Coupled map model for spatio-temporal processing in the olfactory bulb

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Abstract. Odor processing in the animal olfactory system is still an open problem in modern neuroscience. It is a common understanding that the spatial code provided by the activity distribution of the olfactory receptor cells (ORC) due the presence of an odorant is transformed into a spatio-temporal code in the mitral cell (MC) layer in the case of mammals, or the projection neurons (PN) in the case of insects, that is decoded later along the neural path. The putative role of the spatio-temporal coding is to disambiguate the stimulus putting it in a more robust representation that allows odor separation, categorization, and recognition. Oscillations due to lateral inhibition among MC's (or PN's) may play an important part in the code as well as neural adaptation. To shed some light on their possible role in the olfaction processing, we study the properties of a simple network model. Upon the presentation of a random distributed input it respond with a rich spatio-temporal structure where two distinct phases are observed. We discuss their properties and implications in information processing.

Keywords: Odor coding, coupled maps.
PACS: 87.18.Sn, 87.19.Bb, 87.19.La

INTRODUCTION

A very important discovery toward full understanding of olfactory coding was the fact that odor stimulation results in activation of patterns of glomeruli (spherical regions of neuropil gathering a huge amount of synapses) distributed across the surface of the olfactory bulb (OB). However, it is not completely clear how these patterns of glomerular activity are transformed by the circuitry of the bulb, or even which are the crucial elements in these circuits.

Fig. 1 shows the basic circuits of the neuroepithelium in nasal cavity and the OB (the antennal lobe of some insects has a similar behavior, although the cells involved are different). The olfactory information starts at epithelium, when odor molecules get in contact with the olfactory receptor neurons' (ORNs) cilia. These neurons are morphologically uniforms, but their molecular phenotype is highly diverse. For this reason, men have about 100 – 200 different kinds of receptors [1] and rodents have more than 1000 [2]. Subsets of neurons expressing the same olfactory receptor are distributed in a (apparently) random pattern across the epithelium. However, ORNs expressing the same receptor converge their axons to one specific glomerulus inside the bulb, exciting dendrites of mitral cells (MCs), tufted cells (similar to mitral cells and not showed in Fig. 1), and periglomerular (PGCs). Then, MCs are going to transmit information to subsequent cortical regions. However, the information passing through glomeruli
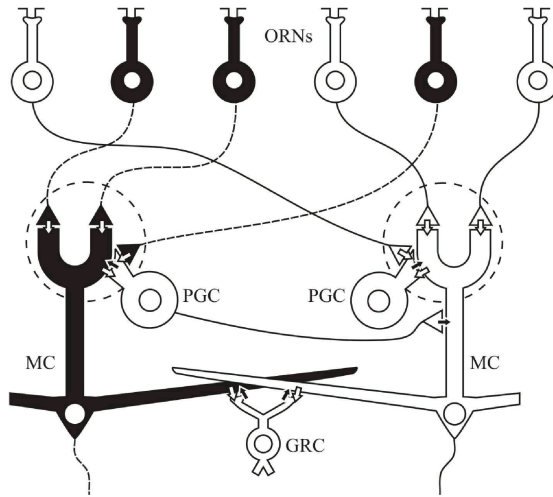
FIGURE 1. Main elements of the olfactory bulb: olfactory receptor neurons (ORN), mitral cells (MC), periglomerular cells (PGC), and granule cells (GC).

and, consequently, through MCs is heavily influenced by dendrodendritic connections between MCs and inhibitory interneurons of the OB.

The dendrites within the glomerulus not only receive the sensory input but are also terminals. The most common patterns are dendrodendritic contacts both from MCs to PGCs (excitatory synapses) and PGCs to MCs (inhibitory).

PGCs are the first type of inhibitory interneuron in OB because it also play an important role in the connection between glomeruli, since the axon of these cells makes inhibitory synapses onto the primary dendrites of MCs (and tufted) as they emerge from the glomeruli. MCs also have dendrodendritic reciprocal connections between their secondary dendrites and dendrites of granular cells (GRCs). These connections follow the same patter of MCs-PGCs synapses, that is, contacts from MCs to GRCs are excitatory and from GRCs to MCs are inhibitory. This kind of connection is responsible for lateral inhibition between glomeruli and MCs and may play an important role in odor coding and neural adaptation [3].

In this work, we investigate the possible function of lateral inhibition and adaptation on the olfaction processing. For this, we study the properties of a simple network model built as a coupled one-dimensional map [4].

