution to the new set of inequalities.

Indeed, each set of inequalities that has no solution is equivalent to a linear separability problem (Quenet et al., 2002). If the activity of an added hidden neuron is such that the linear separability problem is eliminated, then the set has solutions. Let us suppose that there is no solution for the set of inequalities corresponding to neuron i , a simple way to eliminate the linear separability problem for this neuron is to add a single hidden unit whose activity at time $(t-1)$ is *exactly the activity of neuron i at time t* , because the new degree of freedom brought by this hidden neuron (let us call this term w_{ih}) is such that it appears *only* in the group of inequalities whose factor has a positive sign, i.e. when $s_{ti} = 1$.

Constraints can be considered in addition to the ones related to the dynamics itself, for instance when the Dale's principle is introduced in the problem; this principle states that a neuron releases a single neurotransmitter, usually leading to a single effect, i.e. it cannot excite some of its postsynaptic targets and inhibit others (Dale, 1935). These new constraints

can be expressed as inequalities on the synaptic weights or external inputs, therefore, they simply define *a new set of inequalities*. For instance, if we want to impose that neuron 1 in the network is an excitatory neuron, the new inequality which will appear in the sets of inequalities *for all the neurons i* is given in equation 3:

$$W_{i1} > 0 \quad \text{Eq 3}$$

Such new constraints may transform solvable sets of inequalities into non solvable ones. Let us consider a network of neurons, where some hidden units have been added with the appropriate activity in order to allow the network to exhibit exactly the pre-defined sequences, without considering any other constraints than the ones induced by the dynamics. The addition of the constraints related to the Dale's principle may introduce incompatibilities in some sets of inequalities. In such a case, there is again the possibility to add new hidden neurons. The activity of a new hidden neuron will be chosen in such a way that it is active at each time step when the sign in the factor of the synapse is opposite to the one of the added constraint.

With these building rules, *whatever the set of spatio-temporal sequences of some binary units obeying the Dale's principle it is always possible* to find the appropriate activities for hidden units which allow the network to exhibit these sequences.

Next step consists on the definition of a synaptic matrix and of some external input vectors , in other words, finding solutions to the solvable sets of inequalities. This can be done using two different standard algorithms (Ho and Kashyap, 1965; Vapnik, 1995- using Support Vector Machines with a linear kernel²).

Both synaptic weights and external input vectors can be defined simultaneously, or, once the synaptic weight is defined, each input vector corresponding to each sequence can be computed independently.

² Loosli Gaele, <http://asi.insa-rouen.fr/~gloosli2003> Proceedinds ICML 20th International Conference on Machine Learning

Without considering the Dale's principle, the binary activities of two PN recorded in a locust AL have been reproduced with a network of five neurons, as well with MC-P neurons as with H-H neurons (Quenet et al, 2002). The introduction of the Dale's principle increases the size of the network. Here, we present an example of a synaptic matrix and input vectors (Table 1) for a network of ten neurons, which lead the network to exhibit, for its first two neurons, all the binary activities of the two PN recorded in Wehr and Laurent, 1996. In this network, they are five excitatory neurons, including the two ones representing the recorded PN, and five inhibitory ones, i.e. hidden LN.

PN1	PN2	PN3	PN4	PN5	LN 6	LN7	LN8	LN9	LN10	
PN1	2	0	4	4	4	-4	-4	0	-2	-8
PN2	4	8	4	22	0	0	-16	-8	-8	-4
PN3	1	0	0	1	0	-3	-2	-2	-3	-6
PN4	1	0	5	1	6	-2	-1	-2	-1	-4
PN5	0	0	1	1	1	-4	0	-3	-6	-4
LN 6	3	6	3	6	3	-3	-9	-3	-3	-3
LN 7	2	4	1	1	1	-1	0	0	-7	-1
LN 8	2	4	0	4	2	0	-2	-2	-2	-4
LN 9	4	0	0	1	1	-2	0	-2	-3	-7
LN 10	9	3	6	6	9	-3	-6	0	-3	-18
R1	4	4	1	1	1	-16	-3	-2	1	6
R2	4	-4	1	1	1	-15	-1	-1	1	6
R3	4	1	1	1	-1	9	-1	-8	-1	3
R4	2	-4	-2	-1	1	1	-1	-6	1	-3
R5	8	-4	-2	-1	1	1	1	-2	3	-1
R6	1	-4	2	1	2	-3	-1	-4	1	1

