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#### FROM COMPLEX SIGNAL TO ADAPTED BEHAVIOR

A theoretical approach of the honeybee olfactory brain

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## ABSTRACT

The honeybee olfactory pathway is an attractive system for modeling: it is relatively simple, and it is well described functionally and morphologically. Moreover, due to the conservation of the olfactory structure through phylogeny, models may bring information of generic interest. From the point of view of behavior, this system has the ability of encoding the sensory messages into stable representations, and extracting key features from them. The neural bases of these mechanisms are still largely unknown; the purpose of the present paper is to present three different models of the same system, which make use of the same corpus of morphological and electrophysiological data, but which incorporate these data with different levels of details. We show the interrelations between these models and the specific contribution of each of them to the modeling of the olfactory pathway. We show that the design of the simplest model capitalized on the results of the previous ones, and that it suggests mechanisms for simultaneous generation of stable internal representations and key feature extraction.

#### 1. INTRODUCTION

Any system, whether natural or artificial, which has to process signals with high variability in space and time, must make use of robust feature extraction mechanisms, leading to efficient pattern recognition. Since the survival of animals depends critically on fast and appropriate responses to sensory inputs, evolution has selected elaborate neural mechanisms which are not yet fully understood.

#### 1.1. The coding problem

The problem of feature extraction is involved in a more general question about living systems that can be summarized as follows :

How can an input, that may be complex (with a large amount of data) and fluctuating in time, elicit an adapted and stable behavior? Behavior involves both information coding and information storage (and recall). In the present paper, we focus on the coding process, and we investigate possible neural mechanisms whereby a stable behaviour may result from the extraction of the salient features of the stimulus and the generation of a stable internal representation. Symbolically, it can be represented as indicated in Figure 1.





Symbolic representation of the coding problem: an input signal, complex and fluctuating in time may elicit a behavior with a lower degree of complexity and *stable*.

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## 1.2. The olfactory system: why?

Although the goal is to elucidate generic principles which may underlie the information processing mechanisms, it is mandatory to use precise anatomical, neurophysiological and behavioral data as stepping stones towards designing biologically relevant models. Thus, the biological system to be modeled must exhibit general features shared by other living systems, and must be well known experimentally. In this respect, the olfactory system is an attractive candidate. Its discrimination and recognition performances are outstanding : it is determinant for nutrition, reproduction and protection against predators. Moreover, the olfactory signals may be very complex (for example several hundreds of volatile chemicals can be detected by chromatography for a sunflower aroma (Etiévant et al., 1984)), yet the decision based on olfactory information is crucial: the consequences of a mistake can be fatal. It is nevertheless relatively simple, as compared with other sensory modalities. The joint simplicity and efficiency of the olfactory pathway have lead the evolution to conserve its main features through the phylogeny, from invertebrates to vertebrates (Masson & Mustaparta, 1990; Shepherd, 1991; Hildebrand & Shepherd, 1997). The architecture of the olfactory system may be described sketchily as a threelayer structure; of specific relevance to the present work is the intermediate layer (namely, the olfactory bulb and the antennal lobe, in vertebrates and insects respectively), which is known to be involved in contrast enhancement, noise reduction, and feature extraction from the signal transmitted by the receptor cells (Holley & Mac Leod, 1977; Boeckh & Ernst, 1987; Masson & Mustaparta, 1990; Kauer, 1991).

