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The Physics and Biology of Olfaction and Taste

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Traditionally, the chemical senses include olfaction and gustation: olfaction (smell) reports on gaseous substances carried by air over long distances, and gustation (taste) provides information about food material already in the mouth. However, in recent times behavioral, physiological, histological, and molecular studies have increased our understanding of vertebrate chemoreception, and four chemical senses are recognized by some authors, reflecting the diversity in function and physiology (Dulac and Axel, 1995; Eisthen, 1997; Zufall and Munger, 2001; Mombaerts, 2004; Breer et al., 2005). For the purpose of this volume, three chemical senses are important: olfaction, vomeronasal sense, and gustation (Fig. 7.1 in this volume).

It is difficult to distinguish sharp borders between the various chemosensory systems, especially in aquatic vertebrates. For example, the catfish *Ictalurus natalis* carries on its barbels densely packed taste buds. These taste buds appear to report on dissolved substances in the surrounding water (Caprio, 1988). Histologically, the barbels' sensory buds serve taste, but functionally their role seems to overlap with olfaction: catfish successfully orient toward distant "olfactory stimuli" even after bilateral destruction of the olfactory tract (Bardach et al., 1967). A similar quasi-olfactory role has also been described for the tongue of the dolphin *Tursiops truncatus* (Kuznetzov, 1990), and Schmidt and Wöhrmann-Repenning (2004) have reported histological observations indicating a close interaction between taste buds and vomeronasal organ.

Molecular transduction mechanisms of the sensory cells of the olfactory, vomeronasal, and gustatory system are also similar, as are the microstructures of the distal parts of the receptor cells (Eisthen, 1992, 1997; Reiss and Eisthen, chapter 4 in this volume). For mammals a classification based on the molecular genetics of the receptor proteins may be within reach (Mombaerts, 2004; Grus et al., 2005). However, this volume adheres to an anatomical basis for distinguishing between chemical sense organs, as it embraces the inclusion of amphibian, reptile, and bird chemical senses, for which the molecular genetics of olfactory receptors are less well known. As a result, this volume uses a classification based on the innervation by the cranial nerves of the sensory organs.

The sensory cells of the olfactory and vomeronasal systems send out axons passing through the perforated part of the ethmoid bone (the cribriform plate) and terminate in specific glomeruli of the olfactory bulb (Vassar et al., 1993; Belluscio et al., 2002; Pihlström, chapter 7 in this volume). The axons from the main olfactory epithelium project to the main olfactory bulb, while the axons from the vomeronasal epithelia project to the accessory olfactory bulb (Zufall and Munger, 2001; Breer et al., 2005). Afferent axons leaving the main and accessory olfactory bulbs unite into bundles forming the olfactory tract (cranial nerve I). More centrally the olfactory tract divides into many projections contacting different brain nuclei (Shepherd, 1994). The final brain projections from the main olfactory system and the vomeronasal system differ (Smith, 2000).

Receptor cells of the taste buds on the tongue do not form centrally projecting axons; instead they are innervated by thin dendritic sensory endings projecting from specific brain neurons. The taste receptors of the anterior part of the human tongue are innervated by a branch of the facial nerve (cranial nerve VII), while the rear of the tongue is served by the glossopharyngeal nerve (cranial nerve IX). The taste cells of the roof of the oral cavity and the upper esophagus are innervated by branches of the vagus nerve (cranial nerve X). Although diffuse distally, taste is an integrated sensory system as indicated by the termination of nerve fibers in all these taste pathways in the solitary nuclear complex in the medulla (Smith, 2000).

In this chapter, we briefly review the basics of diffusion, the process that underlies the perception of all chemical stimuli. Then, we discuss odorants, and finally the information carried by chemical stimuli. This discussion includes the dimensionless Reynolds number, useful when considering odorant-carrying fluid flows.

The term *odorant* is often used for biologically relevant molecules such as pheromones and alarm substances, and for metabolites unintentionally released by predators or prey animals. Here, we extend the use of the term to include all substances spread in air and water and by direct physical contact, and perceived by the chemical sense organs.

DIFFUSION

Diffusion is the spread of dissolved and gaseous molecules in a stationary medium (here water or air) as a result of random thermal movements. Diffusion is slow and cannot serve detection over long distances. Chemosensory cells, olfactory, vomeronasal, and taste receptors in both terrestrial and aquatic tetrapods are covered by thin layers of mucous. Within this thin 0.1 to 1 millimeter thick unstirred layer, molecules spread exclusively by diffusion (Dusenbery, 1992).

Diffusion is faster in air than in water (Table 2.1); if a micromole (6×10^{17} molecules) of a dissolved substance is released from a point source in still water, the first molecule reaches a point 1 centimeter from the source after approximately 10 minutes. In air, the first molecule reaches a point 1 meter from the source in 10 minutes. These observations can be quantified using diffusion constants, which are approximately 10^{-5} m^2/s and approximately 10^{-9} m^2/s, in air and water, respectively (Dusenbery, 1992). The diffusion constants are generally lower for large than for small molecules, and possible hydrophilic or amphoteric properties of the molecules aid their diffusion through mucous or fluid layers in the nasal and oral cavities (Bradbury and Vehrencamp, 1998). Still, although diffusion may serve communication between microorganisms, this mechanism is too slow to serve long-distance olfaction of

TABLE 2.1

Physical and Chemical Factors Relevant for Spread of Biological Signal Molecules

	IN AIR	IN WATER
Diffusion constant	Small, ca. 10^{-5} m^2/s	Very small, ca. 10^{-9} m^2/s
Odorant-carrying mechanism	Wind of varying velocity and direction	Water current, often predictable velocity and direction
Odorants carried by the medium	Small and medium-sized volatile alcohols, aldehydes, esters etc., with 15 to 20 carbon atoms	Hydrophilic amino acids, peptides, proteins, and nucleotides
Odorants in contact perception	Weakly volatile molecules, e.g., pheromones in sebum	Hydrophobic odorants embedded in slime

larger animals. Taste is different; masticated food in direct contact with the tongue is clearly within diffusion distance from the sensory cells of the taste buds.