Table 1

Weights of the synaptic matrix and inputs (R1 to R6) defining the network of 5 excitatory neurons (PN) and 5 inhibitory neurons (LN) producing the binary codes defined by Wehr and Laurent (1996) according to the firing probabilities of two PN (PN1,PN2) in response to 6 complex odors.

3. Illustration of the solution with a Hodgkin -Huxley neural network

With such an example, we can show that the network properties dominate and produce the identical dynamical behavior for very different neuron models: cellular automaton or

biological plausible units, *just because the synaptic weights, the input vectors, and the delays are the same.*

The H-H neurons and their synapses are designed as described³ in Quenet et al, 2005. They were used in simulations performed with the software NEURON (Hines and Carnevale, 1997). We must stress that the H-H network does not exhibit an intrinsic clock, as is the case in the MC-P network where the clock is represented by the update time step. Therefore, an external clock has been introduced here by sending regular pulses of inputs to the network of H-H neurons.

In fact, the biological networks generate oscillations with regular periods as an *internal clock*, which emerges from the activities of the network itself. Therefore, our aim is now to define a network architecture leading to *the co-emergence of both a code and an oscillation*. We first study the conditions of such a co-emergence in a network of simple neurons, in order to point out the parameters which give such properties to the network dynamics.

4. Optimization of coding capacities with spatial and temporal dimensions

In the computational processes involved in coding mechanisms, an organized timing of spikes is a common property for clusters of neurons firing synchronously, *around the same frequency, independently of the input* (Wehr and Laurent, 1996; Laurent, 1996). Here, we construct networks in which synchrony is easy to achieve for a wide range of parameter values and (initial/random) conditions. According to the Dale's principle, our modified DNF, neurons are either excitatory (as PN) or inhibitory (as LN) as in sparse recurrent networks of Integrate-and-Fire neurons with heterogeneous excitatory and inhibitory connections and (sufficient) different delays which give rise to cyclic attractors (Brunel, 2000). The network is composed of N neurons, from which N_{PN} are excitatory and $N - N_{PN}$ are inhibitory.

³ The HH neuron models constructed with NEURON and synapses which are used here are the ones described in (Quenet et al, 2005) but without the Calcium conductance.

In the connection matrix encoding the synaptic weights (if not nil, these weights are V_{ex} and V_{in} respectively for excitatory and inhibitory connections), every excitatory and inhibitory neuron sends an equal number of contacts, respectively to K_{ex} and K_{in} post-synaptic neurons, chosen at random. This leads to a recurrent synaptic architecture. In addition, a random set of neurons receives an input from K_r units representing the synaptic input from sensory receptors with a V_r weight. A *non-uniform matrix delay* takes into account different synaptic and transmission delays: here $\tau_{ij} = 1$, i.e. one time step of the parallel update of the MC-P units, when neuron j is an excitatory one and $\tau_{ij} = 2$, when it is inhibitory. In our simulations the size of the network is $2N = 200$ with $N=100$ excitatory neurons and $N=100$ inhibitory ones. Some simulations have taken into account a possible "intrinsic" noise, including synaptic and membrane potential fluctuations, whose effect is considered centered at the level of the state function of each neuron (Peretto, 1992). The update rule is modified according to equation 4:

$$s_i(t) = f\left(\sum_{j=1}^N w_{ij} \cdot s_j(t - \tau_{ij}) + R_i - \frac{1}{2}\right) \quad \text{Eq 4}$$

with f , a sigmoid function, replacing the Heaviside one. Here f is chosen as (Equation 5) :

$$f(x) = \frac{1}{1 + \exp\left(\frac{-x}{\varepsilon}\right)} \quad \text{Eq 5}$$

with ε , the factor which governs the level of noise.

