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

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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.

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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 [1–6]. 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].

The nature of the olfactory stimulus is stochastic and non-stationary: wind transports gases by turbulent flows that induce complex filaments [9–11] (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].

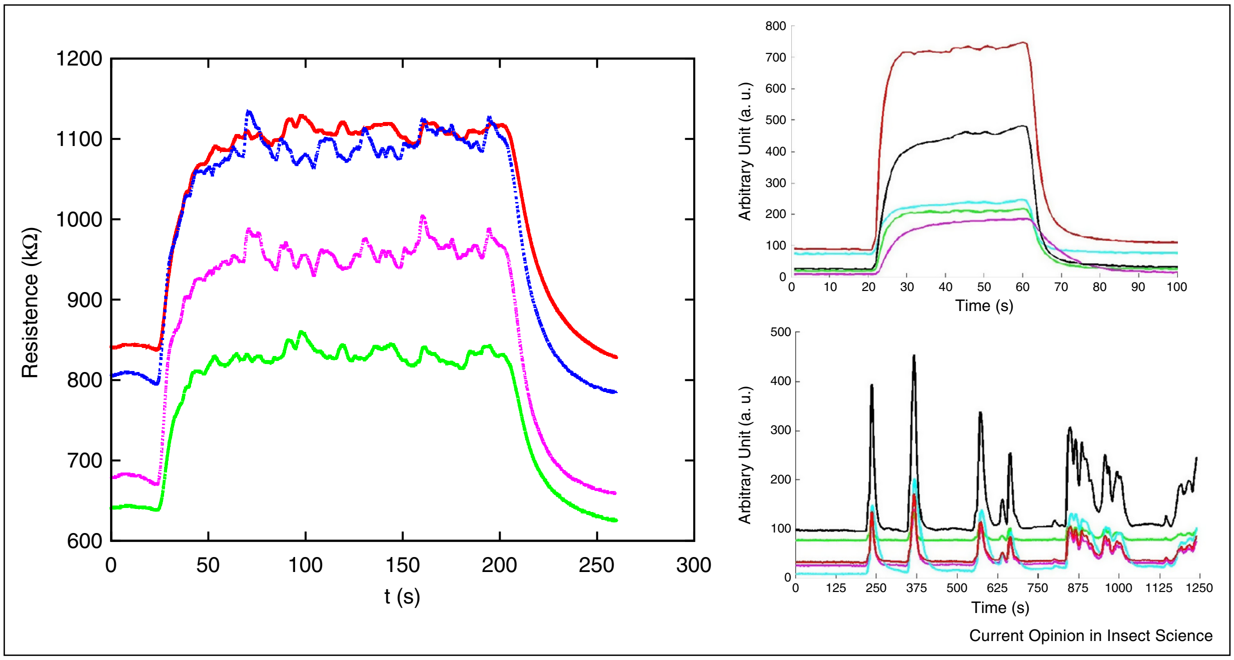
Our goal here is to review the state of the art in computational models in insect olfaction related to decision making functions. Since the main centers of learning and memory are the Mushroom Bodies (MBs) [16,7], this review will mostly concentrate on relating the Antennal Lobe (AL) and MB functions.

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 [13,20–22]. 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 [23–27], resulting

Figure 1



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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 8 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].

from balanced excitation and inhibition in their network [28–30]. Even though mammals and insects can recognize odors fairly quickly [31–33], temporal coding is also present to improve discrimination performance and odor concentration estimation [32,34–36,11].

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 [37–40] 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 [44–46], 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.

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 [4,44,54–56,49], 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 Fig. 2). Connectionists models predicted the need of 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].

Another interesting hypothesis is that the MBs are a large screen where one can easily discriminate objects using