Chapter 1
Introduction to Olfaction:
Physiology

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ABSTRACT

This chapter introduces the basic anatomy and physiology of the neural systems involved in the detection and identification of odors by vertebrate animals. It describes the cellular architecture and function of these systems, tracing the path of sensory signals from the initial steps of sniffing and chemical stimulus transduction in the nose, through to the synaptic processing pathways in the circuits of the olfactory bulb and major areas of olfactory cortex. Included are reviews of the latest research findings and hypotheses shaping our fundamental understanding of olfactory mechanisms, with particular emphasis on mammalian olfaction.

INTRODUCTION

The sense of smell is both ancient and ubiquitous. Olfactory sensory systems have evolved in the simplest and the most complex animals to acquire and interpret information about chemical signals in the environment, a basic need shared by all motile organisms. Many essential biological functions are served by olfaction. The scent of a predator or smoke from a fire can alert an animal to impending danger, triggering life saving avoidance or escape responses. Odor cues may be critical for navigation and the location of food or mates, and for social communication between members of the same species. The olfactory system of humans can also serve these basic biological functions. However, modern man is more reliant on the advanced senses of vision and hearing in daily life. Thus, our media and computer interfaces are universally engineered for visual display and sound, but have not routinely incorporated odor devices. For humans, olfaction seems to be a more primeval sense that nonetheless can significantly enrich our lives in important ways. It adds a flavor dimension to food and enhances the meaning and memory of our experiences through association with odors. This chapter deals with the physiology of olfaction, focusing on vertebrate animals

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and particularly mammals, which have been well studied. We will review how the nose detects odorants and how this sensory information is relayed to the brain. We will discuss current views about how central neural circuits may process this information to enable us to perceive odors.

In seeking to understand the design and workings of any system, it is helpful to specify its operational capabilities. Different species of animals have optimized their olfactory systems to function in different ecological contexts. However, we can list some key capabilities that would dictate the design of these systems: (1) detection of small organic molecules (*odorants*), either in aqueous phase (for aquatic species) or vapor phase (for air-breathing species); (2) wide range of detection sensitivity for odorants: psychophysical studies on vertebrates have reported airborne detection thresholds ranging over ~ $2 \cdot 10^{-18}$ M – 10^{-4} M; (3) wide diversity of odorants, with many hundreds or thousands of different compounds detected and discriminated; (4) fast detection and recognition of odorants; in rodents, detection and discrimination is possible after a single brief sniff lasting < 200 ms; (5) adaptation or habituation to background odorants; (6) shifts in perceived odor quality with changing odorant concentration; (7) identification of new odors in the presence of background odorants; (8) ability to discriminate between very similar odorants; (9) perception of odorant mixtures either as component odors ('elemental'), or as holistic objects ('configural'); (10) dependence of odor perception on prior olfactory experience, context and association with other sensory inputs. Here we will review some of the neural systems and physiological mechanisms that help to accomplish these tasks.

ANATOMICAL ORGANIZATION OF THE OLFACTORY SYSTEM

The structures that make up vertebrate olfactory systems can be divided into peripheral and central components (Allison, 1953). In the periphery, the nasal cavities enclose an *olfactory epithelium* (OE) that is responsible for sampling and detecting chemical cues in the environment. This information is then relayed to central systems by the *Olfactory Nerve* (ON), the first of twelve cranial nerves that interface the brain with the external world. In fish, lamellar folds of the olfactory sensory epithelium occupy a capsule that communicates with the external aqueous medium through a pair of openings or *nares*. In air breathing vertebrates, the olfactory epithelium resides on a series of convoluted shelves of bony cartilage, the nasal *turbinates*, that are housed in a nasal cavity positioned between the oral cavity and the brain (Figures 1a, 2a). The olfactory epithelium is a specialized sensory area of mucus-lined nasal tissues (*nasal mucosa*) (Graziadei, 1971). It contains several million *Olfactory Sensory Neurons* (OSNs), which are specialized neurons with a bipolar morphology (Figures 2b–d, 3c). Each OSN cell body (or *soma*) extends a long *dendrite* to the epithelial surface, where an apical *knob* sprouts fine *cilia* containing the odorant detection apparatus. A thin cable or *axon* extends basally from each OSN cell body (Figure 2c), and axons bundle together to form the olfactory nerve which enters the skull through fine perforations of the bony *cribriform plate* separating the nasal cavity from the brain. The OSNs are embedded in a matrix of *sustentacular cells,* which are positioned between the OSN dendrites.

The olfactory nerve axons project to a superficial layer of the *olfactory bulb*, which is the first major brain center dedicated to processing of odor signals arriving from the nose (Shepherd, 1972). Here, olfactory nerve terminals are organized into hundreds or thousands of discrete ball-like structures, the *glomeruli*, where they make synaptic contact with dendrites of a variety of olfactory bulb neurons (Figure 1b). As its name suggests, the olfactory bulb has an ellipsoidal shape, and its internal construction is laminated like the layers of an onion. The layers are arranged as follows