Morphology and physiological properties of interneurons in the olfactory midbrain of the crayfish

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Summary. 1. Intracellular recording and staining was used to characterize neurons in the crayfish (Procambarus clarkii) brain that respond to chemical stimuli applied to the major olfactory organs, the antennules.

2. Two distinct morphological types of neurons that have major projections in the olfactory lobes (OLs) of the brain were characterized anatomically (Figs. 1, 2, 3; Table 2) and physiologically (Figs. 4, 5, 6; Table 3).

3. Different individual neurons of one type, with similar 'tree-like' projections in the OLs, have somata distributed in at least 5 different cell body clusters of the brain (Fig. 3) and link different subsets of neuropilar lobes through their distributed arbors (Fig. 1, Table 2).

4. Excitatory, inhibitory and mixed responses were recorded in different neurons when odorant mixtures or individual components of these mixtures were applied to the antennules. Response spectra to individual components were broad and overlapping, but not identical in the neurons tested (Fig. 4; Table 3). Mixture interactions appear to be additive in most of the neurons that we tested, but evidence was obtained for mixture suppression in several cases (Fig. 6).

5. Most of the neurons recorded in this study responded only to stimulation of the ipsilateral antennule (Fig. 5), although subthreshold activity to stimuli applied contralaterally was recorded in several neurons that were strongly excited by ipsilateral stimuli.

6. Chemoresponsive neurons without projections in OL's that have all of their branches confined to the brain, or that project an axon in the circumesophageal connective, are described (Fig. 7).

Introduction

The basic organization of the early levels of the olfactory pathway appears to have been conserved in evolution. Maynard (1967), for instance, noted that in both crustaceans and vertebrates, many primary olfactory afferents converge in glomerular neuropil onto many fewer first-order interneurons, whose axons project without synapsing to higher processing centers. A similar glomerular organization exists in the olfactory pathway of insects (Boeckh et al. 1984; Hildebrand and Montague 1986; Christensen and Hildebrand 1987) and at least some molluscs (Chase 1986), suggesting that there may be some fundamental relationship between this type of neural organization and how odor information is processed. If so, the elements of this relationship that are truly fundamental could be expected to transcend species differences.

Antennular chemoreception is considered to be the 'olfactory' sense of decapod crustaceans (e.g. Atema 1977). The antennules bear sensilla called aesthetascs on the lateral filaments that are innervated by multiple, bipolar receptor cells. Axons of these receptor cells project to the ipsilateral deutocerebrum, where they terminate in the surface neurons.
layers of the glomerular neuropil of the paired olfactory lobes (OLs) (Sandeman and Luff 1973; Sandeman 1982). As in the mammalian olfactory bulb (Shepherd 1977), each OL glomerulus is a complex structure in which many, perhaps several thousand, afferents converge on processes of several types of interneurons (Sandeman and Luff 1973). A second major deutocerebral neuropil, the paired accessory lobes (ALs), is also composed of glomeruli, but smaller, more spherical and more numerous glomeruli than found in the OL. The ALs receive no direct olfactory afference. Because the ALs are connected to the OLs via tracts, the former are usually considered to be secondary processing centers for olfactory information (ibid.), although the exact relationship of the ALs to the OLs is unknown.

Although there has been a good beginning characterizing olfactory organization in crustaceans (review: Ache and Derby 1985) the functional organization of the olfactory lobes remains largely unknown. We report here on the physiological responses of several morphological classes of interneurons in the olfactory pathway of the crayfish that respond to chemosensory stimulation of the antennules. Particular emphasis is given to interneurons that arborize in the olfactory lobe. Portions of these data have appeared in a preliminary account (Arbas et al. 1987).

Materials and methods

Crayfish Procambarus clarkii were obtained from a supplier in Louisiana and maintained at 20 °C in shallow trays containing artificial pond water (10% artificial sea water in deionized water. Animals were fed carrots daily. As in deionized water. Animals were red carrots daily.

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