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Cephalopod Olfaction

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Summary and Keywords

Within the Phylum Mollusca, cephalopods encompass a small and complex group of exclusively marine animals that live in all the oceans of the world with the exception of the Black and Caspian seas. They are distributed from shallow waters down into the deep sea, occupying a wide range of ecological niches. They are dominant predators and themselves prey with high visual capability and well-developed vestibular, auditory, and tactile systems. Nevertheless, their perceptions are chemically facilitated, so that water-soluble and volatile odorants are the key mediators of many physiological and behavioral events.

For cephalopods as well as the other aquatic animals, chemical cues convey a remarkable amount of information critical to social interaction, habitat selection, defense, prey localization, courtship and mating, affecting not only individual behavior and population-level processes, but also community organization and ecosystem function. Cephalopods possess chemosensory systems that have anatomical similarities to the olfactory systems of land-based animals, but the molecules perceived from distance are different because their water solubility is of importance. Many insoluble molecules that are detected from distance on land must, in an aquatic system, be perceived by direct contact with the odour source. Most of the studies regarding olfaction in cephalopods have been performed considering only waterborne molecules detected by the "olfactory organs." However cephalopods are also equipped with "gustatory systems" consisting of receptors distributed on the arm suckers in octopods, buccal lips in decapods, and tentacles in nautiluses.

To date, what is known about the olfactory organ in cephalopods comes from studies on nautiloids and coleoids (decapods and octopods). In the nautiloid's olfactory system, there is a pair of rhinophores located below each eye and open to the environment with a tiny pore, whereas in coleoids a small pit of ciliated cells is present on either side of the head below the eyes close to the mantle edge.

Keywords: cephalopods, olfaction, chemoreception, olfactory organs, olfactory receptors, taste and smell

Introduction

Cephalopods are a class of mollusks that includes exclusively marine animals occupying a wide range of ecological niches, from the surface waters to the deep sea. They populate all the oceans and seas of the world with the exception of the Black and Caspian seas.

The most common cephalopods are squid, cuttlefish, octopus, and nautilus. In relation to their numbers and distribution, recent work based on fishery data revealed that cephalopod abundance has recently increased, affecting the distribution mainly of benthopelagic and pelagic forms when compared with demersal species (Doubleday et al., 2016). This increasing abundance has been related to ocean warming, which seems to accelerate their already short life cycle (Pecl & Jackson, 2008; Rodhouse et al., 2014). Given these postulated environmental changes, the sensory capabilities of cephalopods provide them with excellent tools to face their changing external milieu.

The external world of cephalopods is perceived via well-developed sense organs, considered the most sophisticated of all those of invertebrates (Packard, 1972; Messenger, 1977; Young, 1977, 1989; Budelmann, 1995, 1996; Anderson et al., 2010). With the exception of *Nautilus*, they are highly visual animals able to see under a wide range of light conditions (Hanlon & Messenger, 1996; Grable et al., 2002; Yoshida et al., 2015). Cephalopods have remarkable abilities to camouflage themselves on diverse substrates using visual cues alone (Zylinski et al., 2009; Zylinski & Johnsen, 2011) and recently it has been described the mechanism by which cephalopods can achieve color discrimination with only a single photoreceptor (Stubs & Stubs, 2016;). Furthermore, they are equipped with a lateral line (analogous to fishes), low-frequency sensitivity to sound waves, and the ability to detect predators at long distance (Hanlon & Messenger, 1996). Moreover, they have a highly developed vestibular system for directional sensitivity (Budelmann & Williamson, 1994; Williamson & Chrachri, 2007).

Finally, the chemical world of cephalopods also provides an important source of sensory inputs, especially for those that inhabit at light-limited conditions (Nilsson et al., 2012). Chemical cues could work in combination with visual signals, or alone, to inform cephalopods of ecological changes. In cephalopods, the known chemical sensory epithelia are buccal lips and mouth (Emery, 1975), isolated sensory neurons all over the body surface (Baratte & Bonnaud, 2009; Buresi et al., 2014), arm suckers (Graziadei, 1964; Wells et al., 1965; Graziadei & Gagne, 1976), and olfactory organs (von Kölliker, 1844; Von Zernoff, 1869; Watkinson, 1908). In effect, these sensory neurons appear to act as a sophisticated organ (Polese et al., 2016) that plays a crucial role in mate choice (Gilly & Lucero, 1992; Lucero & Gilly, 1995; Lucero et al., 1992, 2000; Piper & Lucero, 1999; Zatynly et al., 2000; Mobley et al., 2007; Cummins et al., 2011; Di Cosmo & Polese, 2014; Polese et al., 2015), predation (Boal et al., 2000), and food odor detection (Boyle, 1983; Basil et al., 2000; Ruth et al., 2002; Anraku et al., 2005).

