

THE CODES OBSERVED IN OSCILLATING NEURAL ASSEMBLIES OF THE OLFACTORY PATHWAY MAY BE REPRODUCED BY A SIMPLE NEURAL NETWORK

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ABSTRACT

The electrophysiological data recorded in the glomerular stage of the insect olfactory pathway show both a coherent global oscillating behavior of the neurons of this stage - carrier waveform? -, and a reproducible complex activity pattern - code? - of some of these neurons, in phase with the global oscillation. We propose a possible interpretation of this type of biological activity patterns, using a simple model of the glomerular stage of the insect olfactory pathway that has been previously designed. This model is analytically tractable, even when synaptic noise, random synaptic weights, inputs or delays are taken into account. This model exhibits the property of coding its inputs through spatio-temporal patterns which are the attractors of its dynamics. These attractors can be long cycles, robust against synaptic noise and also to input fluctuations, provided that the latter occur within well-defined limits. We give an example of a set of adapted synaptic weights and inputs leading our model to the attractors corresponding to a given neuronal code, drawn from experimental data.

1 INTRODUCTION

From a biological point of view, the emergence of *internal spatio-temporal representations* at the output of the glomerular level is now admitted to be the labels of odorant signals. Such 'codes' have been clearly exhibited in (Wehr & Laurent, 1996) where output neurons (or Projection Neurons, PN), transmitting information from a locust's antennal lobe to its mushroom bodies, had been recorded. These neurons appear to fire in synchronization with the Local Field Potential (LFP) recorded in the mushroom bodies; their fine temporal patterns of firing were found to depend reproducibly on the odorant signal applied on the olfactory receptor cells. Moreover, M. Stopfer et al have

demonstrated the role of this synchronization in pattern recognition, by using behavioral experiments in honeybee.(M. Stopfer et al,1997).

From a theoretical point of view, a simple model of the glomerular stage of the antennal lobe has been designed, capitalizing on anatomical, molecular and electrophysiological knowledge acquired so far on the invertebrate olfactory pathway, and taking advantage of previous models of the olfactory pathway (Kerszberg & Masson, 1995; Masson & Linster, 1996, for instance). The model consists of a network of simplified neurons receiving excitatory inputs; one of its salient features is the fact that it is fully tractable analytically (Quenet et al, in press). Based on synchronous dynamics, it codes its inputs with cyclic activities of the neurons, each of them firing according to a precise spatio-temporal pattern. Such a global and cyclic spatio-temporal pattern depends both on the intrinsic characteristics of the network (synaptic weights and delays) and on the external input: it represents an attractor of the dynamics of the model.

The questions that we address in this paper are the following: can we take advantage of our current analytical knowledge of this model of the antennal lobe, in order to build a network able to reproduce this spatio-temporal activities recorded in the antennal lobe of the locust? How can this knowledge be used, in the future, in order to suggest experimental tests of the model?

2 PROPERTIES OF THE MODEL

For brevity, the model will be very sketchily described, the precise analytic tools which are used to analyze and predict the codes will not be explained here in detail. The global structure of the model (schematically represented in figure 1) is derived from anatomical data in invertebrates, which show that the olfactory tract is organized as a three-layer structure (for a review see Masson et al., 1993). The sensory neurons that make up the first layer have dendrites which are in direct contact with the chemicals. These neurons project into the glomerular level, where each glomerulus is a neuropilar structure, site of synaptic contacts between the sensory neurons (mainly excitatory) and the interneurons (mainly inhibitory) of that level. Projection neurons convey information from the glomerular level to a third level, which is generally assumed to be the location of long-term memory (Masson et al., 1993; Menzel et al., 1991). In the model, the glomeruli are modeled as binary units: we assign to each glomerulus one local interneuron whose activity (spiking or quiescent) accounts for the glomerular activity. The Projection Neurons (PN) are supposed here to convey the glomerular activity to the next layer, but not to participate to the dynamics of the glomerular layer. The glomerular units are connected by synapses, with arbitrary delays and synaptic weights. Receptor neurons send excitatory connections to the glomerular units in a one-to-one correspondence, as suggested by the observation that, in vertebrates, sensory neurons which express the same receptor membrane protein project into a very small number of glomeruli (Axel, 1995).