In the deterministic case, the dynamics is usually cyclic with short cycles. When only a fraction of the whole neuronal population exhibits an activity, and if the same group of excitatory neurons is active at each "time step" of the internal clock defined by the cycle itself, we consider the activity pattern corresponding to the input to be a *purely spatial code*,

since the temporal structure is trivial (see figure 4A). Indeed, the spatial information available at the first period is the same whatever the following period: time does not bring any new information. Let us consider the opposite case, where all the neurons are involved in the network activity, i.e. each neuron is active at least once during the total time of observation. Let us suppose that during this time of observation the dynamics defines T time steps, i.e. there are T periods of oscillation of the global activity. If $T < N$, the number of neurons in the network, and if the number of active neurons is about the same in each time bin defined by the oscillation, it is possible to define a "canonical" activity of this network, for which all the time bins are fully useful for coding. Such a canonical activity consists of the activation of a specific subset of about N/T neurons at each time bin, and different from every other subset active during another time bin. As the temporal pattern of activity of the network is invariant with respect to permutations of the neurons, such a canonical activity can be presented ranking the neurons according to the timing of their activity: *it results in a diagonal organisation* as can be seen in figure 2. In this canonical case, there is no pure spatial code, as each of the neurons is active in one bin, but this is really a *spatio-temporal code* as it is based on the combination of the T non-overlapping subsets on the T times bins. Let us call such a matrix a canonical spatio-temporal matrix for T time bins and N neurons, with $N = k \cdot T$. If each neuron is active p consecutive update times, with $p < P$, the number of update times in each time bin, the general term of a canonical matrix is given in equation 6:

$$c_{it} = H\left(i - E\left(\frac{t}{k}\right) \cdot k\right) \cdot H\left(\left(E\left(\frac{t}{k}\right) + 1\right) \cdot k - (i - 1)\right) \cdot H\left(t - E\left(\frac{t}{k}\right) \cdot k\right) \cdot H\left(E\left(\frac{t}{k}\right) \cdot k + p - (t - 1)\right)$$

Eq 6

for $i \in \{1, \dots, N\}$ and $t \in \{1, \dots, P \cdot T\}$. E is the integer part of the ratio, and H the Heaviside function. Each row of the canonical matrix corresponds to the activity of a neuron: the length of a row is the number of simulation update time steps. Each column of the matrix

corresponds to the activity of the network at one simulation time step: the length of a column is the number of neurons in the network.

The concept of canonical matrix has been introduced here in order to define a scalar descriptor able to measure the complexity of an attractor in terms of using the temporal dimension for coding an input. It is possible to “slice” this matrix according to its time bins: to each slice j corresponds an activity vector v_j whose general term is given in equation 7, it is the total number of active time steps of a neuron during this bin.

$$v_{ij} = \sum_{t=(j-1) \cdot k+1}^{(j-1) \cdot k + \frac{T}{n} - 1} c_{it} = \sum_{t=(j-1) \cdot k+1}^{(j-1) \cdot k + \tau} H(i - (j-1) \cdot k) \cdot H(j \cdot k - (i-1)) = \tau \cdot H(i - (j-1) \cdot k) \cdot H(j \cdot k - (i-1))$$

Eq 7

With $j = E\left(\frac{t}{k}\right) + 1$, which means that $j \in \{1, \dots, T\}$.