MODEL

As said in the previous section, the objective of this work is to examine the role lateral inhibition in odor coding inside the OB. However, it's easy to notice that pure and simple lateral inhibition doesn't characterize a real challenge in terms of codification. This would simply make the most active cell in a group of interconnected neurons fires

constantly while the rest of those neurons would be inhibited. But OB doesn't have just lateral inhibition. Connections between MCs and GRCs (or MCs and PGCs inside the glomerulus) also result in auto-inhibition. Fig. 1 shows that the activation of an inhibitory interneuron always results in an inhibitory stimulus to all MCs connected to this.

Our model is a coupled one-dimensional map, where cells have inhibitory connections to their immediate neighbors (first and last elements are also connected, creating a ring). We consider the case of "extreme inhibition" in the sense that once a cell fires it prevents its neighbors of firing it no matter how strong is their inputs. It is in a sense a local "winner-take-all". This concept is only possible if we are careful about the updating order of the maps. Normally the model of a neuron with continuous input would be a differential equation for the potential and auxiliary variables. Since the neuron has a finite membrane capacitance there is a finite integration time τ between the input presentation and firing. Therefore neurons with larger inputs will fire before and win the competition with their neighbors. To incorporate this feature in a time discrete dynamics we proceed as follows, to decide the state of a network at $t+1$, from its state at t

- Only neurons with inputs $h_i(t)$ above certain threshold will fire at $t+1$;
- The firing order is given by neurons' $hi(t)$, that is, the first neuron to fire is the one with the highest internal value, then the second highest value and so on;
- A specific neuron will fire in a time $t+1$ only if no other neighbor has fired yet in the update process.

The input to a neural cell depends on the sum of the olfactory stimulus and adaptation

$$h_i(t) \;\; = \;\; I_i - a_i(t) \tag{1}$$

We consider, as in [3], that the stimulus is logarithmic with the coverage of the available receptors in the olfactory epithelium. The coverage of a given receptor is proportional to the odorant concentration and its affinity to the odorant. We them write the stimulus as

$$I_i = \xi_i + C \tag{2}$$

where ξ_i is an uniform random variable between 0 and 1 representing the intrinsic affinity of the glomerulus i to the odorant and C is the logarithm of the odor concentration. We call C concentration for simplicity. The adaptation $a_i(t)$, who works as the MCs' auto-inhibition, since we don't have granular cells in our model, varies according to

$$a_i(t+1) \;\; = \;\; a_i(t) \; + \; \delta \, s_i(t+1) - D\left(1 - s_i(t+1)\right) \tag{3}$$

The parameters δ and D are responsible for adaptation (or auto-inhibition) and adaptation recovery, respectively. Therefore, each time a neuron fires, it loses δ from its internal value $h_i(t)$. If this new $h_i(t)$ is smaller than any neighbor's internal value or is smaller than θ, the neuron will not fire and its internal value will be increased by D.
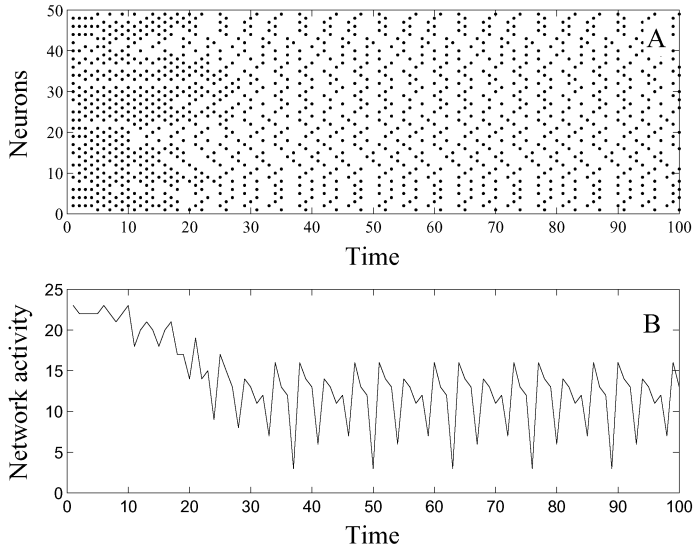
FIGURE 2. Spatio-temporal structure showing two different regimes. In A the raster plot for a network of 50 neurons, in B the corresponding network activity.

