Journal Club

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The Tuning Properties of Antennal Lobe Projection Neurons

Jason Aungst and Marc Spehr

Department of Anatomy and Neurobiology, Program in Neuroscience, University of Maryland School of Medicine, Baltimore, Maryland 21201

Review of Reisenman et al. (<http://www.jneurosci.org/cgi/content/full/25/35/8017>)

The olfactory systems of vertebrates and insects share a number of remarkable similarities both on the anatomical and functional level. In both phyla, a highly organized pattern of axonal convergence of isofunctional peripheral sensory neurons to one or a few discrete glomeruli in the antennal lobe (insects) or olfactory bulb (vertebrates) generates a chemotopic map of odor quality in the brain. Beyond these common principles, general odor information is typically processed by a main olfactory pathway, whereas conspecific chemical signals of social or reproductive status, pheromones, are detected in parallel by a specialized and anatomically separate accessory olfactory system. This functional dichotomy, however, may not be as strict as previously suggested (Xu et al., 2005). Since the beginning of the molecular era in olfactory research, the majority of work in vertebrates has centered on the main olfactory system. In contrast, long-standing knowledge of pheromonal communication in ants, bees, moths, and flies has predominantly stimulated studies on the accessory olfactory pathway in insects (Amrein, 2004).

It is widely held that the sensitivity and selectivity profiles of peripheral sensory neurons, glomeruli, and glomerular output neurons differ between the main and accessory olfactory system. Neurons of

the main pathway are believed to show broad concentration-dependent tuning properties whereas accessory olfactory neurons are characterized by a highly selective molecular receptive field. This concept of “generalists” versus “specialists” is attractive but, at least in insect olfaction, lacks conclusive experimental evidence. Are glomerular projection neurons (PNs) of the main olfactory pathway in insects broadly tuned to a variety of general odors or is the stimulus specificity observed in the accessory pathway conserved across olfactory systems? This question, which goes to the core of the logic of olfactory coding, was addressed recently in an article by Reisenman et al. in *The Journal of Neuroscience*. Using the sphinx moth *Manduca sexta* as a model system, the authors elegantly combined electrophysiological and dye tracing methods to intracellularly record and compare odor response profiles from identified glomerular PNs.

Previous investigations of odor-evoked activity in insect glomerular PNs have primarily been restricted to imaging techniques and thus data interpretation has frequently been hampered by the lack of knowledge of individual neuronal identities. Using sharp microelectrodes, Reisenman et al. overcame this problem by targeting the recently identified isomorphic G35 glomerulus, which is located adjacent to large and sexually dimorphic glomeruli in both males and females. Subsequent to electrophysiological characterization, a given PN was injected with a fluorescent dye to confirm neuronal identity by confocal imaging in brain sections

and three-dimensional reconstruction of the antennal lobe (Fig. 1). This anatomical mapping revealed the same relative positions of G35 and similar morphological characteristics of G35-PNs in the antennal lobe of male and female moths [Reisenman et al. (2005), their Fig. 2 (<http://www.jneurosci.org/cgi/content/full/25/35/8017/FIG2>)].

Having established postrecording staining as a valid tool to determine PN identity in *Manduca*, the authors focused on individual odor response characteristics of G35-PNs. When the moths' antennae were challenged with a panel of several host plant odors, G35-PNs from both sexes preferentially responded to *cis*-3-hexenyl acetate (c3HA), typically displaying triphasic alternations of membrane hyperpolarization and action potential firing [Reisenman et al. (2005), their Fig. 3 (<http://www.jneurosci.org/cgi/content/full/25/35/8017/FIG3>)]. Responses to c3HA were dose dependent with respect to various analysis parameters [Reisenman et al. (2005), their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/25/35/8017/FIG4>)]. PNs in female moths, however, showed a lower c3HA detection threshold, likely because of the higher number of olfactory receptor cells in females. Interestingly, female G35-PNs displayed a pronounced early hyperpolarization when moths were stimulated with linalool, a strong activator of the neighboring large female-specific glomerulus. The authors interpret quantitative differences between c3HA- and linalool-mediated hyperpolarizations [Reisenman et al. (2005), their Fig. 7 (<http://www.jneurosci.org/cgi/content/full/25/35/>)]

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Correspondence should be addressed to Marc Spehr, Department of Anatomy and Neurobiology, University of Maryland School of Medicine, Health Science Facility-2, Room 251, 20 Penn Street, Baltimore, MD 21201. E-mail: mspeh001@umaryland.edu.