Cephalopods are able to detect chemical cues through either contact or distant chemoreception (Boyle, 1983, 1986; Chase & Wells, 1986; Lee, 1992; Boal & Golden, 1999; Alves et al., 2007). The behavioral evidence for distant chemoreception shows that the addition of fish juice to the water causes active movements in octopus (Wells, 1963) and cuttlefish (Messenger, 1977). In this context, cephalopods release the ink that they use as a direct deterrent of predators and as an alarm cue for conspecifics (Palumbo et al., 1999; Di Cosmo, 2003, Di Cosmo et al., 2006; Derby, 2014). Boal (1997) argued that female mating choice in cuttlefish was more likely to be based on olfactory cues than on visual cues. Adding dilute extracts of crabs to the water supply increased the ventilation rate of octopus (Boyle, 1983); typical signs of alarm are shown by octopus when exposed to seawater in which a moray eel had been living (Mac Ginitie & Mac Ginitie, 1968). Furthermore, the ability to detect the sex of conspecifics at a distance, in octopuses, could facilitate reproduction as well as problem-solving ability (Boal, 2006; Anderson et al., 2010). Nevertheless, a blinded octopus will move toward a scent that it perceives as a food source (Chase & Wells, 1986).

More recently, Walderon et al. (2011) demonstrated that octopuses respond to chemical signals from conspecifics and detect a wide range of odors as food or nonfood (seaweed). However, as most coleoids are nocturnal or live at depths where little light is present, the ability to track prey, partner, and predator by scent is crucial to their success (Joll, 1977; Budelmann, 1996). This strongly suggests that the coleoid cephalopods, octopods, cuttlefishes, and squids use distance chemoreception, and the ability to integrate chemical signals with the stimuli perceived by their other sense organs allows them to shape their sophisticated behavior in the sea.

Cephalopod Olfaction Research Through the Years

The first description of the olfactory organs in cephalopods was made by Albert von Kölliker in (1844). He was attracted by a pair of dimples found on each side of the head of both squid and octopus. Initially, these structures were thought to be acoustic organs and only later was their chemoreceptive function, similar to the gastropod osphradium, suggested (Hancock, 1852; Chéron, 1866). Von Zernoff (1869) and Watkinson (1908) provided a detailed description of the olfactory organs in several cephalopods, describing the presence of large cells with a big vacuole. Watkinson (1908) compared the morphology of olfactory organs in 23 species of coleoids, suggesting their analogies with nautiloid rhinophores (Barber & Wright, 1969). The morphology of the organs was described as a flattened pad of cells in *Sepia*, an elongate papilla in *Chiroteuthis*, and a pit of sensory cells in *Octopus*.

In 1974, Woodhams and Messenger provided a partial ultrastructural description of the olfactory sensory neurons (OSNs) in *O. vulgaris*. At about the same time, Emery (1975, 1976) worked on the histology and ultrastructure of the olfactory organ of the squid, *Lolliguncula brevis*, and of the octopod, *Octopus jubini*. He provided a detailed description of different types of OSNs in this species and gave an exhaustive comparative analysis of the OSNs previously described in several species of decapods and octopods (Von Zernoff, 1869; Watkinson, 1908). At the end of the 20th century, Wildenburg (1997) described the structure and histology of the "so-called olfactory organ" in the benthic posthatching stage of *Eledone moschata* and the planktonic paralarva of *Octopus vulgaris*. He concluded that at the posthatching stage, the organ of the benthic species, *E. moschata*, is the more developed of the two.