## 1.3. The honeybee: why?

Since the olfactory tracts have common features across species, a better understanding of insect olfaction is of general biological interest and may be relevant to olfaction in general. In this context, olfaction of the honeybee is particularly appealing: (i) honeybee foraging behavior, which is crucial at the levels of both individual and social survival, is based on discrimination among complex odors which is the result of a process involving the extraction and the recall of key features (for a review, see Masson et al., 1993); (ii) in order to gain insight into the mechanisms underlying the extraction of such key features, a set of neurobiological experiments have been performed at various scales of observation, aiming at understanding how the chemical messages are processed (Masson et al, 1995). Capitalizing on the collected data, several simulation or analytical models of the bee antennal lobe have been proposed (Kerszberg & Masson, 1995; Malaka, 1995; Masson & Linster, 1996; Linster & Smith, 1997; Quenet et al., submitted). These simulations suggest mechanisms for feature extraction in the glomerular layer. Computational models of the insect antennal lobe (Rospars & Fort, 1994) and of the olfactory bulb of mammals (Schild, 1988; Li & Hopfield, 1989; Freeman, 1991; Anton et al., 1991; Linster & Gervais, 1996; Linster & Hasselmö, 1997) point to the same direction.

## 2. BIOLOGICAL DATA

#### 2.1. The concept of key features

It has been shown experimentally that the animal may respond by a stable behavior to variations in the composition of the odorant signal (Masson et al., 1993). In addition, experiments show that animals do not react to the whole set of chemicals present in the stimulus (Pham-Delègue et al., 1990), but to the presence, in more or less specific proportions, or to the absence, of specific components of the odorant mixture; the characteristics on which the animals seem to base their discrimination are called "key features" (Pham-Delègue et al., 1993). Hence, two stimuli which are very different chemically, but exhibit the same key features, may elicit similar behaviors, whereas two stimuli which are very similar chemically, but do not have the required key features, will be considered as different by the animal (Pham-Delègue et al., 1991). Taken together, these experimental observations strongly suggest that the extraction of key features is performed together with the emergence of a stable internal representation, robust with respect to fluctuations of the input signal.

## 2.2. The olfactory pathway

## 2.2.1. The 'three-layer structure'

The olfactory system features two subsystems (Shepherd, 1991; Masson & Mustaparta, 1990), namely, the main olfactory system in vertebrates (or generalist system in invertebrates), and the accessory (vomeronasal) system in vertebrates (or specialist system in invertebrates), devoted to the processing and recognition of sexual odorants (pheromones). Here, we focus on the main (or generalist) system only.

In vertebrates and invertebrates, the (generalist) olfactory pathway can be sketchily described as a three-layer system (Holley & Mac Leod, 1977; Masson & Mustaparta, 1990; Kauer, 1991; Farbman, 1992; Laurent 1996):

- the sensory neurons build up the first layer.
- the second layer (the antennal lobe of insects, the olfactory bulb of mammals) features relay neurons, whose connections with the axons of sensory neurons are located in neuropilar structures called 'glomeruli'.
- the third layer is built up of the cortical regions where axons of neurons from the second layer project (mushroom bodies in insects, piriform cortex in mammals).

It is generally admitted that the first layer encodes the olfactory molecular signal into electrical signals which are conveyed to the second layer. In the latter, an internal representation ('olfactory image') is formed, and discriminant features are extracted from the olfactory signal (Shipley & Constanzo, 1984; Royet et al., 1987; Masson et al., 1993; Cinelli et al., 1995; Joerges et al., 1997). Long-term storage of olfactory images is generally considered to take place in the third layer (Masson & Mustaparta, 1990; Bower, 1991; Kauer, 1991; Hasselmö, 1993; Menzel et al., 1991).

#### 2.2.2. The Olfactory Receptor Neurons

Odor transduction takes place primarily within cilia extending from the dendrites of the Olfactory Receptor Neurons (ORN). In the honeybee, these neurons are located in hairs and placodes on the antennas, while in vertebrates, they form a sensory epithelium in the nasal cavity. When an animal inhales odorant molecules, they are fixed (with the help of Odor Binding Proteins -OBP, whose role is still a matter of research -Danty et al, 1997) on receptor proteins set in the membrane of the receptors' cilia. In vertebrates, activation of olfactory receptors induces responses in olfactory receptor neurons via an adenylate cyclase cascade (Sklart et al, 1989) mediated by specific G-proteins (Jones & Reed, 1989). A similar mechanism is very likely to exist in insects (Breer et al, 1988; Prestwich, 1993). Moreover it has been shown that the honeybees have putative olfactory receptor proteins similar to those

