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

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Abstract

We present a new model of insect antennal lobe in the form of integro-differential equation with short-range inhibition. The learning in the model modifies the odor-dependent input by adding a term that is proportional to the firing rates of the network in the pre-learning steady state. We study the modification of odor-induced spatial patterns (steady states) by combination of odors (binary mixtures) and learning. We show that this type of learning applied to the inhibitory network "increases the contrast" of the network's spatial activity patterns. We identify pattern modifications that could underlie insect behavioral phenomena.
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1. Introduction

Integration across multiple levels of analysis—genetic, molecular, electrophysiological, behavioral—is becoming possible in many biological systems. Because of the complexity inherent in this integration, modeling approaches are becoming increasingly important for representing hypotheses about how different levels interact. An example of how this may be happening is the study of odor interactions in learning of binary mixtures in mammalian and insect olfactory system. Behavioral phenomena must in some way be based on the representations of mixtures and in learning-induced changes to these representations in the antennal lobe of the insect brain (AL; analog of the mammalian olfactory bulb). This hypothesis can now be tested in electrophysiological

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experiments [3]. However, as a first step, it is necessary to investigate what types of odor-related patterns and what changes to them would support our conjecture. We use mathematical modeling to address this question.

Recently, we have developed a minimal spiking model [2] of the antennal lobe that is coupled with the model for the VUMmx1 cell (an identified neuron in honeybee, whose activity is correlated with actual or expected reward, see, e.g. [5]). Olfactory learning is represented in the model by changing the strength of reciprocal connections between VUMmx1 and antennal lobe output neurons. We have shown how activation patterns for mixtures can be modified by learning to produce well-studied behavioral phenomena [2].

In the present paper we consider a different formulation of the model, in which the cells form a one-dimensional continuum and their behavior at time t is described by the activation level $u(x, t)$, which satisfies the integro-differential equation with an inhibitory coupling function. We also introduce a term representing the results of learning. It is proportional to the firing rates in the network in the pre-learning steady state. This model is a very reduced version of the real system, however, it captures the qualitative features of behavioral results and underlies our predictions for physiological experiments.

2. Presentation of the model

We consider $u(x, t)$, the activation at time t of a cell at point x ($x \in \mathbb{R}, t \in \mathbb{R}^+$), to satisfy

$$\frac{\partial u}{\partial t} = -u(x, t) + \int_{-\infty}^{\infty} w(x, y) f(u(y, t)) \, \mathrm{d}y + I(x) + L(x). \tag{1}$$

Models of this kind have been considered in different contexts (e.g. [1,4]) with various assumptions on firing rate and coupling functions, $f(z)$ and $w(x, y)$. We consider three types of $f(z)$: $\max(0, z - a_{\text{th}})$, $H(z - a_{\text{th}})$ (H—Heaviside function), and $1/[1 + \exp(-\beta(z - z_{\text{th}}))]$. We have found no qualitative differences between these cases within the scope of our questions. The coupling $w(x, y)$ is inhibitory ($w \leqslant 0$; for justification see [2]). In simulations and explicit solutions we use $w(|x - y|) = -J/\omega \cdot \max(-|x - y| + \omega, 0)$. The input $I(x)$ is odor-specific, and in this paper it is linear or constant on each of several disjoint intervals, and $\operatorname{supp} I(x) \subset [-I_w, I_w]$. A mixture of odors produces the sum of their inputs. Representation of an odor is the steady-state solution given by the equation

$$u(x) = \int_{-\infty}^{\infty} w(|x - y|) f(u(y)) \, \mathrm{d}y + I(x). \tag{2}$$

We have suggested [2] that learning modifies the strength of mutual excitatory connections between each of the network cells and a special "reward-representing" unit (analogous to VUMmx1 neuron in honeybees [5]),—the higher the cell's activity during learning, the stronger the connection. Therefore, we choose to represent the learning in the activity model in the following way. Let us say that $I_1(x)$ is the input from the

receptors to the network, produced by odor 1, and $u_{ss}^1(x)$ is the corresponding stationary activity pattern. Then, after the odor has been learned (the process itself is not represented in the model), and is presented again in the test trial, each cell in the network will receive additional excitatory input, proportional to the learning-induced strength of connection, which, in turn, is assumed to be proportional to the firing rate of that cell upon the original odor presentation. In other words, for the "naive" network $L(x) = 0$, but for the network that has learned odor 1

$$L(x) = J_L \cdot f(u_{ss}^1(x)),$$

i.e. the learning term changes the odor-specific input to the network for all subsequent odors. The odor representation after learning is the steady state of the network with this new input. Here, for simplification of mathematical treatment we assume that each odor can be learned only once, i.e. the representation corresponding to each particular $I(x)$ can change only once.

Notice that, in contrast to much of the recent work on related models, the connection function $w(\cdot)$ is purely negative; we are looking for a steady-state solution of the inhomogeneous equation (with the input present; as opposed to a solution that persists after the input is gone); and we are looking to see how a steady-state solution is modified in the presence of an additional input of the same type (in the mixture), and in the presence of learning.

