

Convergent connections and information loss: how do insects sense odors?

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1 Introduction and Summary

Insects rely predominantly on their olfactory system to sense their environment, locate resources, and move to areas with food. The American cockroach is equipped with relatively long antennae (40-50 mm) covered by roughly 200 thousand olfactory receptor neurons (ORNs). Each ORN carries a specific olfactory receptor (OR) and all receptor neurons bearing the same OR converge on the same functional unit within the antennal lobe (the first olfactory processing centre, analogous to the mammalian olfactory bulb)(Figure 1a-a). Thus, even if the same odorant can be received in different positions along the antenna, the information of the stimulus location may be lost.

Nonetheless, behavioral observations show that cockroaches are able to accurately sense surrounding odors, and then subsequently follow resource gradients towards areas with higher amounts of food. Because ORNs along the entire length of the antenna converge to a single output neuron, creating an “information bottleneck” which seems to lose information about the local spatial distribution of odors, the prevailing hypothesis is that the animal can only determine the direction of resource gradients by continuously moving and re-sampling average concentration levels [Refs needed]. There are many outstanding questions regarding this: Why would a system evolve an architecture that seems to discard environmentally relevant information? How are movement and active sensing strategies used to enhance gradient detection?

We have recently obtained neural recording data that suggests that despite of the convergent neural architecture, the time-dependent stimulus response of both the ORNs and the output neurons may be tuned to enable local gradient detection within ecologically relevant temporal and spatial scales. Strong odorants elicit stronger and faster neuronal responses, and that stimuli originating on antennal portions closer to the head (e.g. 5 mm) take less time to reach the antennal lobe with respect to more distal stimulations (e.g. 45 mm). Hence, gradients with opposite directions (stronger ahead or stronger behind) could be integrated in different ways, thus allowing the cockroach to encode information about the spatial distribution of an odorant.

To understand the mechanisms for odor processing, we propose a theoretical-experimental collaborative project to develop a computational model of the odor detection system of the cockroach. Work on a model began as part of a course project earlier this year, with the course “Computational modeling in neuroscience and systems biology”, which was jointly taught by Jacob Davidson and Jun-Prof. Tatjana Petrov. The funding will support a computer science master’s student as a HIWI to further develop the model, perform simulations that represent common odor detection scenarios and movement patterns of the cockroach, and to incorporate newly acquired data as part of the input structure of the model. Jacob Davidson will lead theoretical development and simulations, and Einat Couzin will lead experimental analysis and advise on incorporating experimental findings into the model.

2 Preliminary results

A schematic of a simplified model structure is shown in Fig 2. The firing rate of the output neuron is v . Each ORN has a firing rate has a time-dependent firing rate $u_i(t)$, which depends on the odor concentration: strong odors elicit a fast response, while weak odors elicit a slow response. In addition, there is a lag time for the signal to travel from an ORN to the output neuron, based on the distance x_i , which represents a location along the antenna.

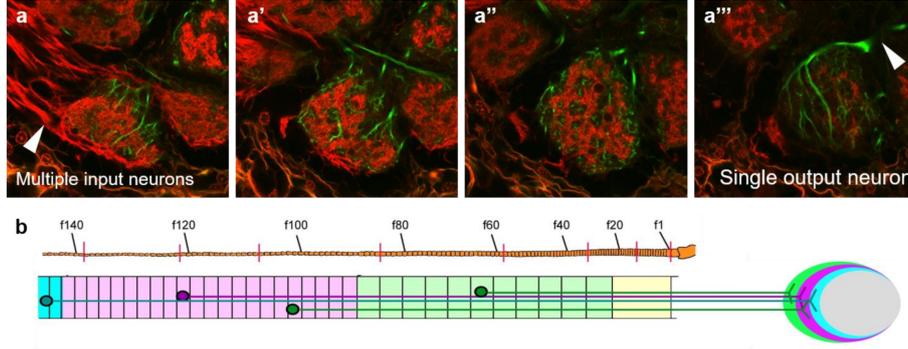


Figure 1: **Neural architecture of the olfactory system.** (a) About 1000 ORNs originating in different antennal segments (red) converge onto a single output neuron (green). (b) ORNs from different location synapse onto different portions of the dendritic compartment of the receiving neuron.

