CHAPTER 7

The Olfactory Sensory Map in *Drosophila*

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**Abstract**

The fruit fly (*Drosophila melanogaster*) exhibits robust odor-evoked behaviors in response to cues from diverse host plants and pheromonal cues from other flies. Understanding how the adult olfactory system supports the perception of these odorous chemicals and translates them into appropriate attraction or avoidance behaviors is an important goal in contemporary sensory neuroscience. Recent advances in genomics and molecular neurobiology have provided an unprecedented level of detail into how the adult *Drosophila* olfactory system is organized. Volatile odorants are sensed by two bilaterally symmetric olfactory sensory appendages, the third segment of the antenna and the maxillary palps, which respectively contain approximately 1200 and 120 olfactory sensory neurons (OSNs) each. These OSNs express a divergent family of seven transmembrane domain odorant receptors (ORs) with no homology to vertebrate ORs, which determine the odor specificity of a given OSN. *Drosophila* was the first animal for which all OR genes were cloned, their patterns of gene expression determined and axonal projections of most OSNs elucidated. In vivo electrophysiology has been used to decode the ligand response profiles of most of the ORs, providing insight into the initial logic of olfactory coding in the fly. This chapter will review the molecular biology, neuroanatomy and function of the peripheral olfactory system of *Drosophila*.

**Introduction**

Sensory systems—touch, hearing, vision, taste, smell—map features of the external world into internal representations in the brain that ultimately allow all animals to navigate their environments. The physical senses of touch and vision use topographic mapping approaches to represent discrete dimensions of the external world. For example, the visual system uses retinotopic mapping to organize the field of view in the lateral geniculate nucleus, such that there is an orderly representation of the visual field in the brain.\(^1\) The somatosensory system uses somatotopic mapping to project not the external world but the body plan onto the somatosensory cortex.\(^2,3\) Thus it is not the environment per se that is mapped, but the various parts of the body, allowing an animal to determine with precision where it is being touched by a physical stimulus. The auditory system maps sound frequencies along a tonotopic axis in the cochlea and the auditory cortex, allowing sound to be broken into its component parts and later synthesized into a coherent representation of what was heard.\(^4,5\) An important feature of the auditory system is the precision by which it permits animals to localize sound in space. This is accomplished by central brain comparisons of input into the left and right ears. These mapping approaches allow visual, somatosensory and auditory cortex to represent important features of visual, mechanical and auditory stimuli and relate them to physical space in the external world.

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The chemical senses—taste and smell—are less well understood than the physical senses but appear to use a different strategy to represent gustatory and olfactory cues encountered in the environment. Instead of mapping primarily the position of the external stimulus and its relationship to the individual, the gustatory and olfactory systems categorize the identity and quality of the stimulus. The tongue can detect at least five different taste qualities—bitter, sweet, sour, salty and umami, the taste of monosodium glutamate. Insects appear to have all of these taste qualities, with the possible exception of umami and the addition of a “water” sense. Each of these taste qualities is perceived by structurally and functionally discrete gustatory neurons in the tongue of vertebrates and labial palps of insects. It is still unclear in the field whether these taste qualities remain segregated into stimulus-specific labeled lines from the periphery to higher brain centers, or whether distributed coding across groups of sensory and central brain neurons allows animals to distinguish tastes of different modalities such as bitter and sweet. There is clear evidence in Drosophila that pathways for bitter and sweet tastes are anatomically and functionally separate senses that elicit innate aversive and appetitive responses, respectively.

The olfactory system is capable of detecting an extremely large number of volatile chemical stimuli, possibly exceeding tens of thousands, although the total olfactory coding capacity of any animal has never been exhaustively catalogued. The ability to recognize such a vast number of odorants is thought to be due to the special properties of the ORs, the large family of membrane proteins that is selectively expressed in OSNs in the olfactory epithelium of vertebrates and antennae of insects. ORs have selective but broad ligand-binding properties, such that a given OR is activated by multiple odors and a given odor activates multiple ORs. This combinatorial coding strategy based on a large family of ORs with broad but selective ligand pharmacology in part accounts for the ability of animals to detect and discriminate a number of odors that far exceeds the number of ORs they possess.

In all arthropods and vertebrates studied to date, the early olfactory system is organized into a large number of spherical neuropil elements, called glomeruli. Olfactory glomeruli represent points of convergence where OSNs expressing the same OR synapse with inhibitory local interneurons and secondary neurons that relay olfactory information to higher brain centers. There is some evidence in mammals that the olfactory system maps odor stimuli along a chemotopic axis in the vertebrate olfactory bulb. Thus neurons responsive to odors sharing an alcohol functional group will tend to innervate adjacent regions in the bulb and these regions appear to be organized by carbon chain length. This type of chemotopy is less apparent in insect systems.

This chapter will review recent progress in our understanding of the organization and function of the adult Drosophila olfactory system. The accompanying chapter by Veronica Rodrigues and Thomas Hummel will address the development and early patterning of the olfactory system. The accompanying chapter by Reinhard Stocker concerns the unique organization of the larval olfactory system.

Olfactory Organs and Olfactory Sensory Neurons of Drosophila

Fruit flies detect odors through two olfactory sensory organs on the head, the antenna and maxillary palp (Fig. 1). These olfactory appendages are covered with a large number of sensory hairs, called sensilla, which house and protect the underlying OSNs that are specialized to detect odors. Olfactory sensilla can be distinguished morphologically from thermo- and hygro-sensitive sensilla by the presence of a large number of small pores that perforate the shaft of the sensillum and which are believed to allow access to odors (reviewed in ref. 33). A total of about 410 olfactory sensilla cover the antenna, while the maxillary palp has about 60 olfactory sensilla. These hairs can be divided into three distinct morphological and functional classes: Club-shaped basiconic sensilla, long and pointed trichoid sensilla and short, peg-shaped coeloconic sensilla (Fig. 1). Further morphological and functional distinctions subdivide both basiconic and trichoid sensilla into additional subclasses, which differ by the size and density of odor pores, the number of neurons housed in each sensillum and their distribution on the antenna (Fig. 1). The different sensilla types are distributed in a highly stereotyped fashion over the surface of the antenna. Large basiconic sensilla are clustered at the medial face of the antenna, while the three types of trichoid sensilla are arranged in diagonal bands across the lateral face of the antenna (Fig. 1).