The length of the vector v_j is the number of neurons in the network. The norm of this vector is:

$$\|v_j\| = p\sqrt{k} \quad \text{Eq 8}$$

For a canonical matrix, we define a distance, D_c , which is a mean value extracted from a distance matrix of size $T \times T$, whose general term d_{nm} is computed as the Euclidian distance between the extremities of activity vectors n and m , corresponding respectively to *the normalized vectors* of activities at time bins n and m respectively (Equation 9).

$$d_{nm} = \sqrt{\sum_{i=1}^N \left(\frac{v_{in}}{p\sqrt{k}} - \frac{v_{im}}{p\sqrt{k}} \right)^2} = \sqrt{\sum_{i=(n-1) \cdot k+1}^{n \cdot k} \left(\frac{1}{\sqrt{k}} - 0 \right)^2 + \sum_{i=(m-1) \cdot k+1}^{m \cdot k} \left(0 - \frac{1}{\sqrt{k}} \right)^2} = \sqrt{2} \quad \text{Eq 9}$$

Therefore, whatever k , p , N and T , $D_c = \sqrt{2}$.

If this matrix is modified in such a way that there is *one* more active neuron in each bin, which leads to an overlap of one neuron between each pair of subsets of active neurons in consecutive bins, the distance $D\left(\alpha = \frac{1}{(N-k)}\right)$ previously defined and computed on this new matrix is smaller than D_c , because of the overlap: the higher the overlap, by adding one by one more active neurons in each bin, the smaller this distance. Let us define *NED* the Normalized Euclidian Distance $NED = \frac{D}{D_c} = \frac{D}{\sqrt{2}}$: the maximal value of *NED* is 1 for a matrix of the canonical form, and its minimum value is 0, when the overlap is complete, which means that all the neurons are active at each time bin. The evolution of *NED* can be computed with $\alpha = \frac{r}{N-k}$, the rate of overlap (with $r \in \{1, \dots, N-k\}$), as indicated in equation 10 (for T odd⁴):

$$NED(\alpha) = \frac{2}{(T-1)} \left[H\left(\frac{1}{2} - \alpha\right) \left(\sum_{\lambda=1}^{1+\alpha \cdot (T-1)} \sqrt{\frac{\lambda}{1+\alpha \cdot (T-1)}} + \sum_{\lambda=2+\alpha \cdot (T-1)}^{\left(\frac{T-1}{2}\right)} (1) \right) + H\left(\alpha - \frac{1}{2}\right) \left(\sum_{\lambda=1}^{1+(1-\alpha) \cdot (T-1)} \sqrt{\frac{\lambda}{1+\alpha \cdot (T-1)}} + \sum_{\lambda=2+(1-\alpha) \cdot (T-1)}^{\left(\frac{T-1}{2}\right)} \sqrt{\frac{(1-\alpha) \cdot (T-1)}{1+\alpha \cdot (T-1)}} \right) + \sum_{\lambda=1}^{\left(\frac{T-1}{2}\right)} \sqrt{\frac{\lambda}{1+\left(\frac{T-1}{2}\right)}} \right] \quad \text{Eq 10}$$

Here, λ is an integer characterizing the degree of neighborhood between two vectors v_n and v_m .

This evolution is independent of N , k and p , and very slightly dependant on T (see figure 2)

⁴ For T even, the value of $D_n(\alpha)$ has to be modified : the maximal value of λ is $T/2$ for which the contributions to the sum have to be multiplied by $\frac{1}{2}$, as there is only *one* neighborhood for this maximal value instead of *two* for the lower values.

Therefore, this *NED* can be considered as an index revealing the overlap between the populations of active neurons among the time bins, hence revealing the use of the time dimension in a spatio-temporal pattern.

As soon as an activity pattern of $M \leq N$ active neurons exhibits an oscillatory behavior that allows the definition of time bins, it is possible to compute a value of *NED*, as defined in equation 11:

$$NED = \frac{\sum_{n=1}^T \sum_{m=1, n \neq m}^T d_{nm}}{\sqrt{2} \sum_{n=1}^T \sum_{m=1, n \neq m}^T (1)} = \frac{\sum_{n=1}^T \sum_{m=1, n \neq m}^T d_{nm}}{\sqrt{2} \cdot T \cdot (T-1)} \quad \text{Eq 11}$$

with

$$d_{nm} = \sqrt{\sum_{i=1}^N \left(\frac{v_{in}}{\|v_{in}\|} - \frac{v_{im}}{\|v_{im}\|} \right)^2} \quad \text{Eq 12}$$

the Euclidian distance between the extremities of activity vectors n and m , corresponding respectively to the normalized vectors of activities at time bins n and m respectively. Comparing this value of with $NED(\alpha)$, using the curve of Figure 3, we can interpret it as an effective rate of overlap between the populations of active neurons among the time bins.

