Evolution of the Chemical Communication and Olfactory System in Animal Kingdom

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Chemical signals transmit a large amount of information about the environment, enabling animals to identify desirable elements (such as food) or dangers to avoid (such as predators) and to locate mating partners. Considering the wide range of different chemicals, it is not surprising that organisms, living in different contexts, use an important repertoire of receptors and signaling pathways to probe their environment. The aim of this work was to describe the major stages in the development of the olfactory organ during the course of evolution. The few cells on the body surface of primitive organisms gave way to an individualised organ, at first rudimentary and then increasingly complex and efficient.

Introduction

Animals used a wide variety of methods to locate vital environmental information or communicate with each other, the most common modes being visual, auditory and chemical communication systems. Until recently, research has focused on the visual and auditory systems, but recent improvements in chemical analysis methods have shown that chemical signals are involved in communication between a large number of organisms in a multitude of contexts (Müller-Schwarze and Silverstein 1980, Bradbury and Vehrencamp 2011). Chemical signals have several advantages over audible and visual signals: they are effective in darkness, around obstacles, and are relatively persistent over time, even in the absence of the transmitter (Alberts 1992). Odiferous molecules are transported by the external environment (air, water) or by the organisms themselves. Some chemicals have no spontaneous informative, appetitive or aversive, value. However, a value can be associated with them through learning. These chemical cues served as a guide for locating environmental information essential for survival, such as detection of food or sources of danger (Table 1) (Ache and Young 2005). Other chemicals have an intrinsic signal value. This is the case for the semiochemicals, which elicit a biological response in individuals of the same species (pheromones) or different species (allelochemicals) (Bakthavatsalam 2016). Pheromones elicit a specific reaction, such as a stereotyped behavior or a developmental process in congeners. Allelochemicals are involved in interspecific communication. Some allelochemicals are beneficial to the emitter of the signal (allomones), others to the receiver (kairomones), or to both the emitter and the receiver (synomones) (Table 1) (Sbarbati and Osculati 2006). All these chemical substances present a great structural and functional diversity,

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requiring the decoding of information by a specialized system. Each animal group, whether invertebrate or vertebrate, has its own chemical signal detection system adapted to its living conditions, which requires a high discrimination power on part of the receiver, in order to allow distinction of an odor among others, and allows it to respond appropriately to chemical environmental information (Wyatt 2014). In addition, chemicals are often produced intermittently, making it difficult for animals to decipher the odor signal. Indeed, animals are subjected to turbulence in the air or water, which disrupts the diffusion of odors and gives rise to highly discontinuous odor plumes. Finally, odors are rarely single compounds, but a combination of molecules, whose treatment is more complex. These different characteristic aspects of olfactory signal decoding give rise to certain organisational similarities between olfactory systems of phylogenetically different species (Krieger 1999, Ache and Young 2005). The aim of this review was to describe the different ways in which olfactory signals are detected and processed in the animal kingdom.

Table 1. *Chemicals Signals Involved in Animal Interaction (Invertebrates and Vertebrates)*

Chemical substances	Effects produced	Types		Examples of biological roles
Chemical cues	Non intentionnel effects	Physico-chemical parameters of the environment as guide to future action		Assess food or water, avoid fire
Semiochemicals	Interspecific effects	Allelochemicals	Kairomones: chemicals that benefit the receiver but not the emitter of the signal	Predation, parasitism
			Synomones: chemicals that favor both the emitter and the receiver of the signal	Mutualism
			Allomones: chemicals that benefit the emitter but not the receiver of the signal	Defence secretions
	Intraspecific effects	Pheromones	Releasers: initiate immediate behavioral responses	Identity of individuals, social status, social group
			Primers: causes physiological, morphological changes	

The Chemosensation in Invertebrates

Most invertebrates use olfaction as their main sensory modality and have a highly evolved olfactory system that enables them to reach an important level of sensitivity and specificity.

In Cnidarians

In most cnidarians, vision is absent and prey is captured by an extraordinarily sensitive chemodetection. Most of studies have focused on jellyfish. Chemicals present on or originating from prey are detected by receptors located on specialized epidermal cells, that activate the cnidocyte mechanoreceptors and the discharge of nematocysts into the prey. The mechanoreceptors and chemoreceptors are neutrally connected and cover most of the exterior surface (Watson and Hessinger 1989, Albert 2011). Archdale and Anraku have shown that other chemoreceptors are located in the lateral tracts of the *Aurelia sp.* jellyfish oral arms, whose function is to select captured objects according to their taste (Archdale and Anraku 2005).