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8017/FIG7)] as indicators of interglomerular inhibition by local interneurons.

How selective are G35-PNs for c3HA stimulation? To address this issue, Reisenman et al. first screened two structural derivatives of c3HA for their stimulatory capacity. The c3HA-related propionate and butyrate evoked fewer action potentials at lower spike frequencies in PNs of both males and females [Reisenman et al. (2005), their Fig. 5 (<http://www.jneurosci.org/cgi/content/full/25/35/8017/FIG5>)]. When an extended panel of 14 plant odors was tested in two female G35-PNs at a relatively high and an intermediate concentration, respectively, the authors confirmed a preference for c3HA in both neurons (higher net number of spikes and longer duration of excitation). However, c3HA selectivity is less pronounced when other response parameters (the peak instantaneous spike frequency and the delay of the response onset) are comparatively analyzed [Reisenman et al. (2005), their Fig. 6 (<http://www.jneurosci.org/cgi/content/full/25/35/8017/FIG6>)].

The study by Reisenman et al. addresses one of the key issues in olfactory coding and processing: the dynamic sensitivity range used by individual uniglomerular output neurons to integrate odor information. Thus far, imaging studies of odor-evoked neuronal activity in the antennal lobe (or the vertebrate olfactory bulb) have failed to provide definite answers to this question because available methods lack single-cell resolution and are frequently limited to reporting pre-synaptic activity. The poststaining and mapping approach used by Reisenman et al. thus represents a major advance toward a detailed physiological description of individually identified PNs. In the present study, the authors were able to demonstrate the morphological and anatomical similarity of a glomerulus-specific subpopulation of PNs in both males and females. Interestingly, G35-PNs in both sexes were preferentially activated by peripheral detection of the same ethologically relevant stimulus, suggesting similarity of physiological principles of central odor processing in the main chemosensory pathway of male and female insects. However, to expand on the selectivity profile and any possible sex differences in G35 or other glomeruli, future studies must in-

Figure 1. Schematic diagram of olfactory processing in the antennal lobe of *Manduca sexta*. Axon terminals of isofunctional peripheral sensory neurons (red) converge on dendritic arborizations of central PNs (brown) to form distinct sexually dimorphic (orange oval) and isomorphic (green oval) glomeruli. The odor tuning of individual uniglomerular PNs is determined by the selectivity profile of peripheral input neurons as well as lateral inhibitory circuits. IN, Inhibitory interneuron; latLFG, lateral large female glomerulus; MB, mushroom body.

clude an extended panel of test odors over a wider concentration range and a larger number of PNs from both sexes. Future research will also address how interglomerular activity affects PN output. Concurrent application of linalool and c3HA could provide interesting insight into the role of lateral inhibition in processing odor information. Moreover, it will be important to learn more about the information content inherent in different PN response parameters. Assuming that, for example, the peak spike frequency encodes important odor information [as reported in *Drosophila* (de Bruyne et al., 1999)], the response pattern of G35-PNs would hardly show obvious odor specificity. Thus far, attempts to decipher the coding logic of central odor processing have suffered from a lack of precise criteria that define the breadth of odor tuning of an individual neuron. Reisenman et al. are now

in an excellent position to develop a rigorous definition for narrow versus broad tuning of PNs in the antennal lobe and to apply these criteria in single-unit recordings as well as large-scale imaging studies.

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