3. Results

3.1. Representation and learning of a single odor

Consider Eq. (2), assuming only $w(z) \leqslant 0$, $f(z) \geqslant 0$, and $f(z) = 0$ for $z \leqslant a_{th}$. Let $u(x)$ be a solution of (2). Then for any x, $u(x) = I(x) + \int w(|x - y|) f(u(y)) \, dy \leqslant I(x)$. In particular, if $I(x) \leqslant 0$ then $u(x) \leqslant 0$. Furthermore, if $I_0 = \sup_x I(x) \leqslant a_{th}$, then $u(y) \leqslant a_{th}$, for all y, and $f(u(y)) = 0$, proving that $u(x) = I(x)$. As a consequence, because we are interested in $f(u(x))$ as a manifestation of activity, and when $f(z)$ is zero for $z \leqslant a_{th}$, we can limit our consideration to $x \in [-I_w', I_w']$, where $I_w' = \sup\{|x| : I(x) > a_{th}\} \leqslant I_w$.

Next, we show that for f as above, and for a small enough inhibition, the steady state solution is unique, for any bounded input $I(x)$.

Proposition. *Assume $w(z) \leqslant 0$, $|I(x)|$ is bounded, f is Lipschitz with constant c, and $f(z) = 0$ for $z \leqslant a_{th}$. If*

$$cW_I = c \cdot \sup_x \int_{x - I_w'}^{x + I_w'} |w(z)| \, dz < 1, \tag{3}$$

then Eq. (2) has a unique solution $u(\cdot) \in L^\infty(\mathbb{R})$.

Proof. Consider the operator $K_I : L^\infty(\mathbb{R}) \to L^\infty(\mathbb{R}) : K_I u(x) = \int w(|x - y|) f(u(y)) \, dy + I(x)$. Using properties of f, $K_I u(x) = \int_{-I_w'}^{I_w'} w(|x - y|) f(u(y)) \, dy + I(x)$. By the Lipschitz
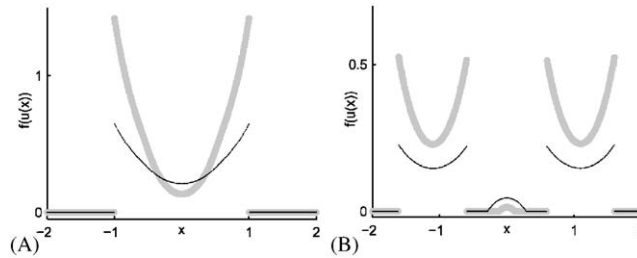
Fig. 1. Response to a single odor before (black) and after (gray) learning. Parameters used: (A) $I(X) = 2.5\mathbb{1}_{[-1,1]}$, $\omega = 1.5$, $J = 2$, $J_L = 2$, $a_{th} = 1$; (B) $I(X) = 1.1\mathbb{1}_{[-0.5,0.5]} + 1.4(\mathbb{1}_{[-1.6,-0.6]} + \mathbb{1}_{[0.6,1.6]})$, $\omega = 1$, $J = 2$, $J_L = 2$, $a_{th} = 1$.

assumption one has

$$|K_I u(x) - K_I v(x)| \leqslant c \int_{-I'_w}^{I'_w} |w(|x - y|)| \, |u(y) - v(y)| \, \mathrm{d}y \leqslant cW_I \cdot |u - v|_\infty.$$

Since $cW_I < 1$, K_I is a contraction on $L^\infty(\mathbb{R})$. The Banach fixed point theorem concludes the proof. □

Condition (3) above can be replaced by the weaker one: $2c \cdot I'_w \sup|w| < 1$. In the case $w(|x - y|) = -(J/\omega) \cdot \max(-|x - y| + \omega, 0)$, condition (3) becomes $cJ(\omega\mathbb{1}_{\omega < I'_w} + (2I'_w - (I'_w)^2/\omega)\mathbb{1}_{\omega \geqslant I'_w}) < 1$, where $\mathbb{1}_A$ is the indicator function.

Even though the above analytical result is only valid under certain assumptions on $w(\cdot)$, I and f, our numerical experiments show that the solution is unique and stable for larger values of W_I and for other types of f. Fig. 1 show examples of response to one odor with 1 and 3 input intervals.

The learning mechanism "increases the contrast" in the firing pattern (Fig. 1A). Namely, it rewards the cells that have already been more active than their neighbors, and they, in turn, inhibit the cells that have been less active. As a result, some of the cells will increase or decrease their firing rate, and spots of firing can appear or disappear with learning (Fig. 1B).

3.2. Representation of a binary mixture

Let us consider odors with inputs $I_1(x)$ and $I_2(x)$ and their mixture with $I(x) = I_1(x) + I_2(x)$. If the intervals where inputs are non-zero are further away from each other than the extent of the inhibition then the odors do not interact, and the response to the mixture is the union of the component responses. However, if the inputs are closer, the mixture representation can have parts that are specific for each of the components, as well as parts that are specific for the mixture. An example of this is shown in Fig. 2A: firing rate representations of odors 1 and 2 (insets) do not overlap, but the mixture evokes activity in intermediate region, which was silent for either of the components. Sometimes the mixture-specific part of the response can be dominant.