In Flatworms (Platyhelminths)

Chemoreceptors are found in multi-sensory structures, the auricles, located near the anterior of the animal, behind the photoreceptors. The auricles contain nerve cells, whose dendritic region in contact with the external environment is ciliated and permits sensitivity to touch and certain chemicals. The chemoreceptors allow the detection of prey and ensure the orientation towards food sources (Mori et al., 2019). For example, *Platydemus manokwari* locates snail slime trails, sometimes even in trees (Yamaura 2008).

In Nematodes

The free-living *C. elegans* can modulate its behavior by reacting to at least 50 odorous substances over a wide range of concentrations. Its olfactory organs consist on the symmetric amphid sensilla in the head and composed of a small number of interconnected neurons, gland cells and supporting cells. Each olfactory sensory neuron expresses many different olfactory receptors and is polymodal (dedicated to several sensory modality). Similarly, the parasitic worms use olfactory cues to find and infect hosts. Studies have demonstrated that their olfactory behaviors are specific to each species, despite the fact that sensory neuroanatomy is approximately conserved across the different nematode species (Rengarajan and Hallem 2016).

In Annelids

The chemoreception is involved in the behaviors of annelids. In polychaetes, the chemicals are detected by the nuchal organs, including ciliated supporting cells, bipolar primary sensory cells and a retractor muscle. Other structures, such as the sensory cells of the parapodial cirri in errantia or the sensory cells of the feeding palps in sedentaria have a chemoreception function in response to specific chemicals signals (Lindsay 2009). In clitellates, the majority of primary sensory cells are located in the body wall. Earthworms perceive diverse environmental chemicals, mainly through chemoreceptor tubercles in the prostomium and anterior segments and through sensory cells in the mouth region. Receptors covering the body respond specifically to salt and pH (Laverack 1960). Their nervous system is made up of a

chain of ganglia that are highly sensitive to any change in the environment, enabling them to identify both food resources and harmful environments (Knapp and Mill 1971, Kiszler et al. 2012, Syed et al. 2017).

In Molluscs

Chemical system is well developed, as indicated by the large number of neurons which it contains, compared to the rest of the nervous system. It compensates for the poorly developed visual system and is used to detect odoriferous molecules at a great distance, providing the animal with information about habitat selection, food finding, interactions with conspecifics, defense, or mating (Emery 1992).

Gastropods are by far the largest class of molluscs (accounting for around 80% of all species) and include between 40,000 and 150,000 species. The sensory perception of terrestrial animals has been relatively well studied. They have two olfactory pathways (Ito et al. 2000). The main pathway involves the perception of olfactory information during long-distance orientation. It is provided by the posterior tentacles. The second pathway, provided by the anterior tentacles, seems to be essentially devoted to contact chemoreception. These two olfactory pathways are structurally very similar, the main differences being their size and the presence of eyes in the posterior tentacles (ommatophores) (Ito et al. 2000). Different studies have shown that structure of the olfactory system of molluscs is very similar to that of arthropods and vertebrates (Chase and Tolloczko 1993, Eisthen 2002). Described in terrestrial animals, it consists of a sensory epithelium, a tentacular ganglion and a tentacular nerve connecting the tentacular ganglion to the procerebral lobe of the central nervous system. The procerebral lobe is directly connected to the buccal and pedal ganglia, respectively the center of feeding and locomotion. It should be noted that the olfactory epithelium contains both lipid glands and protein glands. The nature and location of the latter suggest that they are involved in the secretion of binding proteins associated with the transport of odor molecules to the membrane receptors, as in insects and mammals (Chase and Tolloczko 1993).

Movement and orientation are closely linked to the perception of olfactory stimuli (Gervais et al. 1993). The orientation of terrestrial gastropods towards an odorous source involves different forms of locomotor response. In trail following, the animal uses its anterior tentacles to follow a mucus trail left by itself, a conspecific or an animal of another species. Anemotaxis is involved in homing behavior, courtship and sometimes foraging. In the presence of an air current, orientation is made possible by a single posterior tentacle sampling the air at different times during movement. However, in a calm environment with no air currents, orientation follows a concentration gradient and requires the use of both posterior tentacles (Chase and Croll 1981).

