Progress in Neurobiology 82 (2007) 80–86

progress in Neurobiology

www.elsevier.com/locate/pneurobio

The functional organization of the fish olfactory system

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Received 15 January 2007; accepted 19 February 2007

Abstract

Recent developments in the functional anatomy and physiology of the fish olfactory system reveal three parallel pathways from the sensory epithelium, via the olfactory bulb to the telencephalon. There are three morphological types of sensory neurones spread in a seemingly overlapping arrangement in the olfactory epithelium. The axons of each type of sensory neurones converge to a specific region of the olfactory bulb and connect to separate sets of relay neurones. The axons of these relay neurones leave in three bundles to the telencephalon. Each bundle conveys specific information that elicits sets of characteristic behaviour in response to odours involved in essential life processes in the fish. One pathway is tuned to social cues, another to sex pheromones, and the third to food odours.

Keywords: Olfactory system; Chemotopy; Odorant receptors; Parallell pathways; Labelled lines; Behaviour

Contents

Lord Adrian demonstrated in the early fifties that different odorants induce activity in different regions of the vertebrate olfactory bulb (Adrian, 1951). Since then, the spatial concept of odour representation has been a central theme in discussions on odour discrimination. Our understanding of this subject was greatly improved by the discovery of the odorant receptors (Buck and Axel, 1991) and the subsequent demonstration that olfactory sensory neurones (ORNs) expressing a particular odorant receptor converge to two glomeruli giving a stereotyped spatial map (Ressler et al., 1994; Vassar et al., 1994). There has been a steady increase in our knowledge about the function of particular odorant receptors and also how information is conveyed to higher centres in the brain (Zou et al., 2001). However, the relation between odour, odorant receptors and behaviour has been found to be a complex subject in mammals. In teleosts, the behaviour patterns related to feeding, reproduction and alarm are distinct, they can be quantified, and they are evoked by sets of appropriate odorants. In some fish families, there is a long olfactory tract, which is divided in several bundles connecting the bulb with the telencephalon. These anatomical features permit manipulation that has given us decisive information about the functional organization of the olfactory system.

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0301-0082/$ – see front matter
doi:10.1016/j.pneurobio.2007.02.007

1. Odorants of essential life processes

It is commonly acknowledged that life is dependent upon three fundamental processes, viz. reproduction, feeding and avoidance. In fishes, these functions can be mediated via the olfactory system and by different classes of molecules, i.e., amino acids, bile salts, pheromones. Yet, the odorants are mixed in their natural environment. How can fish distinguish between these complex odorants, and how do the fish know what is the appropriate behaviour pattern at the different seasons? In other words, what are the mechanisms that determine the hierarchy of behaviour patterns? Here, we present anatomical and physiological findings that might form a basis for our understanding how fish perceive its odorous environment.

2. Anatomy

The layout of the olfactory system is demonstrated in the photo of the exposed brain of the crucian carp (Fig. 1). As in all vertebrates the primary sensory neurones are located in the sensory epithelium, which in fishes is called the olfactory rosette, because the leaf-like structures of the lamellae resemble a miniature rose. The sensory neurones have thin axons that terminate in the olfactory bulb in specific synaptic structures called glomeruli. In these aggregates of terminals many thousand axons make contact with a few secondary neurones. The axons of these relay neurones project via the olfactory tract to higher centres in the brain. The olfactory tracts in cyprinids are divided in several nerve bundles, which enter and terminate in different regions of the brain. Such long olfactory tracts are also found in gadids and silurids (cod and catfishes). These long tracts are pathways within the central nervous system and their length makes them suitable for surgical manipulation (Hamdani et al., 2001b, 2000; Kyle et al., 1987; Sorensen et al., 1991; Stacey and Kyle, 1983; Weltzien et al., 2003) and physiological recordings (Døving, 1986).

