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Review

Role of olfaction in *Octopus vulgaris* reproduction

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ABSTRACT

The olfactory system in any animal is the primary sensory system that responds to chemical stimuli emanating from a distant source. In aquatic animals "Odours" are molecules in solution that guide them to locate food, partners, nesting sites, and dangers to avoid. Fish, crustaceans and aquatic molluscs possess sensory systems that have anatomical similarities to the olfactory systems of land-based animals. Molluscs are a large group of aquatic and terrestrial animals that rely heavily on chemical communication with a generally dispersed sense of touch and chemical sensitivity. Cephalopods, the smallest class among extant marine molluscs, are predators with high visual capability and well developed vestibular, auditory, and tactile systems. Nevertheless they possess a well developed olfactory organ, but to date almost nothing is known about the mechanisms, functions and modulation of this chemosensory structure in octopods. Cephalopod brains are the largest of all invertebrate brains and across molluscs show the highest degree of centralization. The reproductive behaviour of *Octopus vulgaris* is under the control of a complex set of signal molecules such as neuropeptides, neurotransmitters and sex steroids that guide the behaviour from the level of individuals in evaluating mates, to stimulating or deterring copulation, to sperm–egg chemical signalling that promotes fertilization. These signals are intercepted by the olfactory organs and integrated in the olfactory lobes in the central nervous system. In this context we propose a model in which the olfactory organ and the olfactory lobe of *O. vulgaris* could represent the on–off switch between food intake and reproduction.

1. Introduction

Olfaction is a vitally important sense for all animals, since how they perceive the environment and make proper behavioural choices are strictly related to their perceptive capabilities. Environmental odours guide animals to locate food, water, and nesting sites, as well as alerting them to avoid dangers. Odours emanating from other species, known as allelochemics (Whittaker and Feeny, 1971), control prey localization, homing, symbiotic associations, territorial marking, predator deterrence and avoidance, metamorphosis and growth. Conspecific's odours are known as pheromones (Shorey, 1976). They can be recognition pheromones to indicate the identity of individuals, social status, social group, and place; as aggregation pheromones to mediate feeding, sex, and aggression; dispersion pheromones to maintain individual spacing and minimize predation; or reproductive pheromones to trigger courtship displays and postures (Ache and Young, 2005; Buck, 2000; Carbone et al., 2013; Eisthen and Polese, 2006).

The chemosensory systems are able to detect chemical stimulus emanating from a distant source. Terrestrial vertebrates and insects detect low concentrations of airborne, volatile chemical substances. Aquatic animals, while not encountering airborne (volatile odorants), possess sensory systems that are anatomically similar to the olfactory systems of land-based animals. "Odours" for these aquatic animals are sapid molecules in solution (Hay, 2009; Mollo et al., 2014). The species share striking similarities in the organization of the olfactory pathway, from the nature of the odorant and receptor proteins, to the organization of the olfactory central nervous system (CNS), through odour-guided behaviour and memory. These common features span a phylogenetically broad array of animals, implying that there is an effective solution to the problem of detecting and discriminating odours that remains a common challenge for all animals (Ache and Young, 2005; Eisthen and Polese, 2006; Laurent, 2002; Mollo et al., 2014; Smith, 2008).

Molluscs are a large and diverse group of aquatic and terrestrial animals that rely heavily on chemical communication. They have generally dispersed senses of touch and chemoreception. Excellent studies at behavioural, neural and biochemical levels on gastropods olfaction has been made and, among the aquatic species, *Aplysia*, *Tritonia* and *Lymnaea* are used as valuable model systems (Cummins and Degnan, 2010; Cummins and Wyeth, 2014).

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Aplysia represents an excellent model in terms of structure and function of olfactory organs in gastropods (Wertz et al., 2006), and the availability of central neuron transcriptomes (Moroz et al., 2006) as well as the genome enables detailed genetic analyses. *Aplysia* and other aquatic gastropods, most important, have no acoustic sense and their world is largely chemically guided so that water-soluble odorants mediate many physiological and behavioural events, leading to aggregation, habitat selection, defence and mating. Mate attraction and subsequent mating is stimulated by the release of conspecific water-borne sexual pheromones consisting of four small proteins named attractin, enticin, temptin and seductin (Cummins et al., 2004; Painter et al., 2004).

The case is quite different in cephalopods, which represent the smallest class among marine molluscs and (excluding *Nautilus*) they are highly visual animals able to see under highly varying light conditions. Cephalopods have remarkable abilities to camouflage themselves on diverse substrates using visual cues alone (Zylinski and Johnsen, 2011). Foraging octopuses use visual cues to camouflage themselves and mimic fishes (Hanlon et al., 2010). They have low-frequency sensitivity and a lateral line (analogous to fishes) to hear and detect at long distance the presence of predator (Hanlon and Messenger, 1998).

Chemical signalling is another possible source of sensory input, which could work in combination with visual signals or alone to inform cephalopods of ecological factors, this is important especially for species that populate light-limited habitats (Nilsson et al., 2012).

In coleoid cephalopods there are three known chemical sensory epithelia: buccal lips (Emery, 1975), arm suckers (Graziadei and Gagne, 1976), and olfactory organs (Zemoff, 1869). The function of sensory epithelia in the buccal lips and arm suckers has been well studied and shows capabilities for both tactile and distance chemoreception (Hanlon and Messenger, 1998).