To guide their navigation behaviour, aquatic gastropods also use chemical cues detected by contact chemoreception or chemoreceptors sampling the water. In this case, odors are transported by advection or diffusion and the aquatic snails and slugs rely on odor-gated rheotaxis and/or chemotaxis to navigate (Wyeth 2019). In addition to tentacles (rhinophores), the primary olfactory organs can be the lips or potentially a single fused oral veil over the mouth. The osphradium, located in the

water entrance of the pallial cavity, in front of the gills, is also chemosensory but it is not certain that it is involved in controlling the direction of movement relative to the odorous sources. It would be used to modulate physiology depending on the presence or the concentration of chemical cues in the environment (Wedemeyer and Schild 1995, Kamardin et al. 1999, Simone 2021, Wyeth 2019).

In Arthropods

Cuticular outgrowths, called sensillae, are sensory organs mediating tactile, gustatory or olfactory modalities. They are consisting of bipolar sensory cells, enveloping cells and a cuticular structure. In decapod crustaceans, aesthetascs are the specialized chemosensory sensilla containing chemosensory neurons, other sensillum types containing mechano- and/or chemosensory neurons. Aesthetascs occur on the lateral flagellum of the first antennae (Steullet et al. 2002, Schmidt 2007). Each aesthetasc includes a large number of primary olfactory receptor neurons (40-500 neurons), that allows aesthetacs to provide the many information-coding channels, needed to adapt to a complex odor environment. The afferent projections of the olfactory receptor neurons transit in the antennular nerve before reaching the olfactory lobe in the brain (Gleeson et al. 1996).

Olfaction is a remarkably sensitive and selective sense for most insects, which used it in a wide range of intraspecific and interspecific communication modes. Pheromonal signals guide many insects to conspecific mating partners and social behaviors. For example, in mulberry bombyx (*Bombyx mori*), bombykol is emitted by the females to specifically attract males. In honey bees, pheromones organize the defense of the hive, recruit foragers and reinforce the primacy of the queen (Paoli and Galizia 2021). Ants used a diversity of volatile substances in different behaviors, such as navigation, alarm or courtship (Jackson and Châline 2007, Hölldobler and Wilson 2009). Pheromones are also necessary for interspecific communication. Odors emitted by host plants attract phytophagous insects, and those emitted by animal hosts attract hematophagous or parasitoid insects. Often, these odors are made up of a mixture of compounds in very specific proportions (Martin et al. 2011).

Despite the great diversity of insect behaviors associated with their olfactory environments, the olfactory system is relatively simple. Olfactory sensilla are mainly located on the antennae, but also sometimes in other parts of the body, such as the maxillary palps in flies (Hansson and Stensmyr 2011). The number of sensilla for pheromone detection is about thousands to tens of thousands among the species (more than 60,000 in *Manduca sexta*) and they show a variety of shapes, but a common structure (architecture). Each sensilla responds specifically to a chemical molecule or a family of chemical molecules, which explains the great morphological diversity. Based on their chemosensory specificity (pheromones *versus* general odorants), various types of olfactory sensilla are described. Sensilla house olfactory sensory neurons (OSN), generally between 2 and 5, although in exceptional cases, the OSN number can be very high, as in the ant *Camponotus japonicus*, where 130 neurons have been recorded (Keil 1999, Nakanishi et al. 2010).

Odorant molecules penetrate through the cuticular pores of the sensilla hair, are dissolved in the aqueous sensilla lymph by Olfactory Binding Proteins (OBPs) and

transported to specific receptors expressed in the dendritic membrane of the OSNs (Plettner et al. 2000, Hansson and Stensmyr 2011). The OBPs are then rapidly degraded, contributing to the dynamics of the responses. Binding of odorant substance to the receptor initiates ionotropic or metabotropic mechanisms, allowing chemical signal transduction into an electric response in the OSN. The sequence of action potentials is then transmitted to primary olfactory brain, the antennal lobe, subdivided into glomeruli. Each glomerulus received the afference of the OSNs with the same receptor type. The output of glomeruli is carried to higher brain centers, in particular the mushroom bodies and the lateral protocerebrum, where odor perception and learning take place (Szyszka and Galizia 2015).

Even if the literature on chelicerate chemical communication is not as extensive as for insects, it is known that the chemical sense of arachnids is well-developed and that many of their behaviors depend on chemical signals (chemotactile or/and olfactory pheromones) (Barth 2001, Uetz and Roberts 2002). For example, jumping spiders (family Salticidae) used, despite their good eyesight, olfactory pheromones to species and sex identification (Cerveira and Jackson 2013). Whip spiders return to their home refuge despite structurally complex tropical environment using the sensory input from the antenniform legs (modified anterior walking legs) (Bingman et al. 2017). In fact, spiders may use chemical signals to avoid predator or locate prey, to recognize congener or sexual partner (Uetz and Roberts 2002). Most of the sensory organs of arachnids are located on their extremities, due to the absence of antennae. The pedipalps and the anterior legs particularly carry chemoreceptors (Foelix 1985).