RESULTS

Upon the presentation of a random distributed input at certain concentration our network responds with a rich spatio-temporal structure where two distinct regimes are observed: a transient and a periodic regime. It's also possible to split the transient regime in two parts. Fig. 2 shows that during the first steps of simulation some neurons fire constantly since they always win the firing contest. But, as said in the previous section, every time a neuron fires its adaptation (or auto-inhibition) value is increased by δ and, eventually, its $h_i(t)$ will become smaller than its neighbors. At this point, the global behavior of the network will change to the second part of the transient regime where neurons alternate firing with neighbors. This is the check board like structure in Fig. 2A, where neurons spike every other time step. If the adaptation due a spike is larger than the subsequent recovery between spikes ($\delta > D$) the alternating competing neurons will continue to adapt until $h_i(t)$ becomes smaller than θ. The firing rate then decreases since once a neuron goes under the threshold it takes longer to recover back, this reflects in the overall network activity, see Fig. 2B. Eventually the dynamics pushes all neuron inputs to the the interval $[\theta - \delta, \theta + D]$. After that the regime changes from transient to periodic, and the firing pattern gets a specific spatio-temporal structure. Depending on the stimulus the pattern period can be a multiple of a minimal period given by

$$T_m = a + b \tag{4}$$

where a and b are the lowest integers such that $\delta/D = a/b$. Of course, if δ and D are incommensurable the pattern is not periodic. In Fig. 3 we display the distribution for
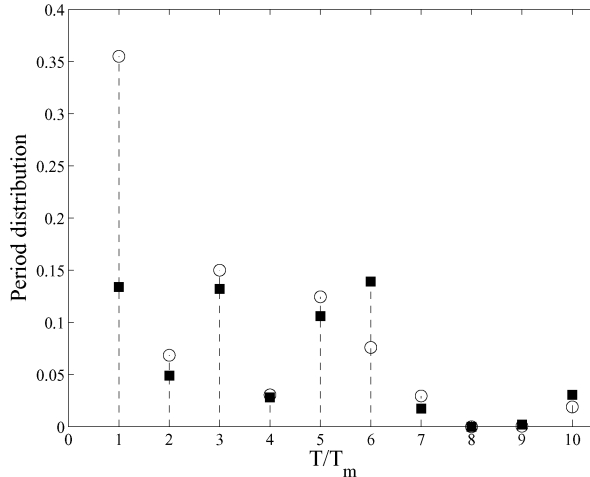
FIGURE 3. Distribution of periods for 2000 random stimuli with concentration $C = 0$ in two networks of $n = 50$ (open circles) and $n = 100$ (solid squares) neurons, $\delta = 0.03$, $D = 0.01$, and threshold $\theta = 0$. Periods for $T/T_m > 10$ are not shown.

the periods obtained upon the presentation of 2000 random stimuli with concentration $C = 0$ to two networks with $n = 50$ and $n = 100$ neurons, and parameters $\delta = 0.10$, $D = 0.03$ and threshold $\theta = 0$. The irregularity in the distribution is not result of poor sampling, and its shape is still a matter of investigation. As the network increase its size from $n = 50$ to 100 the distribution tends to larger periods. We observe that while for $n = 50$ more than 70% of the input stimuli produce a periodic pattern with the minimal period T_m, for $n = 100$ that fraction reduces to less than 30%. Periods for $T/T_m > 10$ are present but we do not display in the graph.

A distribution of periods is certainly a very interesting result for such a simple model. However, if the network is to be a coding stage of a larger network it cannot afford representations that are too wide in time, otherwise the next stage will take too long to process. On the other hand, it is conceivable that for a given pattern with period $T = m T_m$, where m is an integer, not all the neurons have firing periods equal to T. Therefore there are some neurons that are responsible for the larger observed period. If they are few, well before $t = T$ the network already has most of the information that is needed for making a decision. Furthermore if the next stage network has a form of error correction we expect that the effective period of the representation is smaller than T.

In order to investigate that possibility we reprocessed our results introducing a tolerance in the algorithm that finds periods. Basically, we calculate the Hamming distance between two configurations and if it is smaller than the tolerance value, we assume that they are the same. Mathematically, $T(e)$ is a period with tolerance e for a temporal pattern if

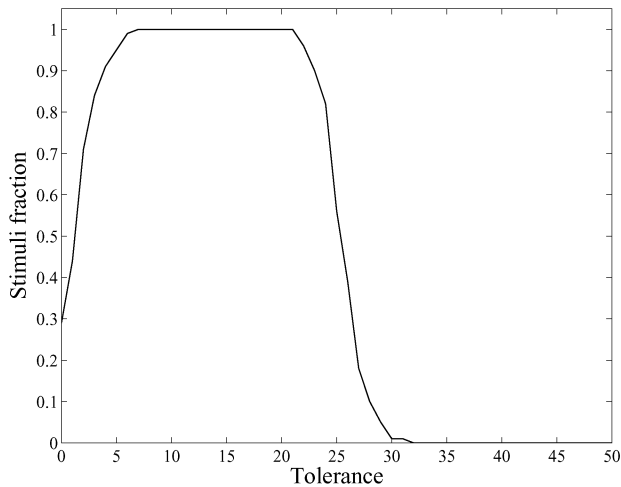$$d_H(\mathbf{s}(t), \mathbf{s}(t + T(e))) \leq e \quad \forall\, t \tag{5}$$

