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Computational models to understand decision making and pattern recognition in the insect brain

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Abstract

Odor stimuli reaching olfactory systems of mammals and insects are characterized by remarkable non-stationary and noisy time series. Their brains have evolved to discriminate subtle changes in odor mixtures and find meaningful variations in complex spatio-temporal patterns. Insects with small brains can effectively solve two computational tasks: identify the presence of an odor type and estimate the concentration levels of the odor. Understanding the learning and decision making processes in the insect brain can not only help us to uncover general principles of information processing in the brain, but it can also provide key insights to artificial chemical sensing. Both olfactory learning and memory are dominantly organized in the Antennal Lobe (AL) and the Mushroom Bodies (MBs). Current computational models yet fail to deliver an integrated picture of the joint computational roles of the AL and MBs. This review intends to provide an integrative overview of the computational literature analyzed in the context of the problem of classification (odor discrimination) and regression (odor concentration estimation), particularly identifying key computational ingredients necessary to solve pattern recognition.

Keywords

Learning; Pattern recognition; Mushroom body; Antennal Lobe; Plasticity

1. Introduction

Decision making is a central process in the brain, enabling living systems to identify objects and scenarios, choose among alternatives, and decide how and when to react [1, 2, 3, 4, 5, 6]. Survival depends on the ability to make decisions and its adaptation to different environments. Such processes commonly rely on two critical components [7]: (i) the prediction of environmental changes (regression), and (ii) the recognition of patterns to discriminate situations (classification). Both functions are solved based on the information obtained by sensory circuits. This sensory modality, present in all forms of life, is central for a wide range of tasks in the insect brain and takes a major share of the neural circuits [7, 8].

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The nature of the olfactory stimulus is stochastic and non stationary: wind transports gases by turbulent flows that induce complex filaments [9, 10, 11] (see Figure 1). Although pattern recognition of gases is challenging for modern artificial sensors [9, 12], evolution has provided even the simplest nervous systems with the ability to extract all necessary information for survival by exploiting the random nature of the stimuli [13, 14].

Our goal here is to review the state of the art in computational models in insect olfaction related to decision making functions. Since the main centers of learning and memory are the Mushroom Bodies (MBs) [16, 7], this review will mostly concentrate on relating the Antennal Lobe (AL) and MB functions.

2. Antennal Lobe function: feature extraction

Thanks to the simplicity of the structural organization, the nature of the neural coding, genetic manipulation techniques, and extensive odor conditioning experiments, the main brain modules involved in olfactory pattern recognition have been identified: the Antennae are sensors, capturing odor information through olfactory receptor cells; the ALs and MBs are respectively feature extraction and pattern recognition devices. Specifically, the AL receives input from the receptor cells that deliver the information into particular sets of glomeruli [17], constructing a genetically-induced chemosensory map that remains the same across individuals from the same species [18, 19]. In principle this peripheral olfactory structure already seems to be able to discriminate among odors at this early stage [13, 20, 21, 22]. However, since the insect is freely moving as odor plumes flow through the air, the signal arriving at the AL is noisy and non-stationary [13] (see Figure 1).

Computational models using realistic AL neuron models claim that odor identity can be encoded quickly for pattern recognition purposes, while the concentration is encoded by the mean latency of the neural response [14]. Moreover, many experiments have demonstrated the presence of spatio-temporal patterns in the first stage of the olfactory system of invertebrates and vertebrates [23, 24, 25, 26, 27], resulting from balanced excitation and inhibition in their network [28, 29, 30]. Even though mammals and insects can recognize odors fairly quickly [31, 32, 33], temporal coding is also present to improve discrimination performance and odor concentration estimation [34, 32, 35, 36, 11].

This spatio-temporal coding regulated by an excitation-inhibition balance in the AL is controlled by Projection Neurons (PNs), which are excitatory, and Lateral Neurons (LNs), mostly inhibitory. PNs and LNs communicate through glomeruli [37, 38, 39, 40] and have been thoroughly modeled over the past few years to investigate robust and reproducible spatio-temporal coding [14, 41, 42], concentration estimation [41, 14], contrast enhancement mediated by lateral inhibition [43], gain control mechanisms [44, 45, 46], and information filtering [47, 48]. There is an agreement that the inhibition provided by the LN neurons improves neural code to make the discrimination task easier. We also know that the inhibitory network is capable of expanding the coding space using spatio-temporal patterns. Yet, we are still lacking the connection between the AL code and the MB function.