Studies on the olfactory system in the Myriapod *Scutigera coleoptrata* have shown that its primary olfactory center is well developed, allowing good odor recognition and discrimination (Sombke et al. 2009). It is interesting to note that the shape of the olfactory neuropils (olfactory glomeruli) is distinct from that in Hexapods and malacostracan Crustacea, suggesting an independent evolution of the olfactory sense in these two phylogenetically separate clades of arthropods (Sombke et al. 2011).

In Echinoderms

Echinoderms are slow-moving animals that rely on waterborne chemical signals to adapt their behavioral responses. Sea urchins can precisely orient themselves towards chemicals emanating from potential food source or from conspecifics, and away from those emanating from nearby predators or crushed conspecifics. They use chemicals to enable external fertilization (Lawrence 2013). Different studies have shown that the activation of the spines, the tube feet and the pedicellariae, equipped with a high number of chemoreceptors, permit a sophisticated chemosensory response (Campbell 1983, Solari et al. 2021). The sea stars can also respond to chemicals and their orientation path is guided by the stimulus field. They possess sensory tentacles on the tips of each arm, enabling them to detect ambient odors and odor plumes (Moore and Lepper 1997, Garm 2017, Motti et al. 2018).

In Protochordates (Cephalochordate and Tunicate)

Sensitivity to external chemical substances has been demonstrated in the non-vertebrate chordates, but it does not always seem to play a role in their behavioral repertoire. In the cephalochordate Amphioxus (*Branchiostoma lanceolatum*), epithelial cells located at the front end of the body enable it to react to various chemical substances (Lacalli 2004). These scattered olfactory cells are homologous to the olfactory epithelium found in vertebrates. In fact, it has been shown that amphioxus has orthologs of vertebrate olfactory receptors, which demonstrates that the vertebrate receptors evolved at least 550 million years ago (Satoh 2005, Churcher and Tylor 2009).

It has not been clearly established that Tunicates are chemosensitive. However, cells that can act as olfactory sensors, are located in the region around the lips in the class Thaliacea (doliolida and salpa), and in the ventral organ, under the lower lip in the class Appendicularia (*Oikopleura*) (Mackie and Burighel 2005).

The Chemosensation in Vertebrates

The main olfactory system of vertebrates shares many characteristics with that of nematodes, molluscs, or arthropods. In general, the olfactory receptor cells detecting the odoriferous molecules are bipolar neurons with a dendrite that protrudes into the fluid medium. The dendrite is covered with cilia and/or microvilli, where are localized the membrane-bound odorant receptors, whose genes are members of a large superfamily. At the opposite pole of the neuron, the axon projects directly into glomeruli of the main olfactory bulb. A third layer of neurons forms the superior olfactory center, involved in multimodal sensory integration (Holley et al. 2013, Eisthen 2002).

However, although vertebrates and invertebrates share commonalities in their strategies to recognize and discriminate odors, differences exist in the olfactory signaling mechanism (odorant receptors and olfactory transduction). In particular, vertebrate olfactory receptors (main olfactory epithelium) are metabotropic receptors, generally belonging to the G protein-coupled receptor family, whereas insect receptors are ionotropic receptors, which of course has major implications for the temporal coding of odors and feedback mechanisms. Moreover, the vertebrate olfactory receptor repertoire is considerably largest (for most of them, 300-1300 olfactory receptor genes) than that of insects (50-160 olfactory receptor genes). A large fraction of the receptor genes in the vertebrate genome are pseudogenes (12% in zebrafish – 52% in humans); the fraction of pseudogenes is low, or non-existent in insects (Nei et al. 2008, Kaupp 2010).

Observation of the olfactory epithelium of various vertebrates has enabled it to be classified into two types: a fish-type olfactory epithelium, observed in flatfish and lungfish, and a mammal-type olfactory epithelium, observed in amphibians, reptiles, birds and mammals (Taniguchi and Taniguchi 2014).