In the 1990s, however, scientific interest in cephalopod olfaction shifted from morphological to physiological approaches. The group that significantly contributed to the physiological aspect of olfaction in cephalopods was led by Mary Lucero and provided many experimental findings demonstrating the chemosensory capabilities of squid OSNs using electrophysiological techniques (Lucero et al., 1992, Lucero & Gilly, 1995; Piper & Lucero, 1999; Mobley et al., 2007, 2008A, 2008B). Based on the morphological typology of OSNs (Emery, 1975), Lucero's group established the odorant responsiveness of all OSN types and suggested the involvement of the adenylate cyclase pathway in squid olfactory transduction (Mobley et al., 2007, 2008A, 2008B).

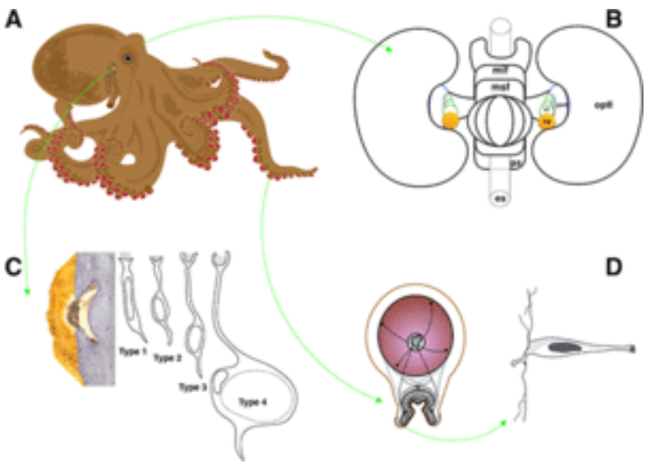

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Figure 1. Octopus chemical senses from whole animal to organ to cells in the organ. A—whole animal in which are visible the olfactory organ and suckers; B—adult *Octopus vulgaris* CNS diagram showing a dorsal view of the lobes involved in chemoreception (msf: median superior frontal; mif: median inferior frontal; ol: olfactory lobe; og: optic gland; ped: peduncle lobe; optl: optic lobe; ps: posterior suboesophageal mass; es: esophagus); C—3D reconstruction of the octopus olfactory organ and the different types of OSNs; D—diagram of segment of the arm of Octopus with a sucker and its chemical sensory cell.

Behavioral studies, which started almost contemporaneously with physiological studies, focused mainly on decapods. These studies demonstrated the role played by olfaction in many aspects of the chemosensory ecology of cephalopods (Boyle, 1983, 1986; Chase & Wells, 1986; Lee, 1992; Lucero & Gilly, 1995), such as mate choice, prey detection (Budelmann et al., 1997; Boal & Golden, 1999; Hanlon & Shashar, 2003), and conspecific odor perception (Walderon et al., 2011; Wood et al., 2008). More recently, Polese et al. (2016) described the detailed morphology of young male and female *Octopus vulgaris* olfactory epithelium. Using a combination of classical morphology and 3D reconstruction techniques, they proposed a new classification for *O. vulgaris* olfactory sensory neurons (Figure 1A, B, C). Using specific markers such as olfactory marker protein and proliferating cell nuclear antigen, they identified and differentially localized both mature olfactory sensory neurons and olfactory sensory neurons involved in epithelial turnover. This suggests that the *O. vulgaris* olfactory organ is extremely plastic, capable of changing its shape, and that proliferation of cells continues in older specimens. Furthermore, an integrative view of the role of chemical perception in the life of *Octopus vulgaris*, at individual, population and ecosystem levels, has been proposed (Di Cosmo & Polese, 2014; Polese et al., 2015, 2016)

Behavioral Evidence for Olfaction in Cephalopods

Spatial orientation in the feeding and reproductive behavior of cephalopods is guided by chemical cues. In nautiloids, the olfactory organ is represented by a pair of rhinophores (Young, 1965; Barber & Wright, 1969; Barber, 1987). These enable animals to follow an "odor" trail to its source in three dimensions. However, if the rhinophores are blocked, either uni- or bilaterally, the 90 thin tentacles can still detect odor, though without providing any spatial information (Basil et al., 2000, 2005).

In tanks, cuttlefishes previously exposed to crab odor perform better on their first attacks on crabs than cuttlefish that were not previously exposed (Boal et al., 2000). This finding suggests that the odors enhance food arousal and improve attention to the odor of the prey of cephalopods, which can then optimize the predatory attack.