5. Co-emergence of both oscillations and spatio-temporal patterns

Simulations have been performed according to the rules defined in the previous paragraph, for a network of 200 units connected by a random sparse matrix where K_{in} is set at a fixed value of 40 and K_{ex} varies from 1 to 100, with $V_{ex}=1$ and $V_{in}=5$. For the input, $V_r=4$ and K_r varies from 1 to 80. From time $t=1$ to time $t=100$, the excitatory and inhibitory neurons are updated

as described in equation 1 (or equation 4, when noise set at a value of 0.1 is added). The delay matrix has also been described previously and contains only two values: 1 for excitatory neurons and 2 for inhibitory ones. The standard dynamical behavior of the network is oscillatory, which is clearly revealed by the sum of the neuronal activity of the excitatory neurons, with a period that is very robust with respect to modifications of the synaptic matrix and the input, but depends highly on the inhibitory delay. In very few cases, there are exceptions with fixed points of the dynamics. Figure 4 illustrates two types of deterministic dynamics that are observed for the excitatory neurons (representing the PN). In a large majority of trials, the oscillations of the summed activities of the excitatory neurons (equivalent to the experimental biological Local Field Potential, LFP) are very regular (Figure 4A), because *the same set of neurons is active in each period*. This situation corresponds to a purely spatial code, as it has been considered above and the *NED* defined in equation 11 is nil. In some trials, the activity pattern is more complex: the set of active neurons is not the same in successive periods (Figure 4B), the activity of the excitatory neurons expresses a spatio-temporal pattern and the values of *NED* is above 0.63 (which means an overlap of 50%): it also reveals an oscillation of the pseudo-LFP, which is less regular than in the previous case but where the dominant period is the same.

We are now looking at the whole results for different values of K_{ex} and K_r , respectively the internal connectivity of excitatory neurons and the external excitation due to the input. For the 4000 trials, the following parameters are measured : 1) the *NED*, 2) the dominant period, 3) the mean number of neurons simultaneously active in each oscillation. The color-coded maps of Figure 4, show the bi-dimensional evolution of these three values versus K_{ex} (x axis) and K_r (y axis) . The period is quite stable between four and five time steps (figure 4C), the number of oscillatory neurons increases as the excitation (internal or external) increases, from

very few neurons (3 or 4, at the minimal excitation) to the whole population (figure 4D). The region of interest for the dynamical behavior corresponds to 1200 trials for which the values of K_{ex} and K_r respectively in the range of 1-30 and 1-40. However, the NED (Figure 4A) exhibits values higher than 0.5 only punctually, the other values being less than 0.3 (which means an overlap higher than 90%). Adding some noise in the dynamics ($\epsilon=0.1$) leads to higher values of the NED, as shown in figure 4B. However, the highest values appears in the region where the excitation is small, i.e where the deterministic attractor contains very few active neurons : in these conditions, the neurons that are active “by error” participate to the emergence of complex activities which explain the higher value of the NED, but such codes *due to the noise*, can not be good candidates to be complex spatio-temporal codes for external inputs, which should be precisely *robust against noise*. In other words, if we want to take advantage of the possible co-emergence of both oscillations and spatio-temporal patterns as codes, for odorants for instance, it is necessary to find *intrinsic conditions* for the network in order to make it able to exhibit *often*, i.e. for *many random realizations*, in *deterministic conditions*, *complex oscillatory attractors with a value of the normalized Euclidian distance around 0.5*.

6. Increasing the probability of co-emergence of both oscillations and spatio-temporal patterns : the “double” synaptic matrix.