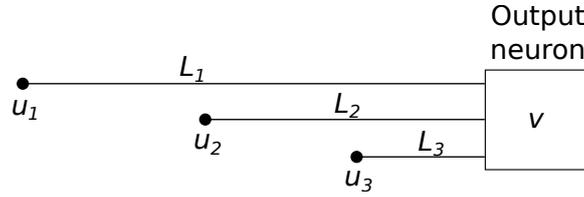


Figure 2: **Model structure.** Multiple input olfactory receptor neurons (ORNs) with firing rates u_j are connected to a single output neuron which has firing rate v . The axial distance L determines the signal lag time from the ORNs to the output neuron.

This model is defined by the following coupled equations:

$$\tau_v \frac{dv}{dt} = -v + \sum_{i=1}^N w_i u_i(t - x_i/\nu) \quad (1)$$

$$\tau_u(s_i(t)) \frac{du_i}{dt} = -u_i + s_i(t) \quad (2)$$

$$\tau_u(s) = \frac{\bar{x}/\nu}{2} + \frac{\bar{x}/\nu}{1 + \exp(\lambda(s - \bar{s}))} \quad (3)$$

where τ_v is the time constant for firing rate changes of the output neuron, ν is the signal transmission speed, w_i are the weights, N is the total number of ORNs, $\tau_u(s)$ is the time constant for firing rate changes of the ORNs which depends on the scent level s , $s_i(t)$ is the time-dependent scent input to ORN neuron i , $\bar{x} = \sum_i x_i/N$ is the average ORN position, $\bar{s} = \sum_i s_i/N$ is the average scent input, and λ is a parameter that describes how much the timescale for changes in the ORN firing rate depends on the scent level.

Setting the sum of the weights to 1, i.e. $\sum_i w_i = 1$, the steady-state response of the output neuron is simply a weighted sum of the inputs: $v = \sum_i s_i/N \equiv \bar{s}$. Using this, we can consider a linear gradient function that depends on the x -position:

$$s(x) = \bar{s} + \frac{1}{N} \sum_{i=1}^N a(x - \bar{x}). \quad (4)$$

By definition, this gives the steady-state output of $v = \sum_i s(x_i) = \bar{s}$. Thus, we can define different gradients, as illustrated in Fig. ??a, which yield the same steady-state output response.

This suggests that the time-dependent response, but not the steady-state firing rate, of the output neuron could be used to distinguish different gradient configurations. To test this hypothesis we simulated a ‘rotation’ of the antennas in a gradient field, where the average odor level stays the same, but after the rotation the gradient along the antenna changes from zero either positive