We have proposed in [2] that this effect underlies the behavioral phenomenon of transs-witching—when the animal learns to respond to the mixture as a unit, distinct from its components.

Our simulations show that two odors produce a distinct mixture if: each of the odor representations has silent units—neurons that get the receptor input, but are inhibited by their neighbors; the silent units for each odor overlap; the combined input to over-lapping silent units is large enough. If these conditions are met, then the silent units do not participate in representation of the components, but, in the mixture, they will be getting the combined input from the components, and can become active and suppress their component-specific neighbors.

3.3. Learning binary mixtures

As we mentioned in the previous section, if the mixture-specific part is dominant in response to the mixture, it will be emphasized during learning, and the resulting representation can serve as a substrate for transswitching. In contrast, if the pattern, specific to one of the components is dominant (odor 2 in Fig. 2B), then, during learning, this dominance is reaffirmed (gray curve in Fig. 2B), and this provides the basis for another behavioral phenomenon—overshadowing. Overshadowing means that after the mixture is learned, the response to one of the components in the test trial is reduced
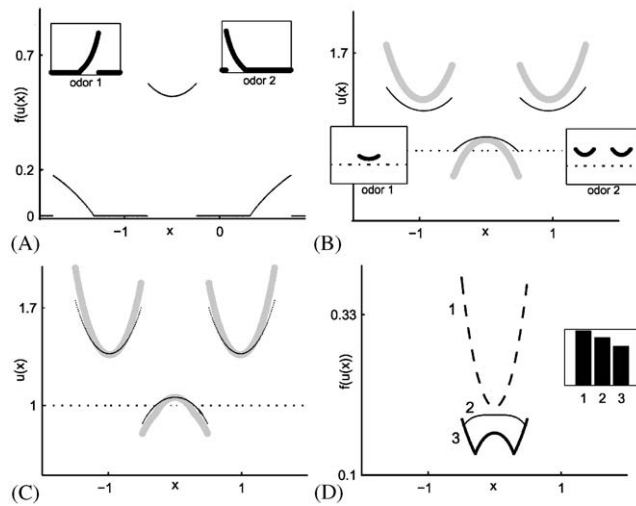

Fig. 2. Responses to mixtures. (A) Mixture with component-specific and mixture-specific parts. Insets: $f(u(x))$ for the components. $I_1 = 1.1 + 0.2x \cdot \mathbb{1}_{[-0.75,0.75]}$, $I_2 = 1.1 - 0.2(x+1)\mathbb{1}_{[-1.75,-0.25]}$, $\omega = 1$, $J = 2$. (B–D) A mixture with odor 2 dominant. $I_1 = 1.4\mathbb{1}_{[-0.5,0.5]}$, $I_2 = 1.8(\mathbb{1}_{[-1.5,-0.5]} + \mathbb{1}_{[0.5,1.5]})$, $\omega = 1$, $J = 2$, $J_L = 2$, dotted lines are $u = a_{th}$. (B) Mixture response before (black) and after (gray) learning. Insets: $u(x)$ for the components, dotted line is $u = a_{th}$. (C) Same as B, but odor 2 is pre-trained. (D) Response to odor 1 ($f(u(x))$) in the test trial with different training histories: odor 1 trained (1); mixture trained (2); odor 2 pre-learned and then mixture trained (3). Inset: total network activity in each of the cases.

(difference between cases 1 and 2 in Fig. 2D). It follows from our simulations that for two odors to produce overshadowing it is sufficient that: regions of inputs for the components have little overlap, but they are within the range of inhibitory connection from each other, and the input for one of the components is stronger.

The next situation we consider is when, in a configuration similar to the case of overshadowing, odor 2 is first learned alone. In this case the system becomes biased to odor 2 response pattern. Consequently, in the response pattern for the mixture (black curve in Fig. 2C) the component specific to odor 2 is even more dominant, i.e. the mixture response is closer to the response to odor 2 alone. This is further emphasized by the subsequent learning of the mixture (gray curve in Fig. 2C). We suggest that this is the basis for the behavioral phenomenon of blocking (the response to odor 1 after learning the mixture is further reduced by pre-learning of odor 2—difference between cases 2 and 3 in Fig. 2D).

4. Conclusions

We have introduced a reduced model of the insect antennal lobe with a learning term that is proportional to the firing rates of the network in the pre-learning steady state. We show that this type of learning applied to the inhibitory network "increases the contrast" of the network's spatial activity pattern by accentuating the differences in firing rates between neighboring groups of cells. We also show that the response pattern for a binary mixture can consist of several parts: regions that are specific to each component, regions that represent both components (overlap) and regions that are unique to the mixture (mixture-specific). Depending on which of these parts is dominant, it can provide neuronal basis for different behavioral phenomena—transswitching (mixture-specific part is dominant), overshadowing and blocking (part, specific to one of the components, is dominant).

Acknowledgements

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