3. The computational blueprints of the Mushroom Bodies

Even in honeybees, insects with no more than a million neurons [8], 35% of its neurons are in the MBs. The MBs integrate multimodal information (idea used in computational models [49]) and are at the focal point of learning and memory [50, 51, 16]. They also undergo significant synaptic and neural changes mediated by behavioral odor conditioning experiments [52, 53, 33].

Before reaching the MBs (see Figure 2), the olfactory information travels from the Antenna (representing 20% of the insect brain) to the AL, which connects the receptor cells to the MBs and constitutes only 2% of the insect brain. Thus there is a compression of information from the sensors to the AL. Subsequently, there is an inflation of sensor information from the AL to the MBs (see Figure 2).

An effective approach to use this information and understand how the insect brain solve pattern recognition problems consists of using a combination of Hebbian learning and mutual competition via inhibition [54, 4, 44, 55, 56, 49], a broadly accepted paradigm [57, 58]. The inhibition leads to competing trends in the output neurons, where the classification is poised at the “winning” neuron(s) (see the output layer in Figure2) . Connectionists models predicted the need of 75 strong lateral inhibition in the output layer of the MBs for classification [59, 54]. Later experimental observations confirmed its presence in the β -lobe neurons in the MBs of the locust [60].

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Another interesting hypothesis is that the MBs are a large screen where one can easily discriminate objects using sparse neural code [61, 62]. The Kenyon cells (KCs) form a projection screen where simple linear discriminants can be used to better classify odors. The idea of using a projection into a large screen for improving discrimination is an old well established idea proposed by Thomas Cover in 1965 [63] and was later also used in Support Vector Machines (SVMs) [64]. Moreover, these screen-like neural structures may be also present in mammalian hippocampus [65].

Simple connectionist models with simplified neurons[66] are often sufficient to understand the roles played by the connectivity, sparse coding, and competitive inhibition. In this framework, the computational problems can be formulated in simple mathematical terms and are amenable to analytical investigation. More specifically, these models are adequate to determine the limits in performance for pattern recognition, estimate optimal connectivities, and calculate the best sparse activity levels in the MBs as shown in [4, 59, 67, 68, 56]. Nevertheless, these connectionist approaches fail to capture the rich dynamical behavior

generated in the AL, which, for example, may be important to estimate the concentration levels. In summary, temporal integration and resolution in the MBs still remain elusive. The integration of the spatio-temporal properties of the AL with continuous models of the MB capable of decoding the random nature of the input is a computational problem capable of providing insightful hypotheses for future research.

4. Mushroom Body function: Pattern Recognition

For illustration purposes let us show how connectionist approaches do indeed solve pattern recognition problems. In [59, 54, 4] a basic model of learning in the MBs based on mutual inhibition in the output layer was proposed. Each component of the N_O -dimension output vector $\mathbf{z}$ of the MB (Figure 2) is

$$z_l = \Theta \left(\sum_{j=1}^{N_{KC}} w_{lj} \cdot y_j - \mu \sum_{k=1}^{N_O} \sum_{j=1}^{N_{KC}} w_{kj} \cdot y_j \right) = \Theta(\hat{z}_l), \quad (1)$$

with $l = 1, \dots, N_O$ and $\hat{z}_l$ being the synaptic input to the l -th output neuron. The function $\Theta(x)$ is a non-linear step function, which defines the spiking threshold. The N_{KC} -dimension vector $\mathbf{y}$ represents the KC state, and μ denotes the inhibition level among output neurons. The $N_{KC} \times N_O$ connectivity matrix is subjected to a “stochastic Hebbian” learning [69, 70, 71] (see Figure 2). The mutual inhibition and Hebbian learning can jointly organize a non-overlapping response of the decision neurons [59, 4].

To implement learning in computational models we need to be aware of the reinforcement mechanisms. A particular set of huge neurons innervate the MBs and receive direct input from gustatory areas [72], which are critical for memory formation [7, 73]. They remain active for long periods of time releasing neuro-modulators into not only the MBs but also the AL and other areas of the brain. They are commonly modeled by a reward signal and different computational approaches converge into a similar formulation [74, 75].

Using the model in [4], we applied this system to a public dataset of recordings from chemical sensors (see Figure 1) [76]. We present our results in Figure 3. Given that the learning rule is stochastic, each point represents an average value. We show that the accuracy for odorant recognition increases with the brain size, reaching $\sim 94\%$. Not unlikely some networks can reach 97%, comparable to the performance of a state-of-art SVM technique ($\sim 99\%$). Moreover, we tested how robust this performance is against the impairment of MB cells: only after more than 90% of the MB is damaged there is a notable drop in performance. Thus, once the insect brain has been trained, damages to MB should not degrade its performance significantly.