of vertebrates (Danty et al., 1994). The mechanisms underlying the initial encoding of general odors in the receptor cells are still poorly understood, and a number of basic questions remain to be solved. Single cell recordings indicate that the antennal olfactory receptor cells of the worker honeybee respond to several olfactory stimuli (Vareschi, 1971; Akers, 1992) like the receptors cells in vertebrates. Yet, a large multigene family encoding odorant receptors on ORNs has been identified (Buck & Axel, 1991), which indicates that odor discrimination may derive, to a large extent, from the differential ligand binding properties of as many as 1000 different receptor types; moreover each odorant receptor gene is expressed by only ~0.1% of the ORNs population, suggesting that each ORN may express only a single receptor type. It is thus possible to define families of ORNs, from the molecular point of view. The ORNs send their axons to the glomerular layer, where they synapse with the dendrites of interneurons in the glomeruli. Molecular investigations also give insight into the topology of the projections of the sensory neurons to the olfactory bulb: it has been conjectured from experimental evidence (Ressler et al., 1994; Vassar et al., 1994) that the axons from sensory neurons expressing mainly a given receptor converge on very few glomeruli, if not a single one.

## 2.2.3. The Antennal Lobe Neurons

The glomeruli are invariant and identifiable neuropilar structures. For instance there are 165 of them in the honeybee, and each of them has a definite, invariant shape and location (Arnold et al., 1985). The first idea about the coding of odors in the glomerular layer was that each glomerulus might be specialized in the recognition of a given odor: it is, for instance, more active (in the sense that the synapses it contains are more active) than the others for that odor. Radioactive tracing experiments have shown that the 'code' at this level is not that simple: for a given input signal (made of pure substances or complex mixtures of molecules, included the odorants that are biologically relevant for the animal, such as the royal pheromone for instance) the activity appears to be widely distributed among the glomerular population, and these patterns of glomerular activities change from one individual to the next (Arnold & Masson, 1987; Nicolas et al., 1993). Nevertheless, the glomerulus is still considered as a functional unit, which is strongly suggested by the above-mentioned molecular results for vertebrates, and also by the relationships between the structure and the function of the interneurons of the antennal lobe in the honeybee (Masson et al, 1993). Local interneurons build up the majority of the neurons in the lobe ( $\sim 90\%$ ), and each category of local neurons (without any axon) and output neurons (with an axon projected to the mushroom bodies) can be subdivided into 2 main types which differ by the spatial distribution

of their branching patterns within the glomeruli (Fonta et al, 1993). All local interneurons are pluriglomerular, but the majority of them (~80%) (localized local interneurons) differ from the others (delocalized local interneurons) by a high density of neurite arborization in one particular glomerulus. Similarly, a part of the output neurons (localized output neurons) have dendrites invading only one glomerulus, whereas the others (delocalized output neurons) are pluriglomerular. From the functional point of view, it has been showed from intracellular recordings (Sun et al., 1993) performed while an odorant -pure or mixture- is applied to the corresponding antenna, that the tendency to respond selectively to odors is expressed only in the category of localized antennal lobe neurons (local and output), as indicated in Figure 2. This might confirm that the related glomeruli represent functional subunits

Figure 2

Sketchy representation of the four different types of honeybee antennal lobe neurons, characterised both morphologically and functionally. The Type A local interneurons and output neurons are the delocalized neurons, with a dendritic tree regularly distributed amongst the glomerular population. The type B local interneurons and output neurons are the localized neuron, with a dense arborization in one glomerulus, exclusive in the case of the output neurons. From the functional point of view, specific responses to odorants are exhibited by the localized neurons only.



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#### 2.2.4. The main functional hypothesis

We have described in section 2.1 the basic observations that we would like to account for, relating the behavior of the animal to the chemical stimulus. The main assumption is the following: the first step of the decision-making process occurs in the olfactory tract, especially at the level of the glomerular layer, where stabilization and key feature extraction are supposed to take place through a spatially and temporally organized activity of the glomeruli. We next focus on three different possibilities to use the ingredients, described in section 2.2, in models of the antennal lobe layer, in order to investigate the emergence of spatio-temporal olfactory images on the 'glomerular pixels'.