During chemical perception in the nasal cavities of terrestrial tetrapods, airborne odorants diffuse both through a thin unstirred layer of air, and through a thin layer of mucous fluid covering the sensory epithelium (Dusenbery, 1992). Slow diffusion results in delays of up to 1 second, which is one factor making olfaction a relatively slow sensory modality compared with hearing and cone-driven vision.

ODORANTS AND THEIR PERCEPTION

The molecular characteristics of odorants determine their solubility in the medium and their volatility, and thus their release and transport toward the sensory epithelium. The spread of molecules is medium specific, and thus the evolution of efficient signal molecules is different in different habitats and for different types of spread: spread in air and water, or through direct physical contact (Dusenbery, 1992).

The physics of the chemical senses is ultimately concerned with interactions between biologically relevant molecules and the corresponding receptor proteins in sensory cells. However, it is unclear whether there are separate groups of olfactory receptor molecules for airborne odorants and for water-soluble substances (Eisthen, 1997; Freitag et al., 1998).

Independent of receptor proteins, aerial olfaction seems to be characterized by olfactory binding proteins in the mucus that covers the sensory epithelia of terrestrial tetrapods. Such binding proteins are also found in the air-exposed cavity of the *Xenopus* (African clawed frog) olfactory system. Olfactory binding proteins are not yet identified in fish, but in terrestrial tetrapods they are supposed to have a carrier role in transporting hydrophobic odorants through the liquid layers covering the olfactory epithelia (Millery et al., 2005).

Airborne odorants are small volatile molecules with few chemical bonds to the substrate. Thus they are easily released by modest thermal vibration, that is, when the thermal energy exceeds the chemical binding energy. Some smelly substances released from biological materials are very small molecules, such as hydrogen sulfide (H_2S) and ammonia (NH_3). These compounds warn at least some mammals of unhealthy food and water, but such small molecules are less suited for signaling between individuals, as important messengers must combine proper volatility with sufficient receptor specificity. Typical airborne pheromones are alcohols, aldehydes, ketones, fatty acids, esters, and steroles with 15 to 20 carbon atoms.

Alarm substances typically have only 6 to 15 carbon atoms and are thus less specific than pheromones. They serve instead as efficient (fast) warning signals (Dusenbery, 1992).

Waterborne odorants are hydrophilic substances ranging from small organic molecules to large proteins. Typical molecules with appetizing effect on aquatic predators are amino acids and nucleotides unintentionally released by prey animals. Waterborne pheromones are usually polar and thus hydrophilic peptides or proteins.

Chemical communication through direct physical contact includes both olfaction and taste; mammals and some other tetrapods transfer sexual pheromones by licking and touching. Direct contact is also involved in territorial markings. An interesting form of contact perception is the use of the snake tongue in following chemical trails (Bradbury and Vehrencamp, 1998). Especially in connection with territorial markings, the longevity of the signal is important, that is, the signal molecules should be released very slowly into the surrounding medium. In terrestrial tetrapods these substances must be weakly volatile pheromones in secreted sebum, while in aquatic tetrapods such as otters and seals they are hydrophobic odorants, sometimes embedded in slime.

STIMULUS STRENGTH AND DETECTION

Over distances longer than those served by diffusion, chemical stimuli are spread by movements of air and water. Essentially, flow in air is similar to flow in water: both media can be considered fluids for the purpose of the receiving sense organs. An important quantity characterizing the type of flow, laminar or turbulent, is the Reynolds number.

When a fluid flows slowly in a narrow channel, the flow is laminar: adjacent layers glide past each other without mixing. Increasing the fluid velocity or the width of the channel leads to turbulent flow. The velocity producing turbulent flow in a given flow field can be estimated by the dimensionless Reynolds number: $R = \rho L v / \mu$, where L is a chosen characteristic length of the flow field, v is a characteristic flow velocity, ρ is the density of the fluid, and μ is its dynamic viscosity (air: 18.3 μPa s; water: 1 mPa s). In all flow fields of similar shape (isometric flow fields) the laminar flow changes to turbulent at equal R values. For example, when a fluid flows in a tube and the tube diameter has been chosen as the characteristic size L, the flow turns turbulent when the value of R is approximately 2300. In narrow channels, flow is usually laminar. Open flow fields correspond to large L values, and in these flow is almost always turbulent, even at low velocities.

Turbulent flow results in efficient spread of odorants. When the source of an odorant is close to the signal-receiving animal, the main medium flow is produced by the animal itself, by its respiratory movements and active search, such as its breathing and sniffing. Differing from humans, many tetrapods have evolved highly specialized anatomical structures for actively collecting air samples for closer scrutiny. For example, among the functions of the elephant trunk is the collection of precisely localized samples of air, and the transport of these samples to a uniquely large and probably very sensitive olfactory organ (Boas and Paulli, 1925; Pihlström et al., 2005). Over longer distances, chemical stimuli are spread by wind and water currents. Water currents are more predictable than those in air.

In turbulent flows odorants do not spread homogeneously in the medium (Dusenbery, 1992). Thus, the rate at which odorant molecules reach an olfactory epithelium varies significantly. High peaks of odorant concentration may increase sensitivity, but the information obtained from such a noisy signal is limited. The type of odorant may be identified, but only a rough estimate of concentration is possible, and precise modulation in time is blurred by turbulence.

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