Within the cephalopods the *Octopus* brain is unique in possessing a chemo-tactile memory system that may have evolved in relation to its benthic life style (Hanlon and Messenger, 1998). Octopods use the arms to explore and detect tactile and chemosensory information functioning as "natural biosensors" (Di Cosmo, personal observation). These proprieties are conferred on the arms by their appendages, with the suckers supplied with receptor cells responsive to tactile and chemical stimuli.

Nevertheless cephalopods possess a well developed olfactory sense. Olfaction plays a role in mate choice of squid and cuttlefishes (Cummins et al., 2011; Gilly and Lucero, 1992; Lucero and Gilly, 1995; Lucero et al., 1992, 2000; Mobley et al., 2007; Piper and Lucero, 1999; Zatynly et al., 2000) and improves predation on crabs by cuttlefishes (Boal et al., 2000). *Nautilus* use olfaction for distant food odour detection and location, and perhaps for mate choice (Basil et al., 2000; Ruth et al., 2002).

Two control systems are involved in decoding the signals coming from the sense organs and in selecting an appropriate behaviour: the nervous and the endocrine systems (Hartenstein, 2006; La Font, 2000; Wells and Wells, 1959; Wells, 1962; Young, 1971). The reproductive behaviour of *Octopus vulgaris* is under the control of a complex set of internal and external molecules. Internal signal molecules such as sex steroids (Di Cosmo et al., 2001; De Lisa et al., 2012), neuropeptides (Di Cosmo and Di Cristo, 1998; Di Cristo et al., 2002a,b, 2005, 2009a) and neurotransmitters (Di Cosmo et al., 2004, 2006) guide the behaviour from the level of individuals in evaluating mates, to stimulating or deterring copulation, to sperm–egg chemical signalling that promotes fertilization (De Lisa et al., 2013). External chemical stimuli are, instead, detected by the olfactory organs and integrated in the olfactory lobes in the central nervous system. The olfactory organ results to play a key role in the development of the switch in behaviour from growth to reproduction (Polese et al., 2012, 2013; Di Cosmo and Polese, 2014). In this context we propose a new integrative approach, that goes over the recent model proposed (Di Cristo, 2013) in which is not considered any environmental chemical involvement in the control of reproduction and that adds the olfactory organ of *O. vulgaris* to the already described olfactory lobe as the on–off switch between food intake and reproduction.

2. Olfaction in *O. vulgaris*

Traditionally the olfactory system in any animal is the primary sensory system that responds to chemical stimuli emanating from a distant source whereas other chemosensory systems generally require physical contact with the source for detection, and this sensory modality is called gustation.

Consequentially, in aquatic environment, ecologically relevant odorants are those compounds that are easily dissolved in water, such as salts, sugars, amino acids, amines, peptides, proteins and functionalized hydrocarbons. Aquatic animals, including crustaceans and fish have a "gustatory systems" (e.g., leg detectors on lobsters and blue crabs, and barbels of catfish) that can detect chemicals dissolved in water as well 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 behaviours (Schmidt and Mellon, 2011; Caprio and Derby, 2008). In *O. vulgaris* the "gustatory systems" consists of receptors distributed on the suckers, considered the aquatic equivalent to taste (Wells, 1963; Graziadei and Gagne, 1973; Grasso and Basil, 2009), whereas chemoreception of water-born stimuli from a distant source seems to be detected by the olfactory organs (Anraku et al., 2005).

O. vulgaris is a predator with high visual capability as well as developed vestibular, auditory, and tactile systems. In some cases, octopuses are also prey for other marine animals, but it is not clear to what degree octopuses perceive danger by visual, tactile, auditory, and/or chemical cues, even though, given the presence of integrative sensory centres, it is reasonable to hypothesize that they use multimodal cues to perceive danger. Interestingly, for most part of their life, octopuses are solitary animals interacting with conspecifics just for reproductive purposes, therefore it is plausible to hypothesize that they use chemical compounds to find a partner. The anatomical descriptions of a putative olfactory organ in cephalopods first appeared in early literature (von Kölliker, 1844), followed by more recently demonstrations of their chemosensory capabilities and sensory mechanisms. To date, what is known about the olfactory organ in cephalopods comes from studies of *Nautilus* (Basil et al., 2000; Ruth et al., 2002) and decapods (Lucero and Gilly, 1995; Lucero et al., 1992, 2000; Mobley et al., 2007, 2008a,b; Piper and Lucero, 1999; Villanueva and Norman, 2008). In squid the olfactory organ is the site of a sensory epithelium resulted of ciliated supporting cells and different types of receptor cells that are bipolar neurons sending an dendritic stalk branch to the surface of the epithelium where sensory cilia are exposed to the marine environment. Each receptor neuron is connected to the 'olfactory lobe' and other areas of the brain with axon leads from their basal surface (Messenger, 1967, 1979). Recently Walderon et al. (2011) investigated the role of the olfaction in the distance chemoreception of conspecifics in *Octopus bimaculoides*, but almost nothing is known about the mechanisms, functions and modulation of the olfactory organ in octopods.

2.1. Olfactory organ of octopuses

In the mid 18th century Albert von Kölliker (1844) was attracted by a pair of dimples found on both sides of the head of both octopus and squid. These openings in the skin were thought