FIGURE 4. The fraction of 100 random stimuli of concentration $C = 0$ that elicit stable periodic patterns with $T = T_m = 13$ as a function of tolerance (in unities of number of cells) for a network of $n = 50$ and parameters $\delta = 0.03$, $D = 0.01$, and $\theta = 0$.

where $\mathbf{s} = (s_1, s_2, ..., s_N)$ is the network configuration and

$$d_H(\mathbf{s}(t), \mathbf{s}(t')) = \sum_{i=1}^{N} (s_i(t) - s_i(t'))^2 .$$

Therefore, the large periodic pattern is just a group of very similar patterns. Fig. 4 shows the fraction of 100 random stimuli of concentration $C = 0$ that elicit stable periodic patterns with $T = T_m = 13$, given a certain tolerance, for a network of $n = 50$ and parameters $\delta = 0.10$, $D = 0.03$, and $\theta = 0$. It indicates that for tolerances between 6 and 20 unities all the stimuli generates periodic patters of firing with the minimal period T_m. Larger tolerances are very permissive, allowing the possibility of detection of smaller periods and eventually for tolerances equal to n the period is 1 for all possible stimuli.

The conclusion coming from Fig. 4 is that if the next stage network is capable of 10% error correction all that is needed it to process the first $2T_m$ time steps after the transient to recognize the pattern.

Another very interesting finding is the effect of concentration. Concentration as modeled here is an additive constant to the stimulus value [3]. As we increase the concentration of the stimuli we observe that there is a sharp transition where all large periods disappear. Fig. 5 shows that for 100 random stimuli and concentration varying from 0 to 2.

This spatio-temporal distribution at the periodic regime is our main concern here, since [5] proposes that OB (and insects' antennal lobe) uses a similar codification for real odors.
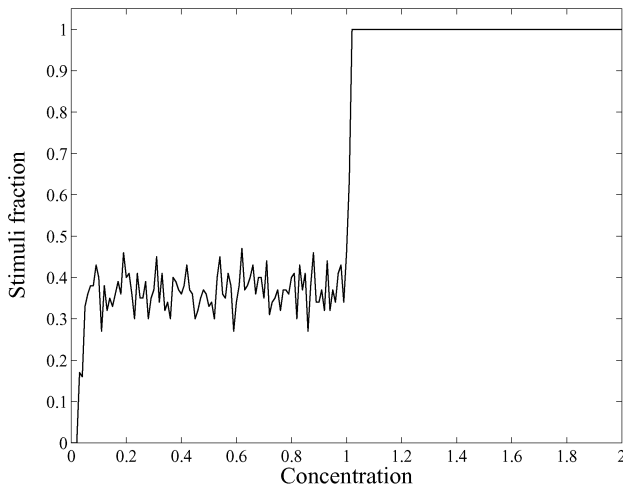
FIGURE 5. The effect of concentration on the fraction of a set of 100 stimuli presenting minimal response period.

CONCLUSIONS

Here we discuss the dynamical properties of a simple network with two ingredients: extreme lateral inhibition and adaptation. The network is a couple-map where each binary neural unity fires depending on its stimulus strength, its internal adaptation state and its competition with the neighbors. We have introduced a update rule where the neurons are updated in order of their input magnitude. Cells that have more input are updated first. This makes the competition between neurons more realistic and interesting since it can result in chain reactions, where the impact of having a neuron released from inhibition can affect neurons many synapses away. This phenomena is more pronounced in one dimensional systems like the one studied in this paper, but it is present in a two dimensional system that is a more realistic model for the olfactory system. In presence of a sustained external (olfactory) stimulus the activity of the network converge, after a transient, to a periodic attractor that can be considered as the network output. The period of the attractor depends on the particular stimulus, and it is always a multiple of a minimal period T_m, determined by the parameters δ and D. For enough tolerance or concentration the activity of the network becomes T_m, independently of the stimulus.

There still much to do to access the relevance of this model for odor processing. The preliminary results show that it produces a rich spatio-temporal response with very well defined transient and periodic phases. Given the model's simplicity the complete understanding on how it comes about is at hand. A rich response, though necessary, is not sufficient to generate a good representation for the odor space. We expect some robustness to noise, and the preservation in the responses of the topological relation of the stimuli. Those will be the next steps on our investigation.

ACKNOWLEDGMENTS

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