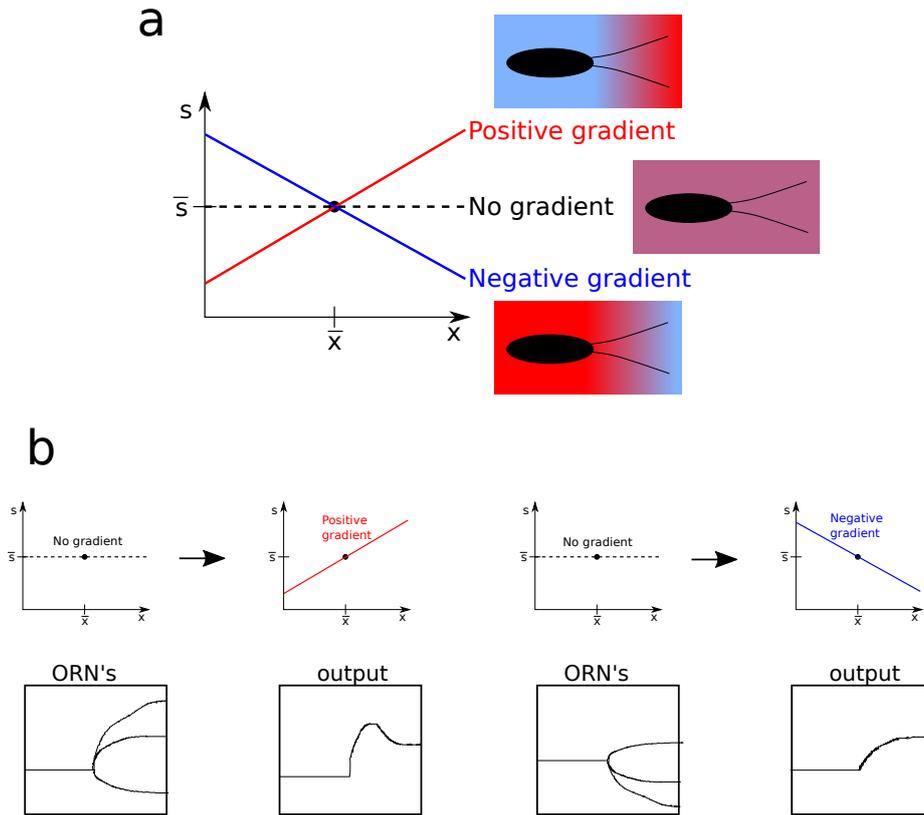


Figure 3: **Preliminary model results** (a) Different gradient configurations (b) Simulation with a change from (left) no gradient to a positive gradient, and (right) no gradient to a negative gradient

or negative. Fig ??b confirms this hypothesis, showing that there can be a difference in the time-dependent response of the output neuron, even if the overall odor level is the same. Thus, in contrast to having to move and sample the ‘average odor level’ to determine a gradient direction, it is possible that the neural properties enable the animal to detect the gradient direction by simply moving its antennas.

3 Planned analysis

The preliminary results suggest that ‘sampling’ movements of the antenna could lead to output that can differentiate gradient direction. However, the results of this simple model depend on tuning of the time and length scale parameters, as well as the nonlinearity of the time-dependent response. In addition, the weights in the model were set equal to 1, for simplicity, and the output was taken as a linear sum. Current experimental work seeks to take recordings of the input odor levels, ORNs, and the output neuron, such that the model parameters and nonlinearities can be directly informed by the data. This also gives the opportunity to use actual recordings from the cockroach ORNs as input to the model, in order to test hypotheses for neural circuit mechanisms. The planned analysis will further develop the computational model to test the sensitivity of gradient sensing to different parameters, configurations, and gradient conditions, incorporate neural recordings from experiments, and constrain input-output properties based on the data.

There are many questions raised by the preliminary results, that we wish to address. How do the timescales of antennal movement and neural activity affect and constrain the gradient sensing ability? What are the limits of gradient configurations, in terms of spatial and temporal properties, that can be accurately detected, and how do these compare with typical environmental conditions? Can nonlinear input-output transformations enhance detection ability, given the constraints of the ‘bottleneck’ architecture? How does noise, in the form of turbulent odor plumes or noisy neural activity, affect detection? What happens if the antenna is damaged?

This project will proceed via a close integration of experimental findings in the computational model. Current anatomical studies are examining synapse size of the ORNs on the output neuron, to ask if connection weights depend on location along the antenna. Behavioral studies with different odor environments will track antennal movement. Electrophysiology experiments yield time-dependent activity of the output neuron ($v(t)$), along with the odor concentrations along the antenna ($s_i(t)$) that elicited this output. We will constrain and modify model structure by the experimental findings, as well as use measured input-output data as a direct test of information processing mechanisms. The proposed collaborative theoretical-experimental project will enable us to ascertain what neural processing mechanisms are needed to distinguish biologically-relevant odor gradients, and to address the evolutionary puzzle of the convergent-divergent anatomical architecture

4 Budget

- 700 euros for conference (include this?)
- * for HIWI, for * months