In addition to the main olfactory system, an accessory olfactory system, the vomeronasal system, is present in most amphibia, reptiles and terrestrial mammals,

although absent in birds, many bats and catarrhine Old-World monkeys (Brennan 2001). It consists of the peripheral vomeronasal organ, the accessory olfactory bulb and its projections to distinct cerebral zones. Depending on the species, the vomeronasal organ communicates with the nasal or the oral cavity to uptake odoriferous molecules, which may be pheromones or non-pheromonal social chemical signals (Halpen 1987, Silva and Antunes 2017). It should be noted that the histological structure of the vomeronasal sensory epithelium is different in snakes, and bears no resemblance to the other vertebrate species (Taniguchi and Taniguchi 2014).

In the primitive vertebrates, the olfactory organ is unique and opens outwards through a single nostril. Then in the course of evolution, the olfactory cavity is formed and communication is established between the olfactory organ and the oral cavity. With the appearance of the Amphibians, the first land animals, the respiratory function was added to the sensory role. Thus, in Tetrapods, the olfactory organ is associated with the respiratory organ, whereas in fish, it is independent of it (Salesse and Gervais 2013).

In Agnatha (Cyclostomata)

The jawless vertebrates have a well-developed olfaction. The olfactory system of the sea lamprey is particularly efficient in the orientation toward prey fish during the parasitic stage and in the migration behavior for spawing (Kleerekoper and Mogensen 1963, Li et al. 1995). It has been shown that migratory mature adults use odors from conspecific larvae to select the best streams for spawning. The larvae produce and release unique bile acids into the water, that function as migratory pheromones that adults specifically recognize at very low detection thresholds ($10^{-12} - 10^{-13}$ M) (Li et al. 1995). Hagfish exhibit positive chemotactic behavior in response to specific decay-related chemo-attractants (Glover et al. 2019).

The olfactory organ consists on an unpaired structure, composed of the nasal duct, the nasal sac and the nasopharyngeal pouch. The nasal tube opens externally as a single nostril localized on the dorsal head surface in the lamprey and above the mouth in the hagfish. A valve of the nasal tube of the adult lamprey's olfactory organ is used to introduce and expel water in the nasal sac recovered with lamellar folds, each fold being lined with the olfactory epithelium. The particularity of the hagfish, compared to the lamprey, is that the nasal sac receives a continuous flow of water from the nostril to the gill openings, the nasopharyngeal duct being open to the pharynx. Moreover, it should be noted that hagfishes have specialized chemosensory structures named the Schreiner organs, in addition to the olfactory system. They are distributed all over the body epidermis (Poncelet and Shimeld 2020).

In *Petromyzon marinus*, from the olfactory sac run two olfactory nerves to the ipsilateral olfactory bulb (Kleerekoper and Erkel 1960). The nasopharyngeal pouch, close to a gill opening, is subject to the rhythmic contractions of the gill chamber due to its soft walls. It allows water to be sucked in or expelled synchronously with gill respiration, enabling water to circulate through the olfactory organ. The olfactory organ is therefore independent of respiration, and evolutionarily we have the first

fully individualized olfactory organ (Dawson 1905, Romer and Parsons 1986, Janny 2011).

In Fish

Olfactory is involved in the regulation of most of behavioral patterns, as feeding, spawning, parental defensive, migration, kin recognition and territorial behaviors (Kasumyan 2004, Maximino et al. 2019, Keller-Costa et al. 2015). Fishes have high sensitivity to a wide spectrum of chemical stimuli, they can detect very low threshold concentrations of chemical substances and can differentiate the smell of conspecific individuals from that of other population or species. The olfactory system is characterized by slow adaptation to the olfactory substance, enabling fish to identify an odor source from a great distance (many dozens or even hundreds of meters) (Hara 1992, Kasumyan 2004).

The olfactory organ consists on a paired structure. The anterior nostril brings water into the nasal cavity, and the water flows out of the posterior nostril. Respiratory movements of the gills activate the circulation of water in the olfactory sac. Olfactory lamellae, covered by the olfactory epithelium, are located at the bottom of the nasal cavity. Some fish have accessory olfactory cavities, primarily used for the ventilation of the nasal cavity, but also to produce olfactory mucus. The olfactory cavity is not linked with the pharynx in most fish, but is linked in Dipnoi or Anguilliformes. Generally, the olfactory organ shows an important diversity, reflecting the ecological habitats (Hara 1994, Kasumyan 2004).

In Amphibians

Amphibians are the first land living emerging vertebrates, and most species combine an aquatic larval stage with a more or less water-independent adult stage. This habitat change requires important adaptations also of the sensory systems. During metamorphosis, anatomical and physiological transformations, cellular and molecular modifications of the olfactory system, make the transition from aquatic olfaction in tadpoles to semi-aquatic or airborne olfaction in adults (Wells 2007, Reiss and Eisthen 2008).