The type of synaptic matrices that have been used for the previous study bring robust oscillations in the DNF with different delays for inhibitory neurons and excitatory ones. In a DNF with uniform delays, some types of matrices may lead to very complex spatio-temporal patterns, with very long cycles, for instance the ones where rows are orthogonal (Elyada and Horn, 2005), each row representing the afferent synaptic weights to a neuron. Let us define a

synaptic matrix where the probability of connection of each neuron to another one, either excitatory or inhibitory is very low (1%), it leads to a very sparse synaptic matrix where the scalar product is nil for the huge majority of couples of rows. In the context of the DNF with different delays, the dynamical behavior induced by this type of matrix is usually complex indeed, and regular oscillations emerge exceptionally. Looking for both properties, oscillations and complexity of the spatio-temporal activity of the neuronal population, we have combined the two synaptic matrices defining a “double” matrix in the following way: a very sparse random matrix with both excitatory and inhibitory weights, stronger than V_{ex} and V_{in} respectively, has been added to the matrix defined in the previous paragraph. With the double matrix, we explored the dynamics of the excitatory neurons for different values of K_{ex} and K_r , as previously done. Simulations were performed as in the case of the primary matrix and the results are shown in Figure 6. The period of the oscillations for the equivalent of the LFP is five for the huge majority of simulations (Figure 6C) and the number of oscillatory neurons evolves according to the same scheme as in the simulations with a primary matrix (Figure 6D). However, the *NED* appears very different with the double matrix than with the primary one (Figure 6A): it exhibits clearly a small region of values of K_{ex} and K_r where the *NED* is above 0.5. The introduction of some noise ($\epsilon=0.1$) increases the size of this region only (Figure 6B). These results indicate that it is possible to define random matrices which leads to both spatio-temporal codes and oscillations, whose period is very robust against changes in the synaptic matrix and in the input vector, and spatio-temporal code, what can be called “Distributed Synchrony” (Levy et al., 2001).

Focusing on the region where *NED* appears higher than 0.5, we performed comparative simulations with basic random matrices only and with double random matrices, in order to have a better insight into the distributions of the values of *NED* in these two cases: Figure 7

presents the histograms issued from such simulations (5000 realizations in each case), together with a zoomed picture of the corresponding matrices, the basic one for Figure 7A, the double one for Figure 7B. These histograms of NED exhibit very different distributions: almost uniform between 0 and 0.5, in addition to the high maximum at 0 (which corresponds to the pure spatial code) for simulations with the basic matrix, while there is a Gaussian distribution around 0.5 for the simulations with the double matrix, which means that this last configuration increases the complexity of the dynamics very significantly.

7. Conclusion

In this paper we address the problem of co-emergence of both oscillations and spatio-temporal codes in recurrent networks. In the first part, we focused on the codes and suggest a tool that may bring a contribution to the following general question: what can we infer about the structure just by looking at the neuronal activity? We based our modeling on two grounds: first, designing a network constructed with MC-P neurons that allows an analytical approach in order to define appropriate synaptic matrix and input vectors, second, replacing the MC-P units by H-H ones, and getting therefore *spiking activities* that exhibit exactly the binary spatio-temporal codes of the MC-P units. In the second part, we focused on the oscillations, and based our modeling on simulations of MC-P neurons.

Synchronization in the presence of random connectivity has been studied extensively in models based on many versions of Integrate and fire neurons (for a review see Vogels et al. 2005). Such studies aimed to understand either the stability of asynchronous states or transitions from oscillatory activities to asynchrony. Here, we show that the simplest neuronal units might provide oscillatory modes with non-trivial dynamics of excitatory neurons, modes that can be very good candidates to be spatio-temporal codes of the input to the network. Looking for a precise feature in the potentially complex oscillatory “distributed synchrony”,

which could not be correctly defined by usual measurements of chaotic features in a pattern (Bertschinger and Natschläger, 2004), we defined an index, the Normalized Euclidian Distance, which is an appropriate descriptor of the temporal use of spatio-temporal binary activity patterns.