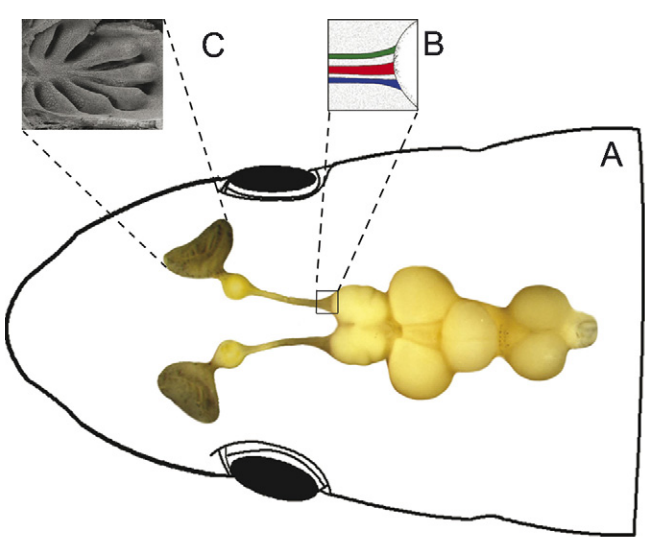

Fig. 1. Overview of the fish brain. (A) Dorsal view of the head of a crucian carp showing the brain and the olfactory system. (B) Schematic drawing of the olfactory tract as it enters the telencephalon, demonstrating three distinct bundles. The medial part of the medial olfactory tract in blue, the lateral part of the medial olfactory tract in red, and the lateral olfactory tract in green. (C) Scanning micrograph of the olfactory rosette.

3. Sensory neurones

The sensory neurones that make up the assembly of cells detecting the odorants in fishes constitute three types with different shapes. These are the ciliated sensory neurones, with long dendrites and a few cilia; the microvillous sensory neurones with shorter dendrites than the ciliated cells and have microvillae extending from their apical surface (Thommesen, 1983; Yamamoto and Ueda, 1979). The third cell type is called crypt cells (Hansen et al., 1997; Hansen and Finger, 2000). These latter cells are spherical or pear-shaped and lay close to the epithelial surface and are equipped with a few cilia and microvillae. Due to the different lengths of the dendrites, the soma of the different cell types lies in distinct depth ranges and forms the pseudo-stratified design of the sensory epithelium. This could be visualized by a single application of the lipophilic tracer carbocyanine dye (DiI) in the olfactory bulb (Hamdani et al., 2001a; Morita and Finger, 1998) (Fig. 2). The morphologically distinct crypt cells are commonly found in layer 1 and the sensory neurones with somas in layers 2 and 3 in Fig. 2 belong to microvillous neurone type. The sensory neurones with somas in layers 4 and 5 are ciliated neurones.

4. Behaviour and tract bundles

The understanding of the chemotopic representation of odour information in fish was initiated when it was shown that electric stimulation of a particular bundle of the olfactory tract evoked distinct behaviours in free swimming cods (Døving and Selset, 1980). The tracts bundles have been given anatomical names due to their anatomical position, viz., medial (MOT) and lateral (LOT) olfactory tract, and each bundle has a medial and lateral portion. Stimulation of the medial part of the medial olfactory tract mMOT induced alarm reaction; stimulation of the lateral part of the medial olfactory tract lMOT induced reproductive behaviour, and stimulation of the lateral olfactory tract LOT induced different feeding behaviours. The results from the cod were reproduced and extended by several subsequent studies, confirming these findings (Kyle et al., 1987; Sorensen et al., 1991; Stacey and Kyle, 1983). In crucian carp, ablation experiments showed that in fishes where the medial part of the medial olfactory tract was cut, the alarm reaction was absent. In contrast, if only the medial part of the medial olfactory tract was intact, the alarm reaction was present. Therefore, the medial part of the medial olfactory tract mediates alarm reaction (Hamdani et al., 2000). Similar experiments demonstrated that the lateral part of the medial olfactory tract mediates reproductive behaviour and the lateral olfactory tract mediates feeding behaviour (Hamdani et al., 2001b; Weltzien et al., 2003). Thus, these studies revealed a correlation between the anatomical organization of the olfactory tract and function.