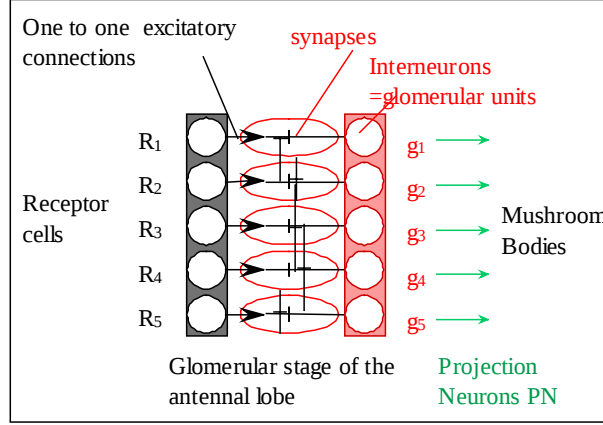


Fig. 1. Structure of the model

Each glomerulus, considered as a functional unit, is the site of synaptic contacts between the sensory neurons and the interneurons. Depending on the activity of the sensory neurons (input), the glomerular units exhibits a dynamics with cyclic spatio-temporal patterns which codes for the input. The Projection Neurons are supposed to simply convey this activity to the mushroom bodies.

The equations that govern the dynamics of the model are, in its deterministic version:

$$h_i(t) = \left(R_i - \frac{1}{2} \right) + \sum_{j=1}^N W_{ij} \cdot g_j(t - \tau_{ij}) \quad \text{and} \quad p(g_i(t) = 1) = H(h_i(t))$$

where $g_i(t)$ is the activity of glomerular unit i at time t , h_i its membrane potential, N the number of glomerular units, W_{ij} the synaptic weight from unit j to unit i , τ_{ij} the synaptic delay from unit j to unit i ; $p(g_i(t) = 1)$ is the probability that $g_i(t) = 1$ (i.e, the probability that glomerular unit i fires at time t), and H is the Heaviside function. It can be shown that any model with various delays has a dynamics that can be entirely described by a larger model (a model with more neuronal units) with unit delays, provided an appropriate choice of the connections has been made. Thus, models with unit delays only can be considered without loss of generality. The dynamics of such models can be described by a pseudo-Lyapunov function:

$$L(\vec{g}(t), \vec{g}(t+1)) = -\sum_{i,j} W_{ij} \cdot g_i(t+1) \cdot g_j(t) - \sum_i \left(R_i - \frac{1}{2} \right) \cdot (g_i(t) + g_i(t+1))$$

The binary vector $\vec{g}(t+1)$ that follows $\vec{g}(t)$ is, amongst all possible binary vectors, the vector that minimizes L . Moreover, in the stochastic version of the model, (where the synaptic noises have been modeled by replacing the Heaviside function in the firing probability of a glomerular unit by a sigmoid function of the value of its membrane potential (Peretto, 1992)), the dynamics can be described as a Markov chain, whose transition matrix T has the following general term:

$$T_{JI} = \frac{\exp\left(-\frac{L(J, I)}{\varepsilon}\right)}{Z(I)}, \text{ with } Z(I) = \sum_K \exp\left(-\frac{L(K, I)}{\varepsilon}\right). T_{JI} \text{ is the conditional probability of observing the network}$$

in state J at time $(t + 1)$ knowing that at time t , the state of the network was I (I and J represent two possible binary vectors, and ε is the parameter that characterizes the noise). Here we clearly see that the vector J that minimizes L is the most probable vector that will appear after I . Since this Markov chain is both homogeneous (T is independent of time) and irreducible (there is a non-zero probability to go from any state I to any state J), it is possible to find an eigenvector with general term $p_\infty(I)$ with eigenvalue 1, such as: $T \cdot p_\infty = 1 \cdot p_\infty$. With these tools, it is easy to compute (and not only to simulate) the most probable cyclic attractor that codes for a given input vector $\vec{R}$, in a given network of connection matrix W , independently of the initial state. In a previous version of this model, where W was supposed to be symmetric, we have shown that one of its relevant features was its ability to exhibit a constant cyclic attractor for quite large domains of inputs, these domains being well defined (Quenet et al, in prep). This property may account for the well-known robustness of an odorant perception while the input signals may vary substantially (Pham-Delegue et al, 1993). With non-symmetric connection matrices, the attractors may be very long, implementing a complex temporal code; nevertheless, the property of robustness to the fluctuations of the input, within well-defined limits, is still conserved, as well as the robustness of this type of code to internal noise.

