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First Order Processing of Complex Olfactory Information in the Moth Brain

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Abstract

As part of a project to develop a novel class of technology for infochemical communication, we investigated olfactory processing in the insect brain to form the basis for a multicomponent detector system able to recover ratiometric odor information deployed in the world. By unraveling neuronal network processing, we support the generation of a tuned detector capable of deciphering chemical signals produced by a biosynthetic chemoemmitter. This chemoemitter/receiver complex establishes an entirely new communication system based on the chemical signaling of insects. Our main challenge is to reveal how complex odor information is encoded in the insect olfactory system. In insects, the initial percept of odors detected by the antenna occurs in the first olfactory center of the brain, the antennal lobe (AL), the insect analog of the mammalian olfactory bulb Afferent input is modified via interneuronal connections (LNs) and the resultant representation is carried by projection neurons (PNs, Output) to higher-order brain centers. Accordingly, the antennal lobe representation of an odor mixture may either retain the single-odor information of blend components, or reveal non-linear interactions due to processing in the AL network. The phenomenon of a non-linear response to a mixture that is not predictable from its component responses is called a "mixture interaction". Combining intracellular electrophysiology, optical imaging, and 3-D morphological reconstruction, we report a highly combinatorial, non-linear process for coding complex host blends in moths that is presumably shaped by the AL network: Blend responses exhibited an array of interactions including suppression, hypoadditivity, and synergism that established a unique blend representation. Our results indicate that each neuron utilizes several different elements to produce the signal representing the entire blend, including the spatial location, rate, latency, and temporal pattern of the response. This suggests that a biomimetic system based on the moth brain can, with a minimum of detectors and processing power, decipher complex odor information on both temporal and spatial scales.

Keywords: odor processing, network, intracellular, electrophysiological recording, single cell

1. Introduction

For many insects, olfactory cues play a major role for survival (e.g. foraging, communication, host localization), and the sense of smell is the most prominent sensory modality. The stereotypic organization of the insect olfactory system and its relative simplicity offers an ideal model to analyze odor-mixture coding. These incredibly small and low power brains contain the full circuitry required to execute elaborate behavioral tasks such as orientation, location of food, and learning and memory. Additionally, the gross structure and connectivity of first order processing is regarded as

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consistent across species and insect and vertebrate olfactory systems share many common properties. Thus, the insect brain provides an effective model for establishing a biomimetic chemical detector system.

In insects, odorant molecules are detected by peripheral olfactory sensory neurons (OSNs) and transduced into electrical potentials conferring information about the odorant molecule to the brain. OSNs expressing the same olfactory receptor protein converge onto the same glomerulus in the antennal lobe (AL), the insect analog of the mammalian olfactory bulb [4,6]. Glomeruli are spherical structures of high synaptic density constituting the functional units of the AL. In the moth AL, the afferent input of roughly 250000 OSNs relay onto two categories of AL neurons: roughly 900 projection neurons (PNs) and 360 local interneurons (LNs) [3]. PNs subsequently relay AL output to higher brain centers including the mushroom bodies and the lateral horn. LNs exclusively branch within the AL, interconnecting glomeruli and providing information processing among glomeruli [2]. Separation of blend information into different OSN channels requires integration of at least a subset of these channels to establish the unique blend percept. Nevertheless, little is known about the mechanisms by which these channels are combined. Therefore, it remains unclear how the insect's olfactory system processes and reliably identifies complex volatile signals in a constantly changing background. As a consequence of OSN targeting, odors are represented as stable, spatial patterns of neuronal activity in the AL [1]. Recent optophysiological recordings in the insect AL show that responses to an odor mixture generally could be predicted from the single component responses at the input- but not at the output level [5]. In our physiological study, we utilized both intracellular electrophysiology and optophysiological recordings. This approach enables us to directly measure how the cellular network of the AL shapes the representation of odor blends. Our combined physiological approach indicates that LNs modulate PN output in the moth AL creating a highly combinatorial, non-linear process for coding complex host blends in the Moth AL.

2. Results

2.1. Electrophysiology

Using a novel multicomponent stimulus system, we performed intracellular recordings of projection (PNs) and interneurons (LNs) in an attempt to thoroughly characterize blend representation and integration by single AL neurons in the moth [7,8]. Response to antennal stimulation exhibited three basic response types, characterized by either an abrupt depolarization with increased spiking (excitatory response), hypopolarization leading to a suppression of spiking (inhibitory response), or a biphasic response with an early excitatory phase followed by a period of hyperpolarization. The fine spatiotemporal representation of blends within and between single neurons in the AL revealed a highly combinatorial, non-linear process for coding host blends presumably shaped by the antennal lobe network: the vast majority of blend responding PNs and LNs showed non-linear spike frequencies in response to an odor mixture, exhibiting an array of interactions including suppression, hypoadditivity, and synergism. Our results indicate that odor blends are represented by each cell as a unique combinatorial representation and there is no general rule by which neurons compute the mixture in comparison to single components. On the single neuron level, we show that those differences manifested in a variety of parameters, including frequency and latency of the response kinetics.

2.2. Optophysiological recordings

We measured odor-evoked calcium responses of AL input and output neurons simultaneously. By applying two different calcium sensitive dyes, we quantified the odor information fed into the network (OSN input) as well as the resultant output of network processing (PN output). With this tool, we are able to directly measure how the cellular network shapes the representation of odor blends across the AL (Fig. 1). Our combined physiological approach indicates that LNs modulate PN output in the moth AL to establish an entirely unique odor representation in *Manduca sexta*.

3. Conclusions

We report a highly nonlinear coding scheme for processing odor blends in the moth brain. An olfactory system incorporating non-linear coding may be advantageous as it can process signals from a "noisy" periphery with input from both specific and broadly tuned receptors. High levels of non-linearity demand broadly tuned receptors where one receptor type may participate in coding for many odors. Thus, the subsequent separation of entities as well as the

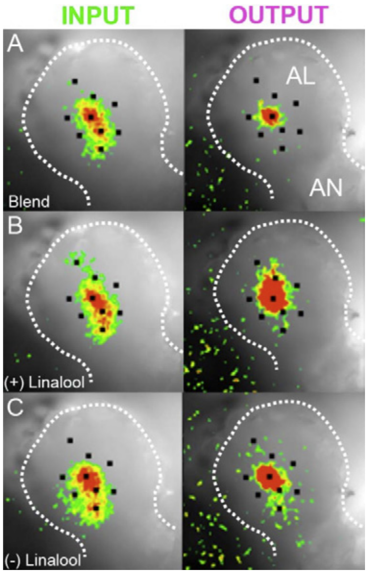

Fig. 1. Calcium dependent response patterns to an odor blend (A) and its single components (B, C) at two different processing levels (Input, left panel and output, right panel). Neuronal activity (calcium increase) was monitored as spatially restricted activity regions of increased fluorescence in the antennal lobe (AL). Clear spatial differences in odor-evoked activity patterns between input and output indicate AL network modulation.

generation of the novel blend percept must be generated by the network. For a neuromorphic processor, this implicates that a minimum of sensors with varying selectivity can already detect complex blends, increasing the processing power of the biosynthetic communication system.

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