# Temporal coding in an olfactory oscillatory model

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## Abstract

We propose a model of the glomerular stage of the insect olfactory pathway that exhibits coding of inputs through spatio–temporal patterns of the type observed experimentally in locust. Making use of the temporal bins provided by the oscillatory field potential we find that it suffices to employ simple little-Hopfield dynamics to account for a rich repertoire of patterns. In particular, we show that we are able to reproduce complex activity patterns from electrophysiological recordings in insects. Biologically plausible mechanisms of synaptic adaptation are discussed. © 2001 Elsevier Science B.V. All rights reserved

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## 1. Introduction

The existence of neuronal temporal coding has been recently demonstrated in the olfactory system of the locust [4,5,10]. These experiments indicate that any two projection neurons that are co-activated by an odor, are so in specific temporal order. Fig. 1A—reprinted from [10]—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. Neuronal spikes are grouped within temporal bins of order 30–50 msec. In the example of Fig. 1A, four bins were used. Thus the odor identity is encoded in this first computational stage of the olfactory system in a spatio–temporal manner. These observations raise many

interesting questions: how does the neural system convert the sensory information into specific temporal sequences? How does the system generate different spatio–temporal codes for different input signals, or conversely generate similar codes for different inputs? Do such operations require a neuronal architecture that relies on many delay parameters? In the model outlined below, we provide an example of how such temporal codes can be created with just one delay of the single time-step dynamics. Our model acts as a dynamical filter, transforming the odor input into a characteristic spiking sequence. From a set of experimentally recorded spiking sequences, we can derive, with appropriate analytical tools, a family of connection matrices that define a family of models, which can reproduce the experimental data. We exhibit such a model, reproducing spiking sequences reported in [10]. We further discuss biologically plausible learning and unlearning mechanisms that allow the model to exhibit more complex spiking patterns.

## 2. The model

The biological motivations of the structure of the model is described in [7]. For simplicity, we limit ourselves to a binary model, i.e. a unit $i$ in the model may either fire, $s_i = 1$, or be quiescent, $s_i = 0$, in a given temporal bin. The LFP serves to define the clock for some finite duration of $T$ time steps. The activity of the $N$ neurons of the model can be simply compared to the activity of some of the 830 projection neurons in the case of the locust antennal lobe. The model has the following little-Hopfield dynamics

$$S_i(t + 1) = H\left(\sum_j w_{ij} S_j(t) + R_i\right) = H(h_i(t)),$$

where $w_{ij}$ is the synaptic coupling matrix and $R_i \geq 0$ is an external constant input (specifying the odor). $H$ is the Heaviside step function. This model can be readily generalized to account for the presence of noise by considering the stochastic definition

$$\text{Prob}(S_i(t + 1)) = \frac{1}{1 + \exp[-(h_i(t) - \frac{1}{2})/\varepsilon]}$$

It is well known that the deterministic system converges onto a fixed point or a two-cycle [6] when the synaptic matrix $w_{ij}$ is symmetric. For non-symmetric matrices, the attractors may be longer cycles giving rise to complex patterns whose robustness with respect to noise can be investigated in the framework of the Markov chain formalism [8]. With these tools, we can solve either the "direct problem" (given a connection matrix, find the most probable cyclic attractor in response to a given input), or the "inverse problem" (given one or several cyclic attractors, find a set of connection matrices and inputs that allow the model to exhibit these attractors). In the next section, we focus on the inverse problem.

## 3. The "inverse problem": An illustration

As an illustration, we consider the experimental results of Fig. 1A. 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 ones. The key point in the derivation is the fact that the conditions on the synaptic weights can be expressed as linear inequalities
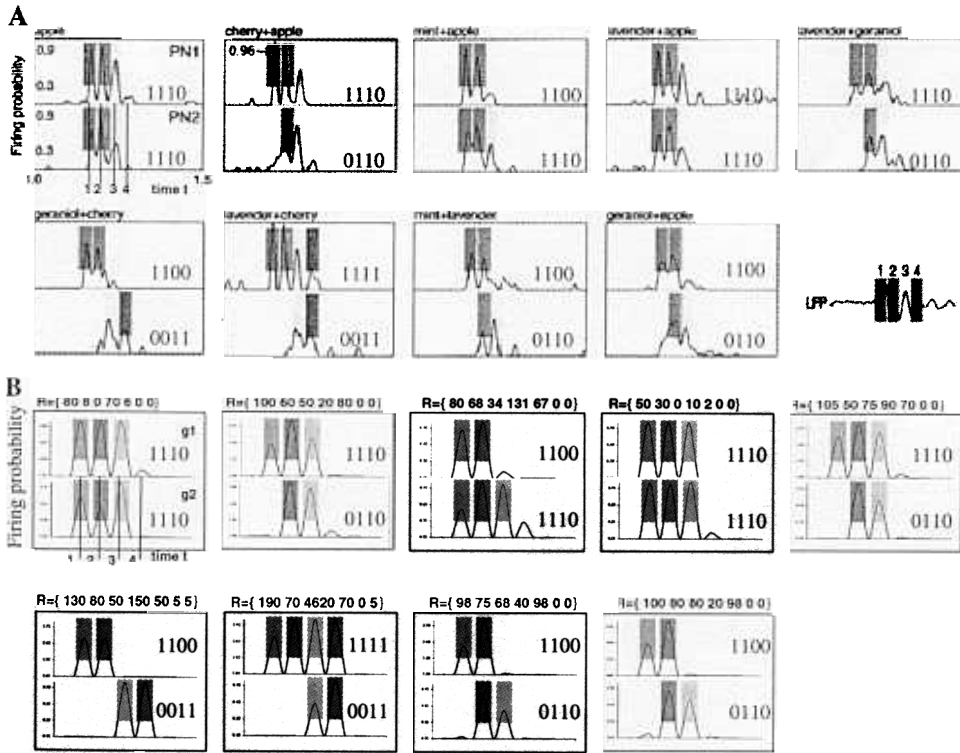