## 3. THE MODELS

## 3.1. A few preliminary remarks on modeling

At present, one of the main difficulties in modeling neural networks is the choice of the complexity necessary for the model to account for experimental results. In physics, this difficulty has long been overcome: it is unquestionable that a model of the behavior of a microprocessor does not require modeling the nucleus of silicon atoms. When modeling a neurobiological system, the situation is not that clear, and the level of details which should be taken into account for modeling a given behavior is still a debatable question. Therefore, any model results from a tradeoff between complexity and plausibility: drastic simplifications may lead to models that are - relatively - easy to understand and analyze mathematically, but which are not plausible from a biological point of view; conversely, models including a lot of details may be intractable mathematically, so that they can be investigated only by heavy numerical simulations which are not guaranteed to give any real insight.

Therefore, at the present time, the modeler has to face the challenge of choosing the appropriate level for his model on the scale of complexity versus plausibility, as shown symbolically on Figure 3. The three models that will be discussed here have different positions on this scale. Their presentation is organized chronologically, in order to show clearly how the results of the first one influenced the second one, and how the results of the second allowed to build the third.

#### Figure 3

Building a formal model requires a tradeoff between various requirements.



## 3.2. A synaptic model of the glomerular stage

This model of the honeybee antennal lobe was built in order to be as close as possible to the biological knowledge. It is completely described in (Kerszberg & Masson, 1995).

3.2.1. The ingredients of the model

In this model,

- each glomerulus is viewed as a group of synaptic contacts between receptor cells, local interneurons and output neurons;
- the circuit is built up in a random fashion, for both the neurons' types and synapses' types and weights, with statistical constraints fitting the anatomical data;
- the four types of interneurons are modeled. The huge majority of local interneurons are localized ,i.e. make synaptic contacts mainly within one glomerulus. The others are delocalized, i.e., have synaptic contacts distributed more or less evenly among glomeruli; the same holds true for the output neurons which have an axon;
- the receptor cells form excitatory axodendritic synapses in the glomeruli with the local interneurons only:
- nonlinearities arise at the synaptic contacts between the interneurons, which are described in great detail. They are either excitatory or (in majority) inhibitory, dendro-dendritic or reciprocal, with a probability of release per unit time depending on the local potential of the presynaptic dendrite according to a sigmoid law;
- the signal propagation along the dendrites is assumed to be passive. Each dendrite section is modeled by a cable equation; inside the glomeruli, the synapses shunt the dendrites to the external medium, which is supposed to be isopotential;
- an input signal is modeled by a series of spikes at a given mean frequency along the axons of the excitatory receptor cells. Two different input signals have different mean frequencies along different fibers (distributed among the whole glomerular population).

A simulation consists in solving the differential cable equations with the nonlinear synapses in a given (random) configuration of the synaptic contacts (according to probabilities compatible with the known biological data), without or with input signals.

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## 3.2.2. Computed quantities

The instantaneous averaged potential of all dendrites in each glomerulus;

- the instantaneous number of active synapses in each glomerulus;
- the membrane potential at the soma of the output interneurons;
- the Fourier spectrum of the above temporal signals.

## 3.2.3. Main results

## 3.2.3.1. A complex spontaneous activity

The mean glomerular potentials as well as the number of active synapses exhibit oscillations, with a high density of Fourier peaks, a few of them being higher than the others. Some synchronization occurs between some glomeruli.

#### 3.2.3.2. Effects of input signals

The application of an input A leads the model to oscillate in a different way than in the previous case: some of the 'eigenfrequencies' of the model seem to be enhanced, while others vanish. Note that these 'coding' frequencies are not necessarily close to the mean frequency of the input signal. Another input B applied on different input fibers with another mean frequency leads to an oscillatory behavior based on other eigenfrequencies. Interestingly, the glomerular synaptic activities exhibit inhomogeneities (some glomeruli are more 'active' than the others), which are not the same when A, B or (A&B) are applied, which is consistent with a non-linear 'glomerular representation' of the olfactory input.