In most anuran amphibian tadpoles, the waterborne odor detection is performed by a dual olfactory periphery, consisting of the main sensory epithelium in the principal cavity (PC) and the vomeronasal organ (VNO). During metamorphosis, a three communicating cavities system appears, consisting of the PC, a newly formed middle cavity (MC) lined with a non-sensory epithelium in most species and the VNO. In adults, the aerial olfaction is provided by the sensory epithelium of the PC. The VNO is connected to the PC by a lateral nasal groove (Reiss and Eisthen 2008, Jungblut et al. 2020).

Unlike the most anuran amphibians, the African clawed frog *Xenopus laevis* is almost completely aquatic: excursions overland occur occasionally (Measey 2016). Adult Xenopus possess the three typical nasal cavities, as in other terrestrial frogs, but the MC contains a well-developed sensory epithelium. Different studies have shown that the PC is used for the detection of airborne odors and the MC for the

detection of aquatic odors: a flap valve directs air or water to one or the other cavity according to the external medium (Altner 1962, Hansen et al. 1998). The olfactory epithelia of both PC and MC show significant differences in histological and molecular levels. Ultrastructurally, the epithelium of the PC contains ciliated sensory neurons, while those of the MC contain both ciliated and microvilli sensory cells, as in the epithelium in larval PC. At the molecular level, each cavity differentially expresses several markers. The adult MC is similar so that of the larval PC and express class I olfactory receptors (found in aquatic vertebrates). The class II odorant receptors, expressed in the PC, are the receptors found in airborne mammals (Mezler et al. 2001, Jungblut et al. 2021). There is evidence that important remodeling occurs during metamorphosis to reorganize the olfactory epithelium in the PC. Massive cell death, replacement of the olfactory neurons and changes in olfactory expression patterns of olfactory receptors are involved (Gascuel and Amano 2013, Dittrich et al. 2016).

In the gymnophiona, all burrowing animals, the olfactory and vomeronasal systems are nearly completely separated; a small connection between the olfactory cavity and the VNO. Chemoreception in the VNO is facilitated by the tentacle. In fact, the VNO is associated with the tentacle, because the tentacular ducts open into it. This association makes olfaction possible, even when the main nasal cavity is closed during burrowing or swimming (Schmidt and Wake 1990, Exbrayat 2000). This system is probably an adaptation to a burrowing life and allows these animals to capture molecules from the environment while keeping their nostrils and mouth closed.

In Reptiles

The position and presence of the vomeronasal organ is extremely variable in reptiles. In crocodilians, the VNO exists during early embryonic development and then regresses to be absent in adults (Weldon et al. 1990, Weldon et Ferguson 1993). In turtles, it is not individualized (Parsons 1970). In squamate reptiles (lizards and snakes), the vomeronasal chemosensory system is an important sensory mode, involved in many behaviors, such as foraging, feeding or reproduction (Graves 1993). In these animals, the VNO is anatomically and functionally distinct of the main olfactory system; the airborne odorant information is collected by the tongue and transmitted to the tiny vomeronasal openings on the palate (Schwenk 1995).

There is no functional vomeronasal system in crocodilians, but the olfaction is well developed and crocodilians can locate prey at great distances (Weldon et al. 1990, Weldon et Ferguson 1993). These semi-aquatic animals are able to breathe through the nostrils, which emerge from the water, while the mouth can remain open underwater. The nasal structure is thus particularly complex, with anatomical dissociation of the respiratory and olfactory noses (Janny 2011). Each nostril acts as a valve, which is closed with a muscular flap during submersion. This prevents the olfactory cavity from being flooded and protects the airways. Olfaction is not employed under water. Another respiratory valve, the buccopharyngeal valve, is formed by the support of the elongated soft palate on the gular fold, which protrudes from the back of the mouth. The inspired air is channeled through the nasopharyngeal

duct. With this flap, the animal can open its mouth underwater without water rushing into the internal nares and the trachea (Weldon and Ferguson 1993, Fleming 2014). Crocodilians can increase their olfactory capacity by gular pumping, which consists of movements of the pharyngeal floor with the glottis and buccopharyngeal valve closed (Pooley and Gans 1976). This mechanism has similarities with the buccal pump phenomenon in amphibians, but the movements are pharyngeal rather than buccal, and the musculature of the nostril is involved during these olfactory cycles (Janny 2011).

