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Chapter 3

Olfaction in Gastropods

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Abstract

Within the Phylum Mollusca, gastropods encompass a large and diverse group of aquatic and terrestrial animals that inhabit areas of the deep or shallow sea, estuaries, lakes, and arid environments. They have no acoustic sense and, for many, little to no visual recognition of objects. Instead, their world is chemically driven so that water-soluble and volatile odorants are key mediators of many physiological and behavioral events. Olfaction, conventionally referred to as the sense of smell, serves to detect odorants at a distance from their source and provides the sensory afference leading to odorant-driven behavioral responses. These exogenous chemicals convey a remarkable amount of information critical to aggregation, habitat selection, defense, prey localization, courtship, and mating. To understand the role of olfaction in behavior, studies have focused on how olfactory systems recognize and interpret information from chemical signals. Researchers have made excellent progress toward understanding gastropod olfaction at behavioral and morphological levels and, more recently, at neural and biochemical levels. In this chapter, we review recent studies and provide insight into the olfactory neurobiology of aquatic (*Aplysia*, *Tritonia,* and *Lymnaea*) and terrestrial (*Achatina, Cantareus,* and *Limax*) gastropods. The three aquatic model systems are distantly related, with previous studies of each tending to have different foci, thereby providing distinct but complimentary contributions to the synthesis of gastropod olfaction research. By contrast, the three terrestrial model systems are more closely related, and their research histories are far more integrated. We continue this integration, taking care to consider the differences within and between aquatic and terrestrial systems in our synthesis effort.

Aquatic Gastropods

Water (including marine and freshwater) covers over 70% of the earth's surface (Ellis 2003), yet our knowledge of how aquatic animals detect water-borne odors in this vast environment is far from complete. This gap in our knowledge is concerning given that many aquatic species dwell on the bottom of bodies of water, where vision and other sensory modalities are at best limited by turbidity or the physical properties of water. Instead, odor cues impact all aspects of aquatic animal life, directly affecting chances of survival and reproduction. Aquatic gastropods exist in marine, freshwater, and brackish water and provide excellent models in which to investigate basic principles of the physiological, biochemical, and molecular aspects of olfaction in aquatic environments.

Aplysia

Aplysia, which are marine opisthobranch gastropods within the family Aplysiidae, are unique among molluscs in that they are highly characterized at multiple levels and therefore fulfill many of the requirements necessary for investigating the biological basis of olfaction. Their primary cephalic sensory organs are two pairs of tentacles located in the head region. All Aplysiidae possess a pair of short retractable rhinophores and oral tentacles (Klussmann-Kolb 2004; Cummins et al. 2009a) (Figure 1), allowing them to locate and discriminate food (Audesirk 1975), conspecific pheromones (Levy et al. 1997), and predators. Upon stimulation of the cephalic sensory organs, animals may orient and move towards the source (Leonard and Lukowiak 1986; Painter et al. 2004). Rhinophores were first described as olfactory organs by early nudibranch researchers (Agersborg 1925) and more accurately defined through the discovery that their ablation reduces, although does not abolish, food-finding (Audesirk 1975). Rhinophores are required for long-distance chemoreception, with oral tentacles generally thought to be close-range chemoreceptors (Boudko et al. 1999), although rhinophores appear to be as effective as oral tentacles in detecting food odors (Preston and Lee 1973). Other proposed functions of rhinophores and oral tentacles in other gastropods are photoreception and mechanoreception (Bicker et al. 1982; Keunzi and Carew 1991), the latter which allows for orientation within water currents.

Prior to the year 2000, there were few ultrastructural studies of the cephalic sensory organs of any opisthobranch, although it was established that sensory cells are the principal cell type, which may be of primary or secondary origin (Emery 1992). Light microscope histological analysis revealed two receptor cell types in the epithelium of the rhinophore groove, while a small rhinophore ganglion is present at the base of each darkly pigmented rhinophore groove (Figure 2) (Emery and Audesirk 1978). More recent studies describe that *Aplysia punctata* possesses three different cell types at the epidermis of the rhinophore groove: supporting cells, ciliated cells, and mucus cells (Gobbeler and Klussmann-Kolb 2007). The surface of the rhinophore groove differs markedly from the relatively smooth outer surface (Gobbeler and Klussmann-Kolb 2007; Cummins et al. 2009b). Scanning electron micrographs of both the rhinophore groove and oral tentacles demonstrate the presence of long cilia (Figure 1), with ciliated cells of the rhinophore occurring once every 5-

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