Wells (1963) proposed that *O. vulgaris* can distinguish between objects based on their chemical differences alone. He described the animal's ability to perceive chemicals using arm suckers as "taste by touch." He previously proved that the responses of blinded animals to sardine blood were quite unaltered by removal of the olfactory organs (Wells & Wells, 1956). It seems that the *O. vulgaris* gustatory system consists of receptors distributed on the suckers, where the aquatic equivalent to taste takes place (Wells, 1963; Graziadei & Gagne, 1973; Anraku et al., 2005; Grasso & Basil, 2009) (Figure 1D).

Chemical sensing also plays an important role in cephalopod reproduction. For example, *Nautilus pompilius* females extend their tentacles fully when tracking male odors (Basil et al., 2002), while sexually mature males are attracted to females by excretions of the rectum (Westermann & Beurlein, 2005). Cuttlefish females choose their mates based on chemical cues (Boal, 1996, 1997), while chemical cues from squid egg capsules stimulate aggressive behavior related to competition for mates in male squids (King et al., 2003). These data demonstrate the importance of chemical perception in cephalopod reproductive behavior. In 2011, Walderon et al. demonstrated the role of olfaction in distance chemoreception of conspecifics in *Octopus bimaculoides*.

Integrative View of Chemical Perception in Cephalopods

All the sense organs contribute to animal life, but the relative importance of each sense was established during evolution. The apparent difference in the importance of one sense over another is strictly related to the ecological niches that the animals occupy. Cephalopods are described as animals that rely on their visual sense for most of their activities (Hanlon & Messenger, 1996). This prevailing view, together with sophisticated behavior exhibited by cephalopods, almost completely drove the attention of researchers to give chemical perception a secondary role. But even complex and sophisticated animals like cephalopods that occupy many ecological niches of the sea, including the deep sea with low light conditions, must integrate their sensory information appropriately to achieve evolutionary fitness.

The integration of multimodal sensory inputs may occur at central and/or peripheral levels, at the output neurons converging to final behavior, or at any intermediate point along the processing path (Di Cosmo & Polese, 2016). It is clear that the localization of the neuronal mechanisms underlying multimodal processing is not an easy task. Recent research (Di Cosmo & Polese, 2014; Polese et al., 2015, 2016) examining the central control, anatomical pathways, and molecules involved in

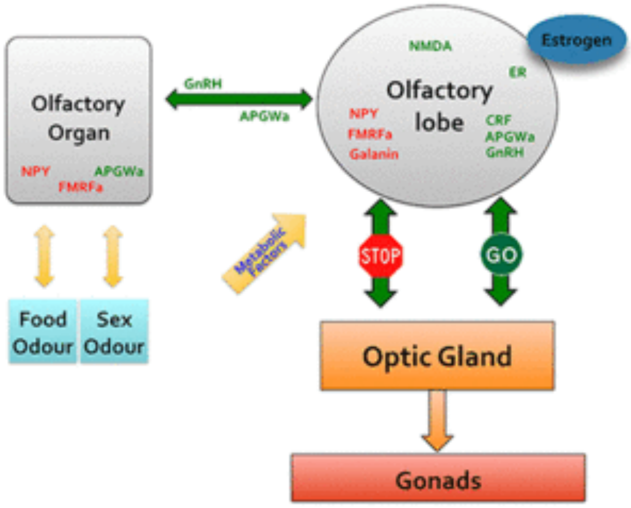

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Figure 2. Control of reproductive behavior based on chemical cues. The olfactory lobe acts as a switch between growth and reproduction. In addition, the olfactory lobe modulates the olfactory organ to be more sensitive to food or sex odors via the molecular players identified: (in red) FMRFamide, NPY, and Galanin inhibit reproduction and stimulate food intake; (in green) GnRH, APGWamide, ER (estrogen receptor), and NMDA stimulate reproduction inhibiting sensitiveness to food odors.