In Birds

Birds do not exhibit specific behaviors indicative of dependence on olfactory cues, and it has long been thought that they don't smell very well. However, many recent studies have demonstrated that birds are equipped with a functional olfactory system (paired nasal olfaction chambers, olfactory epithelium, olfactory nerves, and olfactory bulbs) that allow them to detect odors in a variety of ethological contexts (Roper 1999, Caro and Balthazart 2010, Corfield et al. 2015). For orientation, homing pigeons and other birds can smell atmospheric gases in trace amounts to find their way back home after moving passively over hundreds of kilometers of unknown terrain (Papi 1989, Wallraff 2005). For foraging, it can be noted that various species of procellariform seabirds (petrels, albatrosses and shearwaters) are attracted by indirect cues such as dimethylsulfide (DMS) associated with their prey. The DMS is effectively emitted by phytoplankton when ingested by zooplankton, and it indirectly indicates to birds the presence of fish feeding on zooplankton (Bonadonna et al. 2006). In fact, a large number of bird species can use olfaction to foraging, as the great tit *Parus major*, which can differentiate a caterpillar-infected tree from and uninfected one on the basis of volatile emissions (Amo et al. 2013). For communication, olfaction is used in a variety of social contexts. The uropygial gland of birds produces an odoriferous secretion that birds spread over their feathers. This preen oil is used in intraspecific contexts, such as species discrimination, sexual mate distinguishing or kin recognition (for review, Grieves et al. 2022). In the context of reproduction, olfaction is involved in the choice and synchronization of partners, the selection of nesting materials and the care of eggs and offspring (Caro et al. 2015). In addition, it has been shown that olfaction of birds is well developed *in ovo*: chicken embryos can perceive olfactory stimuli through the shell pores and memorize this chemosensory information. So, the mother's diet can generate specific odorant properties in the egg yolk and guide the feeding behavior of the young chicken after hatching (Bertin et al. 2010, Bertin et al. 2012, Aigueperse et al. 2013).

In Mammals

The mammalian olfactory system is an evolved sensory system, enabling most species to detect a very large number of chemical molecules necessary for survival and reproductive success (Wilson and Stevenson 2006). However, significant differences in olfactory abilities characterize species. For example, Cetaceans and

Pinnipeds, which are aquatic mammals, have reduced olfactory faculties and their olfactory organs have regressed (Pihlström 2008). In contrast, Ungulates, Carnivora or Rodents are microsmatic animals, with an extremely acute sense of smell (Wackermannová et al. 2016).

Most mammalian species possess the two parallel circuits, the vomeronasal system and the main olfactory system, to process olfactory information. In some species, there are two additional olfactory subsystems, the septal olfactory organ, described in several placental and marsupial species, and the Grueneberg ganglion, particularly well developed in mice (Taniguchi et al. 1993, Storan and Key 2006).

The vomeronasal system is specialized to the pheromone detection, which provide information about the social or sexual status of other individuals in the species. However, recent data suggest that the vomeronasal system also responds to certain non-pheromonal chemical signals, at least in rodents. Furthermore, evidence shows that the main olfactory system also detects a range of volatile odorants that function as pheromones to facilitate reproduction (Brennan and Keverne 2004, Baum and Cherry 2015). In humans, the VNO has regressed and is no longer a sensory organ, as evidenced by the absence of neurons and nerve bundles (Trottier et al. 2000).

The aim olfactory system detects a wide variety of environmental odorant molecules. It seems to play a key role in food detection, in social recognition, in maternal behavior and in offspring recognition at birth (Popik et al. 1991, Keller and Lévy 2012). For example, infants rapidly recognize their nursing mother by her odor signature, or distinguish between a pleasant smell (such as vanillin) and an unpleasant one (such as butyric acid) (Romantshik et al. 2007). The high olfactory capacity of most mammals is clearly linked to the significant development and the complexification of the nasal cavities. The surface area of the olfactory mucosa is particularly increased in mammals by the presence of ethmoturbinals arising from the ethmoidal bone. Interspecies variations in the number and shape of ethmoturbinals could easily be linked to differences in the animal's sense of smell (Smith et al. 2015). In anthropoid primates, as the brain increases in size and the eyes are brought closer together for a better vision, the nasal cavity is both reduced and modified. The number and size of the ethmoturbinals are reduced, resulting in a smaller olfactory surface. In fact, it is likely that the arboreal life characteristic of primates has distanced individuals from the many chemical stimuli present on the ground (food, various olfactory trails) and has therefore made the olfactory system less necessary for survival. So, the olfactive surface area in humans is estimated at between 2.5 and 4 cm^2 (by comparison in dogs, it is 150 cm^2) and represent only 1.25% of the total nasal mucosa (Stoddart 1980).