Many questions can be tackled with the model developed here: as the number of parameters is reduced, related only to the network, it is possible to study the dynamical behavior of the model in an exhaustive way. Moreover, as this model is analytically tractable, we can hope to get a deeper insight into the relationship between the complexity of the dynamics and the structure of the synaptic matrix, the input vectors and delay matrix. Concerning the coding possibilities, we assume here that the higher the temporal dispersion of the spatio-temporal activity pattern, the higher the labeling and classification power of the network, with respect to its inputs, however, this is something which needs further analyses, in terms of projections from the space of inputs to the space of “outputs”, at the level of the excitatory neurons studied here, and representing PN in the AL, and, mainly, at the level of the neurons of the next step in the olfactory pathway, i.e., the Kenyon Cells.

Finally, this study opens the door toward theoretical studies oriented to what can bring learning rules modifying the synaptic weights. Here, they have been considered as fixed values during the simulation time for each trial : which means that, so far, our model could represent a biological network in its stabilized state, next step being to try to implement synaptic modifications in order to model what has been observed in the locust AL, i.e., the fact that coherent network oscillations emerged with repeated odor presentations and PN respond with decreasing intensity, but increasing precision (Bazhenov et al., 2005, Laurent, 2002).

MC-P neuronal networks constitute very appealing flexible models as they might provide complex dynamical behaviors and nevertheless remain simple tools in order to formalize many biological constraints extracted from experimental data.

APPENDIX

HODGKIN-HUXLEY NEURONES IN NEURON

Neurons : Two compartments

Geometry :

Soma :	diameter	= 30 μm
	length	= 30 μm
	surface area	= 2826 μm^2
Dendrite :	diameter	= 2 μm
	length	= 100 μm
	surface area	= 628 μm^2

Biophysics :	Soma	Dendrite
Membrane Conductance (Gm) (S/cm ²)	0.0003	0.0003
Axial Resistance (Ra) $\Omega\cdot\text{cm}$	30	30
Membrane Capacitance (Cm) ($\mu\text{F}/\text{cm}^2$)	1	1
Resting Potential (Vr) (mV)	-59	-70

Somatic membrane mechanisms

Na ⁺ :	Equilibrium Potentiel = 45 (mV)
	Maximal Conductance (g _{max}) = 0.34 (μS)
K ⁺ :	Equilibrium Potentiel = -70 (mV)
	Maximal Conductance (g _{max}) = 0.1 (μS)

Synapses : alpha function $g = g_{\text{max}} \cdot \frac{t}{\tau} \cdot \exp\left(1 - \frac{t}{\tau}\right)$

	Excitatory synapse synapses	Inhibitory
Equilibrium Potentiel (E) (mV)	45	-90
Maximal Conductance (g _{max}) (μS)	0.0055	
0.0024		
Time constant (τ) (ms)	2	20
Delay Δ (ms)	198	180

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Figure Captions

Figure 1.

Action potentials in a network of ten H-H type neurons obtained with a NEURON simulation. The activities of the first two neurons reproduce one the sixth binary code for PN1 and PN2. PN3 PN4, PN5 correspond to 3 excitatory hidden units and LN1, LN2, LN3 LN4, LN5 correspond to 5 inhibitory hidden units.

Figure 2.

The upper panel represents a canonical activity matrix, for 100 binary neurons during 100 update time steps. They are 20 groups of 5 neurons firing together, every five time steps, a new group of neurons is active for two consecutive time steps. When summed over the whole neuronal population (as in the biological Local Field Potential- LFP), the neuronal activity reveals a regular oscillation that is shown in the lower panel.

Figure 3.

Plot of the Normalized Euclidian Distance (NED) computed as in Eq. 10 as a function of the overlap rate α . It has been computed for four values of T (15,21,51,101). The four curves are almost superimposed and define a region of overlap where the decrease of NED is linear. This region corresponds to $NED \in [0.5, 1]$ and $\alpha \in [0, 0.73]$.