Moreover, the membrane potential at the soma of the localized output interneurons also exhibits input-specific responses, consistently with electrophysiological recordings (see section 2.2.3). Finally, the most striking observation concerns the responses of localized output neurons during the application of an input signal : when two (or more) localized output neurons have their dense dendritic arborization in the same glomerulus, the evolution of their somatic membrane potential in time are almost identical.

#### 3.2.4. Transition to the next model

With the same symbolic representation as introduced in section 1.1, the main result brought by this formal model of the olfactory pathway can be summarized in Figure 4. If the principles of the coding can be understood as a sort of selection of some spontaneous dynamical states by the input signal, *the relationship between the input signal and the membrane activities of the local output neurons is intractable: the complexity of their behavior is too high.* A fortiori, this model cannot be helpful in order to find the conditions that input signals have to fulfill in order to lead to a stable behavior of the output neurons.

Nevertheless, the last result mentioned in section 3.2.3.2 is particularly interesting since it gives a *new argument for considering a glomerulus as a 'functional unit'*.

If we want to address the questions of the coding of the input signals and of the transfer of this information to the next step by the localized output neurons, A we do not need to consider more than one such neuronal unit per glomerulus. Extending this argument to the localized local interneuron leads to the second type of model, described in the next section.

#### Figure 4

The symbolic representation of the main results of the synaptic model of the glomerular layer. A) without input signals, its spontaneous behavior is oscillatory with a high number of frequency components. B) With an input signal at a mean frequency, some of the previous eigenfrequencies are enhanced while other vanish.



## 3.3. A simplified synaptic model - towards a neuronal model of glomeruli

This model of the two first stages of the honeybee olfactory pathway includes the receptor layer. The glomerular layer has been simplified in comparison with the previous one: all types of interneurons are represented, but *there is only one unit per glomerulus which models the localized interneurons* (related to that glomerulus) and another unit modeling the localized output neurons. Various versions of this model have been described in (Linster et al., 1994; Linster & Masson, 1996; Masson & Linster, 1996).

## 3.3.1. The ingredients of the model

#### 3.3.1.1. The receptor layer

According to the commonly assumed 'across fiber code' of the peripheral representation of an odor stimulus (Vareschi, 1971; Ackers & Getz, 1993), each

formal receptor neuron models a type of ORNs with similar molecular sensitivity; the different receptor neurons have overlapping molecular spectra. These receptor neurons are thus more or less excited by a mixture of odorants modeled by a vector of binary values (0 or 1). They project to the glomerular layer in the following way: since the number of receptor neurons is smaller than the number of glomeruli in the model, a single receptor neuron send the same excitatory input to several glomeruli (the same number of glomeruli per receptor neuron).

## 3.3.1.2. The glomerular layer

- Each glomerulus is the site of the synaptic contacts;
- the four types of interneurons are modeled in a fixed architecture, with the constraint of having only one localized local interneuron per glomerulus (it receives excitatory inputs from its glomerulus and sends inhibitory inputs to the other glomeruli), and one localized output neuron (it receives excitatory or inhibitory inputs from its glomerulus, depending on the variant of the model); moreover, there is only one delocalized local interneuron and one delocalized output neuron in the whole model;
- there is an additional localized local interneuron which is excitatory with synapses only in its corresponding glomerulus<sup>1</sup>;
- nonlinearities occur at the level of the neurons themselves. A firing probability
  is assigned at each time step to each neuron, as a function of its membrane
  potential at this time; the membrane potential obeys a difference equation
  including a discrete-time integrator of all the inputs to the neuron at this time<sup>2</sup>;
- the receptor neurons form excitatory connections with the local interneurons only (excitatory and inhibitory)
- the synaptic weights and the transmission delays are chosen randomly around mean values.
- an input signal in this model is a vector of M components, equal to 0 or 1, modeling a chemical input signal, mixture of M 'molecules' (1 if the molecule is present, 0 if it is absent) applied to the receptor neurons which, in turn, send an excitatory information to the glomeruli. The chemical input signals, and consequently the receptor activities, are constant in time during a simulation.