The human olfactory epithelium accommodates approximatively 6 million of sensory neurons, each of them expressing a single type of receptor. Around 340 human genes encoding potentially functional receptors have been identified. This number is much lower than in rodents (around 1000 genes) or dogs (870 genes), which are animals with a highly developed olfactory sense. Nevertheless, the number of human receptors is sufficient to recognize over 10,000 different odorants. Recent studies even put the number at 1000 billion (Bushdid et al. 2014). The odorous molecules are perceived using a combinatorial coding, in which one olfactory receptor

is able to recognize several odorants, while different odorants are recognized by different combinations of olfactory receptors. In addition, an odorant can act both as an activator of certain olfactory receptors and as an inhibitor of others, making olfactory coding even more complex. So different odorants, or different concentrations of the same odorant, active unique sets of olfactory receptors and generate a specific response (Kurian et al. 2021).

The sensitivity and quality of human olfactory perception varies greatly from one individual to another. This variability is linked to significant genetic polymorphism in ORs (mutations, single nucleotide polymorphisms, copy number variations, pseudogens), associated with a gene segregation in different human ethnic groups. The fact that each individual has a specific repertoire of functional genes and that certain genes are more frequently invalidated in one population than in another suggests that different selection pressures have shaped chemosensory repertoires in distinct populations (Menashe et al. 2003, Hasin-Brumshtein et al. 2009, Ferdenzi et al. 2016).

Scents are powerful stimuli that can evoke emotional states and promote learning and memory. The singularity of the anatomy of the olfactory pathway explains the strong connection between odor and emotional memory. Indeed, the olfactory information does not pass through the thalamus to the cortex, but is relayed directly to the limbic system, which is the region of the brain typically associated with emotional process and memory (Soundry et al. 2011). This gives olfaction a powerful and unique ability to influence mood, cognitive mobilities, and the learning of new elements related to the environmental context. The odors can modulate complex behaviors and lead the animals to adjust their survival decisions (Sullivan et al. 2015). These adjustments involve brain plasticity phenomena, modifying the number or efficiency of neuronal synapses and creating new neurons (Ming and Song 2005). In humans, odors are also essential for learning about situations, and they constitute efficient cues for recalling episodic emotional memories (Livermore and Laing 1996, Wilson and Stevenson 2003). Existence of connection between odor, emotion and memory explains why odors are increasingly used for therapeutic purposes, for example to bring back memories and emotions, or to free up the speech of patients who have suffered memory or speech trauma.

Conclusions

All living organisms have senses that enable them to interact with their environment, with other organisms of the same or different species, or with physical objects. These senses have diversified over the course of biological evolution, becoming important adaptation factors directly linked to the lifestyle of each organism.

Olfaction is one of the most important senses in the animal kingdom. It appears very early in biological evolution and the broad role for odors appears highly preserved across species. Olfaction is heavily involved in survival behaviors, such as foraging, danger detection or communication between individuals of the same or different species. Olfaction based on the reception of chemical molecules is reminiscent of certain aspects of communication in bacteria, protists or archaea

(Miller and Bassler 2001, Lami and Teyssedre 2019). In these unicellular organisms, there is a key mechanism for cooperative behaviour, the quorum sensing, which is based on the emission and detection by the cells of small signal molecules. The concentration of these chemicals in the external environment increases with that of the unicellular organisms, and above a certain concentration threshold in the external environment, the cells switch to a different, cooperative mode of functioning.

In addition to the functions mentioned above, the sense of smell can be a source of pleasure and well-being for humans. Among odorous molecules, perfumes have multiplied since their origin at the discretion of perfumers, who offer constantly renewed, complex scents with proven emotional effects. Some molecules, such as essential oils, can have therapeutic effects. The hedonic value that humans attach to certain scents and the pleasurable or spiritual activities with which they are associated contribute to their well-being. Indeed, the loss of the sense of smell affects a number of physiological parameters, including emotions, reminding us of the importance of another sense, hearing, and the effects of sounds and music (Brun and Exbrayat 2022). The study of the senses, at the interface of science and art, also shows the immense possibilities and plasticity of living beings.

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