3 INTRODUCTION TO THE 'INVERSE PROBLEM'

In the previous section, we discussed the "direct problem", i.e. the possibility of finding the code, as a cyclic attractor, in response to a given input $\vec{R}$ (or a family of inputs $\vec{R}$) in a given network, with fixed weights. Since precise experimental information on the input signals and on the synaptic weights is not available, it may be argued that the solution of the direct problem is not of immediate interest for the validation of the model. Conversely, if a few neurons are simultaneously intracellularly recorded, in such conditions that their precise spatio-temporal patterns of firing, in response to various stimuli, can be accessed, it may be of interest to know (1) the minimal network size required to elicit the observed patterns, (2) the sign and the range of the synaptic weights of such a network, (3) the input stimuli that can lead to the observation of the patterns of interest. As a first step into the analysis of this problem, we define the following 'inverse problem': given one or several cyclic attractors, is it possible to find all the combinations (or at least one of them) of both synaptic weights and inputs able to produce this or these attractors? As an example, we consider the recent experimental results obtained by (Wehr & Laurent, 1996) who report intracellular recordings of two output neurons in the locust antennal lobe. We look for a family of networks and of inputs such that two units of the network exhibit responses that are similar to the observed responses. The key point in the derivation is the fact that the conditions that the weights of the network must satisfy to exhibit the desired attractors can be expressed as linear inequalities which are independent on the input signals. Therefore, the derivation includes the following steps:

- derive the set of linear inequalities that must be satisfied in order for the network to exhibit the desired attractors,

- using the simplex algorithm, optimize with respect to some constraints if necessary (for instance, optimize in order to obtain as sparse as possible a connection matrix),
- in input space, find the volume that contains the inputs that may produce the desired responses.

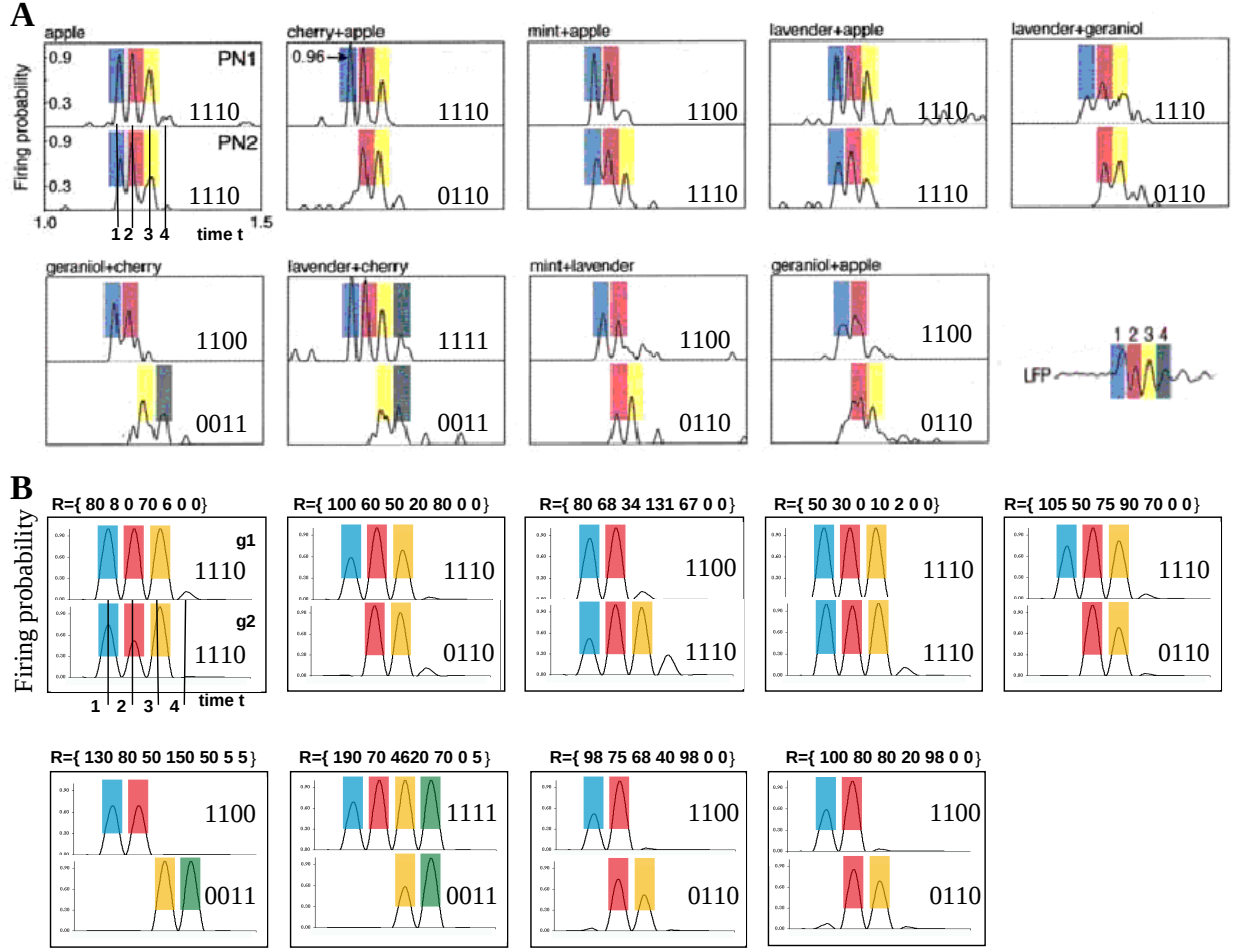
If a specific input is chosen, the techniques developed to solve the direct problem, as described in the previous section, may be used in order to compute the firing probability of the neurons of interest. Figure 2 illustrates a result of the above procedure. Figure 2A (reprinted from (Wehr & Laurent, 1996)) shows intracellular recordings of two projection neurons of the locust antennal lobe, in response to various odorants. The observed neurons fire in synchrony with the oscillations in the mushroom bodies, so that time steps are defined with respect to these oscillations. Each odorant has been applied 21 times, so that firing probabilities can be estimated. A binary code has been defined as follows: the activity in a given time step is taken equal to 1 if the firing probability is larger than 0.3, and it is taken equal to zero otherwise. Figure 2B shows the firing probabilities of two glomerular units of a network of 7 units, as computed by the model (with noise parameter $\varepsilon = 3$); these activities correspond to stable cyclic attractors whose lengths are larger than or equal to 4 time steps. The computed codes are identical to the observed codes.

