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Differential Processing by Two Olfactory Subsystems
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Abstract—Among insects, Hymenoptera present a striking olfactory system with a clear neural dichotomy from the periphery to higher order centers, based on two main tracts of second-order (projection) neurons: the medial and lateral antennal lobe tracts (m-ALT and l-ALT). Despite substantial work on this dual pathway, its exact function is yet unclear. Here, we ask how attributes of odor quality and odor quantity are represented in the projection neurons (PNs) of the two pathways. Using *in vivo* calcium imaging, we compared the responses of m-ALT and l-ALT PNs of the honey bee *Apis mellifera* to a panel of 16 aliphatic odorants, and to three chosen odorants at eight concentrations. The results show that each pathway conveys differential information about odorants' chemical features or concentration to higher order centers. While the l-ALT tract primarily conveys information about odorants' chain length, the m-ALT tract informs about odorants' functional group. Furthermore, each tract can only predict chemical distances or bees' behavioral responses for odorants that differ according to its main feature, chain length or functional group. Generally l-ALT neurons displayed more graded dose–response relationships than m-ALT neurons, with a correspondingly smoother progression of inter-odor distances with increasing concentration. Comparison of these results with previous data recorded at AL input reveals differential processing by local networks within the two pathways. These results support the existence of parallel processing of odorant features in the insect brain. © 2018 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: insect, antennal lobe, parallel processing, projection neurons, optical imaging.

INTRODUCTION

Olfaction provides animals with crucial information in a variety of behavioral contexts that are common across species, like mating, feeding or detecting danger. The anatomical architecture of the olfactory system shows, therefore, a remarkable interspecific similarity (Hildebrand and Shepherd, 1997; Ache and Young, 2005). The primary olfactory center (the olfactory bulb in vertebrates, the antennal lobe (AL) in insects and the olfactory lobe in crustaceans) is composed of numerous functional units termed glomeruli (Pinching and Powell, 1971; Hansson and Anton, 2000). Each glomerulus receives input from many olfactory receptor neurons (ORNs) expressing one type of olfactory receptor (Gao et al., 2000; Vosshall, 2000; Imai and Sakano, 2007).

Local, mostly inhibitory, interneurons interconnect glomeruli and thus reshape the olfactory message (Puopolo and Belluzzi, 1998; Seki et al., 2010; Grabe et al., 2016; Nagel and Wilson, 2016). This local processing involves both a gain control that avoids saturation of the signal and asymmetrical inhibition qualitatively reshaping the olfactory representation (Tabor et al., 2004; Bhandawat et al., 2007; Deisig et al., 2010; Adam et al., 2014; Kim et al., 2015). The olfactory message is then conveyed to higher olfactory centers by mitral/tufted cells in vertebrates, or by projection neurons (PNs) in insects (Haberly and Price, 1977; Kanzaki et al., 1989). These neurons usually project to several brain centers, such as the amygdala and the piriform cortex in vertebrates (Mori and Sakano, 2011; Igarashi et al., 2012), or the lateral horn and the mushroom bodies in insects (Laurent, 2002; Tanaka et al., 2004; Kirschner et al., 2006).

Parallel processing is defined as the coding and processing of different features of the same stimulus by distinct neural pathways and has been demonstrated in several sensory modalities in both insects and vertebrates (Rauschecker and Tian, 2000; Yamaguchi

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et al., 2008; Nassi and Callaway, 2009). As it is ubiquitous in neural systems, it may represent an adaptive strategy for living organisms, ensuring more efficient and rapid processing of inherently complex sensory stimuli. Olfactory systems are especially interesting for the study of parallel processing because within the general architecture detailed above, they harbor several distinct pathways in which the reshaping of odor information may differ (Galizia and Rössler, 2010; Rössler and Brill, 2013). Among insects, this is particularly true in Hymenoptera like the honey bee, which exhibit an olfactory system with multiple PN tracts: the median (m-ALT), the lateral (l-ALT) and three smaller medio-lateral tracts (ml-ALTs) (Abel et al., 2001; Müller et al., 2002; Kirschner et al., 2006; Galizia and Rössler, 2010; Zwaka et al., 2016). The m-ALT and l-ALT are particularly remarkable as they are of almost equal size in terms of neuron numbers (~400 vs ~500) (Rybák, 2012) and project both to the mushroom bodies and the lateral horn, but in reverse order. As each PN type collects information from segregated subsets of AL glomeruli, m-ALT and l-ALT may be envisaged as forming part of two different subsystems. Here we will adopt the term *m-subsystem* to define the olfactory pathway proper to m-ALT PNs, starting at the receptor level and finishing at the PNs themselves. In the same way, we will adopt the term *l-subsystem* for the olfactory pathway corresponding to l-ALT PNs, from the receptor level to the PNs. These subsystems have been the focus of numerous neuroanatomical and neurophysiological studies, which reported differences in odor specificity, response latency, concentration dependence or coincident activity (Müller et al., 2002; Kroficzek et al., 2009; Yamagata et al., 2009; Brill et al., 2013, 2015; Carcaud et al., 2015). Yet, if and how different chemical features of odorants are processed within each subsystem and if the reshaping of the odor message imposed by local AL networks differs between the two subsystems remains largely unknown.