chemical perception via the olfactory organs found that they are often shared with those of other sensory modalities. In fact, the olfactory lobe, which receives nerve fibers coming from the olfactory organ, appears to be at the crossroads of different sensory pathways. This lobe, situated on the optic tract, close to optic gland, is organized in three interconnected lobules (Figure 1B). The olfactory lobe also receives fibers from the dorsal, basal, and optic lobes and sends fibers to the basal and subpedunculate lobes (Messenger, 1967). Based on these neuroanatomical connections, it constitutes a center of convergence and interception of fibers coming from lobes involved in the control of vision, motor programs, and reproduction (Young, 1971; Wells, 1978; Hanlon & Messenger, 1996; Di Cosmo & Di Cristo, 1998; De Lisa et al., 2012a, 2012b; Di Cosmo & Polese, 2013, 2014). The integrative function played by the olfactory lobe has only recently been highlighted by assigning a crucial role to chemical perception in the physiological and behavioral control of cephalopods (Di Cosmo & Polese, 2016; Polese et al., 2015, 2016) (Figure 2). Several experimental findings on chemical perception were presented in the past, but they must now be read in light of this new integrative perspective.

Chemical Cues and How They Are Perceived by Cephalopods

Traditionally, the olfactory system in any animal is the primary sensory system that responds to chemical stimuli emanating from a distant source. The other chemosensory sense is gustation or taste, which generally requires direct contact with the source for detection.

Cephalopods possess sensory systems that have anatomical similarities to the olfactory systems of land-based animals, but the molecules perceived from a distance source are different because their water solubility is of importance.

Consequentially, in the aquatic environment, have been considered ecologically relevant odorants water soluble compounds such as salts, sugars, amino acids, amines, peptides, proteins, and functionalized hydrocarbons.

To perceive this kind of molecule, on the one hand, the relaxed and erect postures of the octopus olfactory organ result in an intrinsic capability of movement that allows the animal to orient itself to detect the spatial gradient of these chemical cues, which help in navigation and trigger spatial memories (Huffard, 2013; Polese et al., 2016).

On the other hand, many insoluble molecules that are detected from distance on land, generally compounds with a molecular weight (MW) smaller than ~300 Da (Mollo et al., 2017; Mori et al., 2006; Touhara & Vosshall, 2009), must be perceived by touch in aquatic systems if they are not carried by micelles or rafts, but are just held or laid on a substrate. For example, compounds known to contribute to the smell of terrestrial plants have been isolated in marine invertebrates that use them as defensive chemical weapons (Giordano et al., 2017; Mollo et al., 2014), they could be “smelled” by an octopus or any other aquatic animals just when they are touched.

It has been demonstrated that aquatic animals, including crustaceans and fish, have “gustatory systems” (e.g., leg detectors on lobsters and blue crabs, and barbels on catfish) that can detect chemicals dissolved in water without the requirement of physical contact with an object other than the chemicals themselves. These gustatory systems can respond to very low doses of those chemicals and evoke behaviors (Caprio & Derby, 2008; Schmidt & Mellon, 2011). Although it has been shown that both crustacean and fish are able to detect hydrophobic compounds by a tactile form of chemoreception (Giordano et al., 2017); in particular, they show that little shrimp (*Palemon elegans*) and also fish (*Danio rerio*) use their chemosensory mouthparts to perceive typical odiferous compounds usually smelled by humans. In the same way, other benthic animals, such as octopus, could follow, or avoid, chemical trails adherent to the substrate by recognizing gradients of concentration.

The debate about the terms *taste* and *olfaction* in relation to the various chemosensory systems of marine and aquatic species requires further elaboration, but it is important to avoid making any assumption based solely on organ topology (Mollo et al., 2014, 2017). The traditional view of the chemical senses based on their spatial range is being supplanted by a new vision based on the natural products that are the actual mediators of the chemosensory perceptions.

The majority of the studies regarding the olfaction of cephalopods have considered prevalently waterborne molecules that are detected by the "olfactory organs." However, cephalopods use "gustatory systems" located on the arm suckers in octopods, the buccal lips in decapods, and the tentacles in nautiloids, which are able to detect molecules by contact. In light of the fact that the majority of volatile odorant molecules are insoluble or have a very low solubility in water, octopuses, as all the other aquatic animals, exhibit a peculiar performance that can be provocatively described as "smell by touch." This would be supported by the demonstration of the presence of olfactory receptors on their "gustatory systems."

However, taste and olfaction are part of a multimodal system of information transfer. The synchronous use and integration of different signals using different channels have the advantage of improving recognition, discrimination, and memory of inputs by the environment.

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