Fig. 1. Firing probabilities of two glomerular units of the model: (A) Temporal evolution of the firing probabilities of two PN's in response to 9 complex odors (Fig. 3 in [10]); the corresponding binary code (as defined in the text) is indicated in each box. (B) Temporal evolution of the firing probabilities of two neurons $s_1$ and $s_2$ in a network of seven units, computed for 9 different excitatory activities of the receptor neurons; these units belong to a model with seven glomerular units with the connection matrix $W$ (given below).

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

that are independent of the input signals. If the inverse problem is "well-posed", i.e. if all the activities of the network are known, the complete set of the synaptic weights compatible with these activities can be exhibited. The inverse problem of Fig. 1A cannot be solved without introducing hidden neurons whose activities are unknown: this inverse problem is "ill-posed". One of the ways of solving such a problem is to generate networks with a large enough number of neurons and adapted synaptic weights in order to identify the desired activities of the known neurons with the activity of some units in the networks.

Fig. 1A displays firing probabilities, as estimated by Wehr and Laurent [10] after applying each odorant 21 times. It includes also binary codes defined by them as follows: the activity in a given time step is taken to be one if the firing probability is larger than 0.3, and zero otherwise. Fig. 1B shows the computed firing probabilities of two glomerular units in a model network of seven units whose synaptic weights and inputs are indicated. The noise parameter was set at $\varepsilon = 3$. The computed codes are identical with the observed ones.

## 4. Discussion

Clearly none of the solutions of Fig. 1B corresponds to either fixed-points or two-cycles that can be generated by symmetric $w$ matrices [6]. They must all correspond to cycles of length 4 or higher. Since the LFP may oscillate for 20 or 30 times before it levels off, and no experimental observations have reported cyclic temporal-coding yet, we have to work with synaptic matrices that generate cycles that are larger than the number of observable temporal bins. Therefore, it is relevant to investigate the generation of matrices leading to arbitrarily large cycles. It was shown [1] that the synaptic matrix in this case is one whose elements are random with zero mean.

As a model of the biological problem we suggest that synaptic connections are developed during an early plastic period when the system is subjected to noisy arbitrary inputs. This training should lead to synaptic connections close to the desired random matrix, after which this matrix is frozen. We may envisage two types of learning principles that are helpful in this direction, one at the synaptic level and the other at the neuronal level. At the synaptic level, a generalized Hebbian rule can be used, taking advantage of LTP and LTD phenomena [11] to unlearn fixed points or short cycles in an unsupervised fashion. Furthermore, at the neuronal level, the constraint of having synaptic matrices with zero mean can be enforced through neuronal regulation [2], a process whereby a pyramidal neuron performs homeostasis, i.e. multiplies all the synapses on its dendritic tree by some factor so that its average excitatory input remains at a preset baseline [9]. To apply it to our problem it would seem natural to separate the synaptic weights into excitatory and inhibitory ones, and constrain their sums to be equal and opposite.

The technology of solving an "ill-posed" inverse problem is currently under investigation. A straightforward approach is building the network step by step, testing after each addition of a hidden neuron the existence of a solution for the synaptic matrix

[3]. A systematic exhaustive search for the minimal set of hidden neurons needed to reproduce the observed behavior is quite complex. In the problem of Fig. 1A we know that the minimal network has to have at least 4 neurons (i.e. 2 hidden neurons), but the minimal solution that we could find this far is of size 5 [3]. The size of the minimal neural network can serve as a measure of the complexity of the spatio–temporal binary code that it reproduces.

To summarize, we have shown that a very simple binary model with unit delays is able to generate complex spatio–temporal patterns in response to fixed inputs. We have been able to reproduce experimental data from the locust antennal lobe. Possible mechanisms of generating matrices leading to arbitrarily long cycles are being investigated.

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