<sup>&</sup>lt;sup>1</sup> Such an element can be assumed to exist according to some experiments (Malun, 1991a; Malun,

<sup>1991</sup>b, Kirn & Boeckh, 1994), but without any experimental evidence.

 $<sup>^2</sup>$  From an electrophysiological point of view, the spiking or non-spiking character of a local interneuron is still a matter of discussion.

A simulation consists in solving the differential membrane equation at the soma of the different neurons, taking into account their non-linear firing probability, in the presence or absence of inputs.

## 3.3.2. Computed quantities

- The instantaneous activities of the different neurons;
- the averaged activities of the different neurons.
  - 3.3.3. Main results

#### 3.3.3.1. The similarity between simulated and experimental neuronal activities

The simulated and experimental intracellular 'time-recorded' neuronal activities are comparable from two points of view: the formal delocalized output neurons exhibit a time-dependent activity which is only slightly affected by the application of an input signal, which is consistent with experimental observations. On the contrary, the localized neurons, local (inhibitory) or output, have a clear response (by an increase or a decrease of the spiking frequency, depending on the variant of the model) to the application of an input signal, which is also consistent with the biological data.

#### 3.3.3.2. The emergence of stable patterns of the averaged neuronal activities

Due to the lateral inhibitory connections, localized local interneurons compete with each other. This competition may eventually lead the neurons to a stable pattern of activities, in which some local interneurons 'win' and stay activated and others 'lose' and stay inhibited by their neighbors. These patterns of stable activities have been observed both for the localized local (inhibitory) interneurons and for output neurons (Linster et al., 1994). At this level, it is very remarkable that the patterns of activities of the localized local (inhibitory) interneuron and the corresponding localized output neuron (they intensively invade the same glomerulus) are closely related. Depending on the variant of the model, they are either almost the same (both are highly active simultaneously), or almost in opposition (only one of them is very active)

#### 3.3.3.3. Other results

Three additional results are of interest here. First of all, the effect of the modulation of the lateral inhibition is the following: the higher the lateral inhibition, the sparser (and thus the clearer) the pattern of activity of the output neurons. Then, the variant of the model which considers an inhibitory action on the localized output neuron by its glomerulus leads to neuronal activities whose statistical distributions are close to the experimental ones (Masson & Linster, 1996), the comparison is much better than when an excitatory action is taken into account. Finally, this model can easily

exhibit a property of short term memory, thanks to its assumed excitatory localized local interneuron (Linster & Masson, 1996).

## 3.3.4. Transition to the next model

Figure 5 shows symbolically the main information conveyed by this model about coding. The receptor layer forms an intermediate step of coding which is also represented here. The coding principles are clearer in this case than in the first model: (i) the patterns of activities of the output neurons may be stabilized in response to a stable input signal; (ii) if the output neurons convey the information to the next layer, *the elements that are responsible for the formation of the stable activity patterns are the localized local inhibitory neurons*. Both the activities of these last neurons and the weights of their synaptic interactions determine for the coding pattern.

This model suggests a transition between the expression of the glomerular activity in terms of synaptic activities inside the glomerulus, and the expression of the glomerular activity in terms of spiking activity of its corresponding localized local inhibitory interneuron (which indeed represents a family of such biological cells). This model, however, is still too complex to convey a clear picture of the input-output relationship, which is the only way towards expressing a condition of output invariance. Thus, the understanding of the coding properties of a formal olfactory-like model requires additional simplifications.

From the conclusions drawn from the above two models, one may infer that it might be legitimate to retain in the model the formal localized local interneurons only, each of them modeling now a functional glomerulus. This is the first step towards the third proposed model of the glomerular layer, described in the next section.

