Odor interactions and learning in a model of the insect antennal lobe

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Introduction

Insect antennal lobe (AL, the primary processing site in the insect olfactory pathway) has been a subject to multiple recent anatomical, behavioral, and physiological studies. Here, we present a minimal mathematical model that tries to reconcile some of the data across these different levels. We use the model to study odor interactions, as manifested by the antennal lobe cells' responses. We also study how responses in the antennal lobe may be modified by learning.

We show that a model AL with reciprocal modifiable connections between its output neurons (projection neurons, PNs) and a modulatory neuron (VUM, [1]) can produce responses that correspond to well-characterized behavioral phenomena ([5]), even if only spatial odor coding is considered. In contrast to an earlier model by Linster and Smith ([3]), we use the scheme of intra-AL connectivity recently proposed by Sachse and Galizia ([4]).

Model

Each unit in the model represents a projection neuron (PN) whose activity reflects the activity in the corresponding glomerulus:

$$\dot{V} = -g_L(V-V_L) - g_{Na}m_\infty^3(V)(1-n)(V-V_{Na}) - g_K n^4(V-V_K) + I_0 + I_{syn},$$

$$\dot{n} = \phi(n_\infty(V) - n)/\tau_n(V).$$

Here, V is the membrane potential, n is the activation of potassium and inactivation of sodium currents, and $m_\infty(V)$ is the (instantaneous) activation of sodium. Input from olfactory receptors, I_0, and synaptic input I_{syn} are described below.

The units in the model are all-to-all connected with fast inhibition and locally connected with slow inhibition. To create this connectivity pattern we implicitly made the following assumptions: (i) As proposed by Sachse and Galizia ([4]), there are 2 classes of interneurons. One class is GABA-ergic: each cell receives excitatory input from one PN, and sends inhibitory output to all other PNs. The other class of interneurons is histamine-ergic: each cell receives input from one PN and sends inhibitory output locally, with some footprint. (ii) Output spike trains of interneurons are the same as their inputs, i.e. there are no synaptic delays, no bursting, adaptation, saturation, etc.

The receptor input is modelled by setting I_0 of some units to a constant positive (depolarizing) value. Therefore, each odor is characterized by a set of I_0s. In mixtures of odors, if a unit gets input due to two or more components, these inputs add.

All model PNs have reciprocal excitatory connections with modulatory VUM cell. Pairing of an odor with a reinforcement (sucrose) is modelled by injecting a constant depolarizing current into the VUM cell to induce its firing. Simultaneous firing (on tens of milliseconds time scale) of a VUM neuron and of a PN cell leads to an increase of weight of the connection between these two cells. In the absence of reinforcement, weights do not change.

Summary of results

In the present model an odor is coded by a distributed spatial code, i.e. by identity and firing rates of the activated units. But the coding is neither linear, nor time-invariant. For example, as a result of interactions in the inhibitory network, a mixture of two odors may activate units that were not activated by either odor alone. Moreover, the odor representations change as a result of learning, as cells may increase or decrease their activity.

It was suggested recently ([2]) that temporal response features (in particular, transient synchronies of subsets of PNs) are important for antennal lobe odor coding. Our model cells also exhibit transient synchronies: many firings occur near-simultaneously, yet there are no lasting synchronized ensembles. In the model this is achieved by having slow inhibition that tends to synchronize the cells, counteracted by heterogeneity in external inputs and localized connections. Whereas, we do not exclude that fine temporal structure of responses may be important for odor coding, the particular implications of the odor interactions and learning on the temporal patterns still need to be investigated.

To address consequences of odor interactions and learning on model responses, we employ the behavioral paradigms of blocking and overshadowing ([5]). Both paradigms address the question of how well an odor can be learned if other odors interfere with it in the process of learning. The model network can exhibit both blocking and overshadowing, but it does not happen for all odors. The ability or failure of the pair of odors to generate overshadowing and blocking mostly depends on the pattern of olfactory inputs that each of the odors generates and on the pattern of connectivity in the antennal lobe. Examples are demonstrated in figure 1. Here, the firing rate of the VUM cell is considered to represent the quality of learning ([1]). Figure 1 shows the firing rate of the VUM cell in response to the same odor

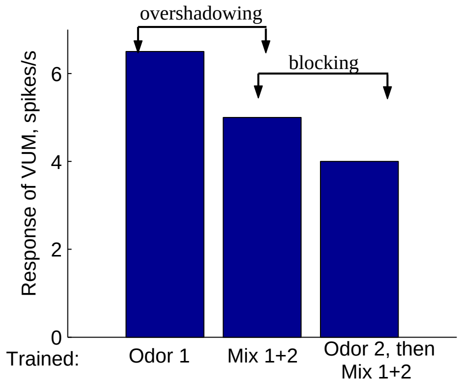

Figure 1: An example of blocking and overshadowing. Responses of VUM cell to odor 1 with three different histories. Substance used for training is specified under the axes. Difference in height between the first two cases manifests overshadowing. Difference in height between cases 2 and 3 demonstrates blocking.

(O1), but with different training histories. In the first case the network has been trained with O1 itself. In the second case the network has been trained with a mixture of O1 and O2, and the response to O1 is diminished, demonstrating overshadowing. In the third case, the network had been pretrained with O2 (to "bias" the connections to that odor) and then trained again with a mixture of the two odors. As a result, the odor 1 has been learnt less than with a pure mixture training, demonstrating blocking.

We use the model to investigate which properties of the odors allow them to produce or not overshadowing and blocking. In particular, we study the role of the relative patterns of inputs from the olfactory receptors that each odor produces, and the structure of the underlying network (e.g., under what conditions and how the presence of GABA-inhibition blocker will affect the odor-interaction).

References

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