We addressed these questions in the honey bee by recording via *in vivo* calcium imaging the activity of m-ALT and l-ALT PNs to a standard panel of aliphatic odorants differing in two chemical features (functional group and carbon chain length) or in their concentration (Fig. 1A). We then compared PN responses to our previous recordings of AL activity dominated by ORN signals and provided, a fair approximation to AL input activity (Carcaud et al., 2012). Our results show that the reshaping of local odor information within the AL network differentially affects the two subsystems, with a more significant reshaping occurring in the m-subsystem. Our data also reveal that each PN type conveys different, but complementary, information about odorants to higher order centers.

EXPERIMENTAL PROCEDURES

Animals

Honeybee workers (*Apis mellifera* females) were collected at the entrance of an outdoor hive. They were chilled on ice until they stopped moving, and were then placed in recording chambers using low temperature

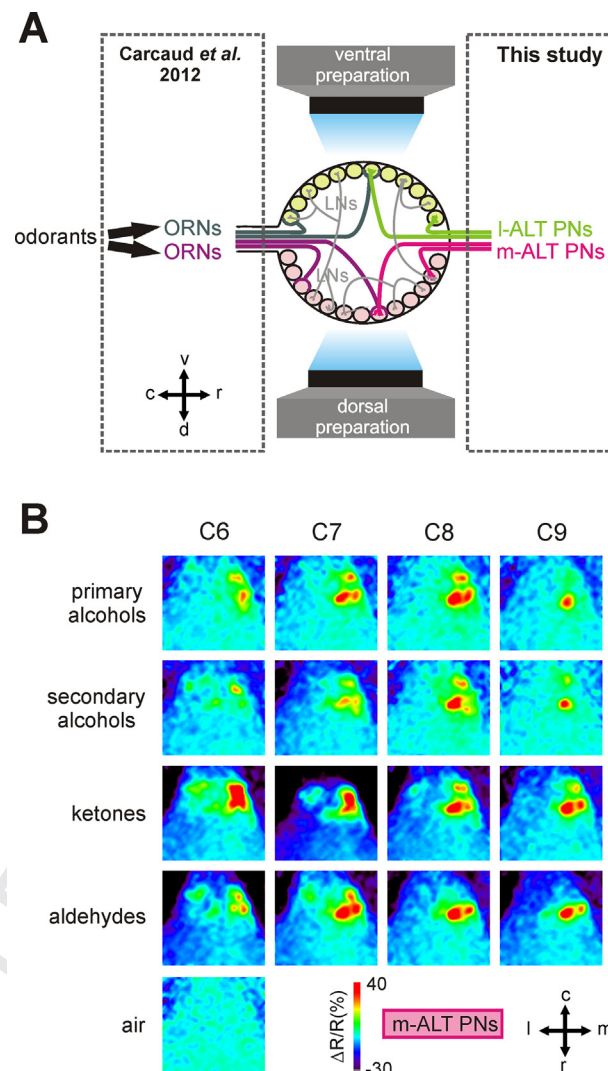


Fig. 1. Calcium signals from m- and l-ALT PNs in the AL. (A) Schematic drawing of the AL network. Odorants molecules are detected by ORNs on the antenna, which send olfactory information to the antennal lobe. ORNs convey their information either in the ventral surface of the AL (l-subsystem, light green) or in the dorsal surface of the AL (m-subsystem, light pink). Within the AL, local neurons (LNs, gray) interconnect glomeruli. Then, projection neurons (PNs) convey information to higher brain centers, the mushroom bodies and the lateral horn, through two main tracts of PNs, the m-ALT (magenta) and l-ALT (green). Responses of PNs were recorded in the present study, from both AL subsystems. Data were compared to ORN responses recorded in a previous study (Carcaud et al., 2012). (B) Odor-induced calcium signals in glomeruli innervated by m-ALT PNs, to a panel of 16 aliphatic odorants varying according to their chemical functional group (primary and secondary alcohols, aldehydes and ketones) and their carbon chain length (C6–C9). Relative fluorescence changes ($\Delta F/F\%$) are presented in a false-color code, from dark blue to red. Different odors induce different glomerular activity patterns in glomeruli innervated by m-ALT PNs. c: caudal, r: rostral, v: ventral, d: dorsal, l: lateral, m: medial. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

melting wax. Different animals were used to record l-ALT and m-ALT PNs since visualizing each subsystem requires a different preparation. To record activity from glomeruli innervated by the l-ALT PNs, we employed the

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