#### Figure 5

The specificity of the neuronal model of the glomerular layer is that it shows the possible stabilization of the neuronal activities in response to a stable input. The intermediate signal represented in the figure reminds that the receptor layer is modeled here.





## 3.4. An analytically tractable neuronal model of glomeruli

This model of the honeybee antennal lobe is based on a further simplification of the previous ones. As a consequence, the new model is fully tractable analytically; therefore an in-depth understanding of its coding properties can be gained. A detailed presentation of the model and of its properties can be found in (Quenet et al., 1997)

3.4.1. Ingredients of the model

- As in the previous models, a glomerulus is still the site of synaptic contacts, but it is represented functionally by a single unit which corresponds to its localized local inhibitory interneuron;
- a receptor neuron send excitatory inputs to a single glomerulus and a glomerulus receives inputs from a single receptor neuron: this bijective connection is in accordance with the results of molecular biology obtained in vertebrates, as mentioned in section 2.2.2, assuming that a receptor neuron figures a group of ORNs expressing the same protein on their membrane surface;
- the only formal interneuron modeled here, the localized local interneuron, receives excitatory inputs from the receptor neuron corresponding to its glomerulus and inhibitory inputs from its neighbors. It sends in turn inhibitory inputs to them. It can be called a 'glomerular unit';
- the 'glomerular unit' is a binary unit characterized by a probability of being at 0 or 1 which is a non-linear function of its mean potential, computed by adding all the excitatory and inhibitory inputs it receives. This function is either a sigmoid (thereby modeling the presence of internal noise) or a Heaviside function (thereby assuming that no internal noise is present);
- for simplicity, all synaptic weights between the glomerular units are equal to -1, all delays between neurons are equal to 1; the update dynamics is synchronous;
- an input from the receptor neurons to the glomerular layer consists of a vector of integers proportional to the number of active cells in the families of ORNs represented by the receptor neurons.

A simulation consists in applying an input, stable or changing with time, and in computing at each time step the successive vectors of activity of the glomerular units. However, the essential feature of this model is that simulations are used as illustrations only, since the behavior of the model can be understood analytically.

#### 3.4.2. The main properties

It is known that the steady states of a system of binary units with symmetric connections are cycles of maximum length two (Peretto, 1992). Thus, for a given input, when a steady state is reached, the activity of a glomerular unit, integrated on two update steps, is independent of time. It can also be proved that the glomerular 14

units that oscillate in the steady state, do so in phase. Finally, it is possible to define a two-time Lyapunov function which is a non-increasing function of time, constant in steady states.

When there is internal noise in the model, the dynamics of the glomerular units can be described by a Markov Chain (See for instance Seneta, 1981), whose limit vector of probability of transition between two instantaneous states can be expressed as a Boltzmann-like function of the Lyapunov function of these two states (Quenet et al, 1997.)

3.4.3. The measured quantities

- The activity of the glomerular units integrated during 2 update times;
- the euclidean distances between the vector of the integrated activities and a reference.

## 3.4.4. The main results

# 3.4.4.1. The effects of the lateral inhibition on the coding is completely understood, without and with internal noise.

It is well known that the lateral inhibition introduces competition between the neuronal units, leading to a contrast enhancement of their activities. In the present case, for a model with N glomerular units, we suppose that the receptor neurons have a fixed activity represented as a vector of integer values. This input signal can be viewed as an 'image' of N pixels with N+2 'gray levels' (there is a saturation at N+1). When the steady state is reached, the output consists of cycles of maximal length 2; since the glomerular units are binary, this output may be viewed as a spatio-temporal image with only 3 'gray levels'. The gray level reduction between the input and the output is obtained by thresholding the input to each glomerular unit by two thresholds, which are the same for all glomerular units. The values of the thresholds depend both on the initial glomerular activity and on the input pattern itself. In the absence of noise, a single input pattern may elicit more than one glomerular image, depending on the initial state. In the presence of internal noise, the effect of the initial state vanishes in the steady state, which is the glomerular image that minimizes the Lyapunov function. Note that this minimum can be degenerated. As a consequence, whatever the input vector, for a given noise level, it is possible to compute (without any simulation) the probability of emergence of an output image. Conversely, given an output image, one can find the conditions an input vector has to verify in order to possibly elicit this precise output pattern. In other words, we have now a possible approach to the problem of the invariance of the glomerular activity pattern, as shown in the next section.