Additionally, from equation (1), the synaptic input $\hat{z}_k$ arriving into the k -th output neuron can be compactly written as

$$\hat{z}_k(\mathbf{x}) \equiv \hat{z}_k(\mathbf{y}) = \langle \mathbf{w}_k, \mathbf{y} \rangle - \mu \sum_l \langle \mathbf{w}_l, \mathbf{y} \rangle, \quad (2)$$

with $\mathbf{w}_k = (w_{k1}, w_{k2}, w_{k3}, \dots)$. This equation can be situated in a SVM formalism [77, 78], in which the solution is a particular combination of weights (synaptic connections) $\{w_{kj}, j = 1, 2, 3, \dots\}$ can be optimized to solve odor classification. The learning algorithm is also guided by reward/penalty signals but the key differences lie in the manner the synaptic changes are applied. In the SVM formalism the synaptic changes due to reward signals are applied only if the odor is not well classified over an arbitrary margin.

5. Discussion

An insect, during the decision making process, requires to know at least three important pieces of information to choose an action: odor identification or pattern recognition (what food), estimating concentrations (how much food), and distance to source (how far). The odor discrimination function is employed to know whether the odorant is of interest to the insect, the problem of regression or odor concentration estimation is required to know how much food is available to harvest, and the distance is central to evaluate if the effort of searching the source is cost effective. Mechanisms involved in solving these three functions together remain scarce. Nevertheless, we have integrated the current knowledge on computational insect olfaction that can be relevant for pattern recognition purposes, particularly identifying the mechanisms underlying decision making.

Computational models based on the MB architecture can be helpful to make hypotheses. For example, connectionist models predicted that strong inhibition in the output of the MBs and Hebbian learning from the Kenyon cells (KCs) to the output layer were critical for pattern recognition. These theoretical requirements, which are widely used in computational models, were later empirically verified in the MBs [54, 60]. It can be also used to understand memory resilience in brain circuits subjected to trauma and strong perturbations. Computational models provide a unique way to test the sources of brain resilience. As an example, we provide evidence that the main source of resilience may lie in the MBs. In Figure 3 the model shows that killing KC neurons does not impair the ability to classify odors unless the massive neural damage is present.

On the other hand the question of how to incorporate time integration effectively into realistic MB models for pattern recognition is still challenging. There are quite many dynamical models for the AL investigating problems like neural coding, time decorrelation, gain control, and even classification using machine learning algorithms. However, there is a gap to achieve an integrated model of AL and MBs using the characteristic spatio-temporal code observed in their neural activity. We are also missing a model that combines all three basic odor components (what odor is present, how much odor there is, and how far the source is) into a unique decision making device. This means that we are still scraping the surface of the computational power of the insect brain.

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Figure 1.

Time series recorded using artificial sensor arrays designed for discriminating volatile organic compounds and quantifying concentrations in a wind tunnel. **Left:** Dataset from an array of 72 metal-oxide gas sensors in presence of carbon monoxide, publicly available at UCI Machine Learning Repository [9]. **Right:** example of the traditional three phases sampling process applied under controlled conditions (shown on top) and a few time series recorded by a mobile robot in an uncontrolled environment (bottom)[15].

Figure 2.

To construct a simple model for pattern recognition based on the insect brain architecture, one can consider four main populations of neurons: (i) the olfactory receptors in the Antenna, the Antennal Lobe (AL) that filters, compresses and decorrelates information; (ii) the Kenyon cells in the Mushroom Body (MB); and the output neurons, where the decision take place. As the figure depicts, the AL is much smaller than the other two populations. The red lines in the output layer of the MB represents mutual inhibition, which creates a competition important to form responsive group of neurons to a particular stimulus set. The green lines, innervation from KCs to the output layer, are subject to Hebbian learning in most models (see Section 4).

Figure 3.

An example of a hypothesis generated by the computational models. A connectionist model as given by equations (1) is applied to a real dataset of chemical sensors exposed to 10 odorants at different concentrations [76]. The accuracy is defined as the fraction of right answers in a test dataset. **Left:** performance during the classification of odor type when the number of Kenyon Cells increases, indicating that larger brains can learn more. **Right:** accuracy as function of random elimination of Kenyon Cells. 90% damage level needs to be reached before the accuracy sharply drops. This fan-out structure of the MBs provides natural resilience to biological damage.