4 DISCUSSION

We have shown in the present paper that, although the proposed model is simple enough to be analytically tractable, quantitative comparisons with experimental biological data are possible. Moreover, the complex spatio-temporal codes exhibited by the model in the form of periodic attractors, are more robust, with respect to internal noise and to initial conditions, than chaotic models and/or transient spatio-temporal trajectories. The hypothesis of a synchronous dynamics can be justified by the observation of oscillating LFP in the mushroom bodies, which can be interpreted in terms of an "internal clock".

The fact that, thus far, cycles of activity have not been observed during the LFP oscillations (30 to 32 time steps in length) (G. Laurent, personal communication) is not inconsistent with the model: if the number of neurons is large, and if the connections J_{ij} and J_{ji} have no correlation, the length of the cyclic attractors may increase sharply (Gutfreund et al, 1988). Therefore, it may be argued that the observed responses can indeed be parts of long cycles.

Another general concern stems from the use of binary units in the model: are the codes derived from the model still valid if more realistic neurons are implemented in the model, thereby making it essentially intractable? In a recent study (Quenet et al, in prep), we have shown that a network of two Hodgkin-Huxley neurons (simulated with the Genesis simulation software) exhibits the cyclic spatio-temporal behavior predicted by the model made of binary units, *on the whole range of possible inputs*. This is an indication that the codes derived from the model may be robust with respect to the complexity of the basic units of the model.



(A) Temporal evolution of the firing probabilities of two PN's in response to 9 complex odors (Fig. 3 in (Wehr & Laurent, 1996)); the corresponding binary code (as defined in the text) is indicated in each box. (B) Temporal evolution of the firing probabilities of two glomerular units g_1 and g_2 , computed for 9 different excitatory activities of the receptor neurons; these units belong to a model with seven glomerular units with the connection matrix J (shown opposite).

$$J = \begin{pmatrix} 30 & 30 & -87 & 30 & -97 & -50 & 0 \\ 30 & 30 & -37 & 30 & -97 & 50 & -50 \\ 30 & 30 & 3 & 30 & -97 & 0 & 0 \\ 30 & 30 & -91 & 28 & -97 & 0 & 0 \\ 30 & 30 & 30 & 30 & -97 & 0 & 0 \\ 0 & -10 & 0 & 0 & 0 & 0 & 0 \\ -10 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

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