## 3.4.4.2. Stabilization and key feature extraction from a sequence of inputs without and with internal noise

A given glomerular activity pattern can be generated by a very large number of input signals on the basis of the amplitudes of the receptor activities. Therefore, if a sequence of such inputs is presented when the corresponding glomerular image is already present, then this image will not change, irrespective of the fluctuations of the inputs, provided the latter comply with the threshold conditions that uniquely define the glomerular image. Hence, the model exhibits *two properties* which are essential in the context of olfaction: when presented with a sequence of inputs, the model *extracts the key features* (in terms of receptor activities) which are common to the stimuli of the sequence, if any, *and, at the same time, produces a stable glomerular pattern* which codes for these common features. These two properties are clearly apparent on the example of Figure 6. Note that the addition of a small amount of internal noise not only does not suppress this very interesting property, but it even allows the system to find the key features earlier than it does in the absence of noise.



#### Figure 6

The properties of stabilization of the glomerular image and key feature extraction. Despite the clear differences between the successive input patterns, common features are present in the whole sequence (high activity of receptor 7 and relatively low activity of receptors 14 and 17). With the deterministic model, after presentation of 7 different inputs, the system *stabilizes* in a spatio-temporal pattern of activity featuring a persistently high activity of glomerulus 7 and a persistent quiescence of glomeruli 14 and 17. The presence of a small internal noise even helps the model to code earlier for the key features mentioned before: in that case the glomerular image appears slightly spoiled.

#### 3.4.4.3. The quasi-linear property of the model with noise

We have seen in the section 3.4.4.2 that a small internal noise leads the glomerular layer to an essentially stable spatio-temporal pattern which codes for the underlying key features of a stable input pattern or a sequence of different inputs. When this noise is high, all the coding properties are blurred out: the glomerular layer becomes insensitive to the inputs. Between these two extreme cases, there is a noise regime where the model exhibits the following property: the mean activity of the glomerular units comes close to the mean activity of the receptors themselves. It is shown by the evolution, versus the noise level, of the distance between the mean activity vector of the glomerular units and the activity vector of the receptors neurons: it exhibits a minimum. It is possible to compare this effect to the well known dithering effect in the signal processing domain (see for instance Sklar, 1988). Thus, a modulation of the noise level, may lead the same model to fit more or less precisely the activities of the receptor neurons, the extraction of key features being performed at low noise level.

#### 3.4.5. Conclusion

The behavior of this model is represented symbolically on Figure 7. Unlike the previous models, this one is simple enough that it allows an analytic treatment of the coding properties, of key feature extraction, and of stabilization when the input signal fluctuates, even within large limits. We have also seen how key feature extraction and stabilization can be considered as two aspects of the same phenomenon, i.e. the dynamical property of the model to reach a stable cyclic attractor; moreover, the conditions on the input signals applied to the model to let it reach a given attractor can be computed (without simulations).

## 4. CONCLUSION

In the present paper, we have presented three models of the olfactory tract, with various degrees of complexity and biological plausibility. The deterministic version of the last model is at the bottom of the scale introduced in Figure 3. The addition of an internal noise has pushed it a notch higher, without sacrificing the analytical approach. The future steps up this scale will be a relaxation of such constraints as the single value of the synaptic weights and delays, and the synchronous dynamics. It may be conjectured that the understanding gained with the present model will be very helpful in understanding the properties of these future versions.

#### Figure 7

The analysis of the simple neuronal model of the glomerular level allows an understanding of its code and an access to a condition of output invariance. It may be viewed as a step towards understanding how an output can be stable while the inputs exhibit a high variability.



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