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Review

Drosophila Chemoreceptors: A Molecular Interface Between the Chemical World and the Brain

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Chemoreception is essential for survival. Feeding, mating, and avoidance of predators depend on detection of sensory cues. *Drosophila* contains diverse families of chemoreceptors that detect odors, tastants, pheromones, and noxious stimuli, including receptors of the odor receptor (Or), gustatory receptor (Gr), ionotropic receptor (IR), Pickpocket (Ppk), and Trp families. We consider recent progress in understanding chemoreception in the fly, including the identification of new receptors, the discovery of novel biological functions for receptors, and the localization of receptors in unexpected places. We discuss major unsolved problems and suggest areas that may be particularly ripe for future discoveries, including the roles of these receptors in driving the circuits and behaviors that are essential to the survival and reproduction of the animal.

Trends

Odorant receptors (Ors) have been found to activate an increasing number of behavioral circuits.

Gustatory receptors (Grs) are expressed in a wide diversity of organs. Emerging results reveal roles in an expanding repertoire of functions, extending beyond chemoreception.

Ionotropic receptors (IRs) are expressed not only in olfactory organs but also in taste organs. A large clade has recently been found to be expressed in all taste organs of the fly.

Ors, Grs, and IRs all have roles in the sexual behavior of the fly.

The Problem

Animals in their natural environments are immersed in a sea of chemical compounds. Some of these compounds signal the presence of nutrients, while others signify the danger of poisons. Some compounds indicate the proximity of a mating partner, while others warn of a predator. Animals must be able to detect and identify a wide variety of meaningful signals among the vast complexity of their chemical milieu.

In addition to chemical identity, chemical intensity can also be critical to an animal. The quantity of a sugar in a food source reflects its nutritive value, just as the quantity of a bitter compound such as strychnine may reflect its toxicity. Moreover, some stimuli are attractive at low concentrations and aversive at high concentrations. The temporal pattern of the stimulus is also important. For example, it may inform an animal of the proximity of an odor source.

This, then, is the problem: how to detect and interpret a wide variety of chemical signals amid a cacophony of chemical noise. The signals are enormously diverse in chemical and temporal structure, and the ability to identify and quantitate them may be a matter of life and death.

This review discusses recent progress in understanding chemoreception, which is the foundation of all the perceptual processes and behavioral responses that follow. We focus on the chemoreceptors of *Drosophila*, which provides a powerful genetic model for the study of chemosensory reception. Although there has been great progress in the field, it is clear that critical problems remain to be solved and that major discoveries are in store.

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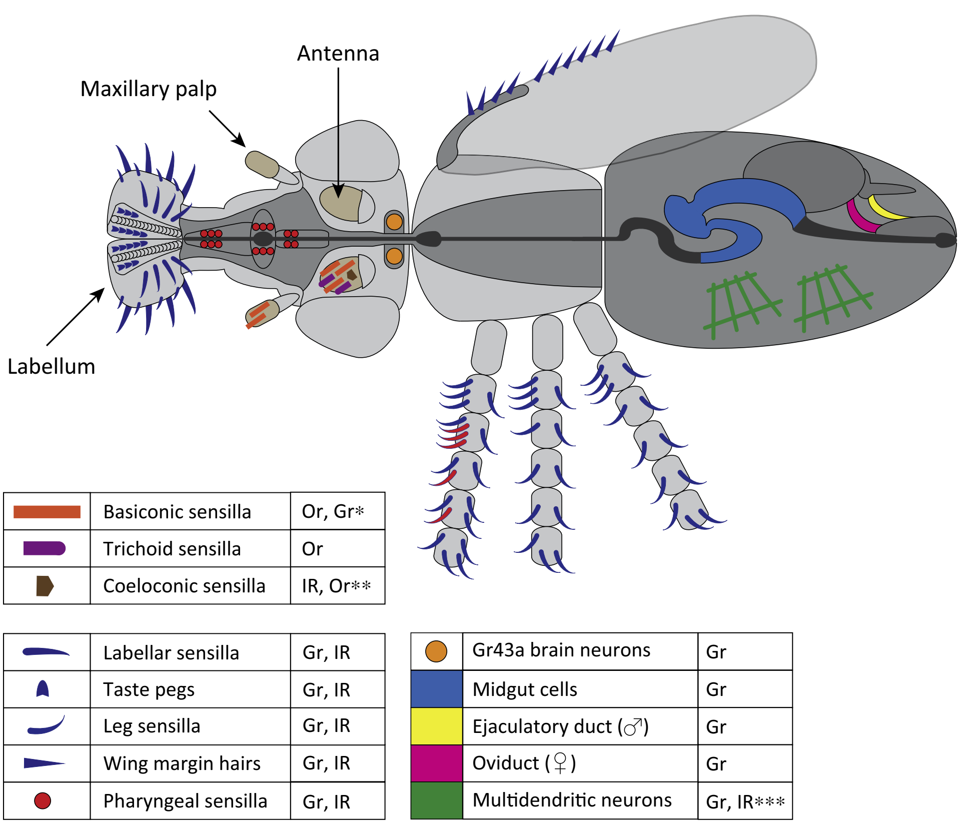
The Cellular Context of Chemoreception

Volatile compounds are sensed by olfactory receptor neurons (ORNs) of the olfactory system, whereas non-volatile compounds are detected by gustatory receptor neurons (GRNs) of the taste system. However, the conceptual wall dividing olfaction and taste has been increasingly assaulted by a barrage of experimental results that establish new links between the two sensory modalities.

The Adult Olfactory System

The fly contains two olfactory organs, the antenna and the maxillary palp (Figure 1). Both are covered with sensilla, sensory hairs that contain the dendrites of up to four ORNs (Figure 2A) [1,2]. The shafts of sensilla are perforated by numerous pores, or channels, through which odorants can pass. The ORN cell bodies lie below the sensillar shafts, adjacent to accessory cells. These cells secrete odorant-binding proteins (OBPs) into the lymph that bathes the ORN dendrites [3]. OBPs are widely believed to carry odorants to odor receptors in the dendritic membranes, although other functions have been proposed (Box 1). ORNs project axons to the antennal lobe of the brain, where signals are processed and transmitted to higher-order centers [4].



Trends in Genetics

Figure 1. Expression of the Three Largest Chemoreceptor Families in *Drosophila*. Light-gray coloring indicates the exterior of the fly; dark-gray coloring indicates the interior. Tan highlights the antenna and maxillary palp, which primarily house olfactory neurons. Leg sensilla indicated in red are male specific. Gustatory receptor (Gr) expression in the gut occurs in enteroendocrine cells as opposed to neurons. Multidendritic neurons are subcuticular. Expression of Grs and ionotropic receptors (IRs) is based in most cases on expression of *Gr–GAL4* and *IR–GAL4* drivers. Expression of odor receptors (Ors) is based on *Or–GAL4* drivers and *in situ* hybridization. Classes of receptors that have been identified in each corresponding sensillum type or tissue are indicated at the right of the labels. *Antennal Grs include *Gr21a* and *Gr63a* in basiconic sensilla neurons and others [62,85]. **A single Or has been localized to one neuron of one coeloconic sensillum. ***A single IR has been localized to multidendritic neurons in the abdomen.