Figure 4.

Two types of spatio-temporal patterns observed in a recurrent network, where MC-P type neurons are connected by a random matrix. The upper panels show the activities of the 100 excitatory units (PN) for 100 time steps and the lower panels show the oscillation of the global activity (number of active neurons).

A : a regular synchrony (period=5 time steps) characterizes the 17 active units: $NED = 0$

B : an irregular synchrony (period=5 time steps) is seen for a variable number of units (1 to 18). Some of them show a reduced activity in the 45-75 time steps period. $NED = 0.63$

Figure 5.

Colormaps for Normalized Euclidian Distance (NED), period and number of oscillating neurons in dependence of two variable network parameters : the connectivity K_{ex} and K_r for a random matrix. The parameter space was sampled on a grid with values increasing from 1 to 40 for K_r and from 1 to 30 for K_{ex} , K_{in} being set to 40; $V_{ex}=1$, $V_{in}=5$. The values are linearly color-coded to define equidistant contour lines according to the colorbar on the right.

A: Contour maps of NED for a deterministic network (noise=0), there are very few points with values of $NED > 0.5$.

B: Contour maps of NED for a stochastic network (noise =0.1). Numerous values of $NED > 0.5$ are found exceptionally in the region defined by $K_r = 1$ to 12 and $K_{ex} = 1$ to 20

C: Contour maps of the oscillating period for the network corresponding to the NED values shown in A. In the region with small values of K_{ex} , there are spots where the network is out of the oscillating state which correspond to periods > 10 .

D: Contour maps of the number of oscillating units in the stochastic network illustrated in B.

A similar colormap (not shown) was observed for the deterministic network illustrated in A.

Figure 6.

Colormaps for Normalized Euclidian Distance (NED), period and number of oscillating neurons in dependence of two variable network parameters: the connectivity K_{ex} and K_r for a primary random matrix. The parameter space was sampled on a grid with values increasing from 1 to 40 for K_r and from 1 to 30 for K_{ex} , K_{in} being set to 40.

For the secondary matrix composing the double matrix, the connectivity values are fixed :

$$K_{ex}=1, K_{in}=2; V_{ex}=20, V_{in}=10.$$

The parameter space was sampled and color-coded as in figure 5.

A: Contour maps of NED for a deterministic network (noise =0), the points with values of $NED > 0.5$ are restricted to a region delimited by small values of $K_{ex} \in [1, 10]$.

B: Contour maps of NED for a stochastic network (noise =0.1), there is a greater region with $NED > 0.5$.

C: Contour maps of the oscillating period for the network giving the NED values shown in A. For a large majority of points, the network is in an oscillatory state.

D: Contour maps of the number of oscillating units in the stochastic network illustrated in B. A similar colormap (not shown) was observed for the deterministic network illustrated in A, it is similar to the colormap shown in figure 5.

Figure 7.

Properties of the random synaptic matrices and their effects on NED distributions.

A: The left panels show portions of the two types (primary and double) of random synaptic matrices used for simulations.

B: NED distributions for two random samples of 5000 trials. The networks were characterized by the fixed parameters ($K_{ex}=4$, $K_{in}=40$; $V_{ex}=1$, $V_{in}=5$; $K_r=10$; $V_r=4$) but are defined by two different types of synaptic matrices: primary (upper panel) and double (lower panel).

Upper panels: Pattern of the excitatory and inhibitory connections (The values as shown in the color-coded right bar are respectively 1 and -5) for a primary random matrix and histogram showing the *NED* distribution. It presents a high peak at 0, a smaller hump, a plateau between 0.1 and 0.5 then it decreases towards 0 for larger values of *NED*.

Lower panels: Pattern of the excitatory and inhibitory connections for a double random matrix. (The values as shown in the color-coded right bar are respectively 1, 20 and 21 for the excitatory ones and -5 , -10 and -15 for the inhibitory ones) and histogram showing the *NED* distribution on the right. It presents a small peak at 0 and a wide hump with a maximum at 0.5.