Neuroanatomical Evidence for Electroreception in Lampreys

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The patterns of the anterior lateral-line afferents of *Lampetra fluviatilis* as revealed by transganglionic transport of horseradish peroxidase are described. The afferents form two roots in entering the rhombencephalon. Fibers of the dorsalmost root can be traced to a short dorsal fascicle which runs along the dorsal nucleus. The ventral roots form two fascicles adjacent to the nucleus intermedius. Comparison with urodeles indicates that lampreys, like urodeles and other anamniotic vertebrates are electroreceptive.

The sense organs of the lateral-line system are present on the head and the trunk of almost all anamniotic vertebrates. They can be subdivided into two receptor types: the mechanoreceptive neuromasts and the electroreceptive ampullary organs [1, 2]. Within the last few years, the sense of electroreception which was once thought to be restricted to some teleost fishes, sharks and rays was found in all major anamniotic taxa [1, 2]. Northcutt [3] and McCormick [4] argued on histological grounds in favour of electroreception in lampreys. This claim was recently supported by electrophysiological evidence [5, 6]. In fact, lampreys are in an interesting phylogenetic position. Besides Myxinoids they are the sole extant species of jawless fish or agnathans which have been separated more than 400 million years of evolutionary history from the electroreceptive gnathostome species. If we do not consider that electroreception has been invented separately by the ancestors of gnathostomes and agnathans, we are faced with the fact that electroreception is as old as all the other major sensory modalities of craniote vertebrates.

Besides a preliminary note [17] no experimental data exist on the lateral-line projection of lampreys. For this reason we have undertaken the study of the anterior lateral-line afferents in this fish, particularly since a detailed comparison of the lateral-line projection patterns between lampreys and urodeles may provide further evidence for electroreception in lampreys and the ancienty of this system.

Five specimens of *Lampetra fluviatilis*, ranging from 28–34 cm in length were used for this study. The animals were anaesthetized in tricaine methanesulfonate, the nervus buccalis [7] of the anterior lateral-line system was surgically exposed on both sides (*i.e.* 10 projection patterns were analysed) in the orbit and cut after all bleeding was stopped. Horseradish peroxidase (HRP, Böhringer Grade I) was applied to the cut nerve for five minutes. After surgery the animals were kept five to seven days at 4 °C in their tank. They were subsequently reanaesthetized and perfused through the heart. The brains were removed and processed according to the whole-mount method described elsewhere [8].

Labeling of the anterior lateral-line nerve afferents was successfull in 7 (out of 10) cases. Further, the trigeminal nerve was labeled in 5 cases. The absence of label in some cases occured if strong bleeding had followed surgery.

In all labeled specimens, the anterior lateral-line nerve showed a clearcut segregation of the afferents into three fascicles within the rhombencephalic alar plate: a short dorsal fascicle (about 0.7 mm long) and two more or less separated long ventral fascicles (about 2.2 mm long). The afferents which form the dorsal short fascicle enter the rhombencephalic alar plate *via* a separate dorsal root of the anterior lateral-line nerve (Fig. 1); the afferents forming the ventral long fascicles enter it *via* a ventral root of the lateral-line nerve. All traceable afferents bifurcate after entering the medulla to form an ascending and a descending limb in their respective fascicle. The descending limb of the short dorsal fascicle can be followed up to the entrance of the posterior lateral-line nerve, the ascending limb up to the entrance of the trigeminal nerve. Only in one case could a single afferent fiber be traced to the midline. The descending limb of the long ventral fascicles extends almost to the obex region whereas the ascending limb can be followed to the midline of the cerebellum (as

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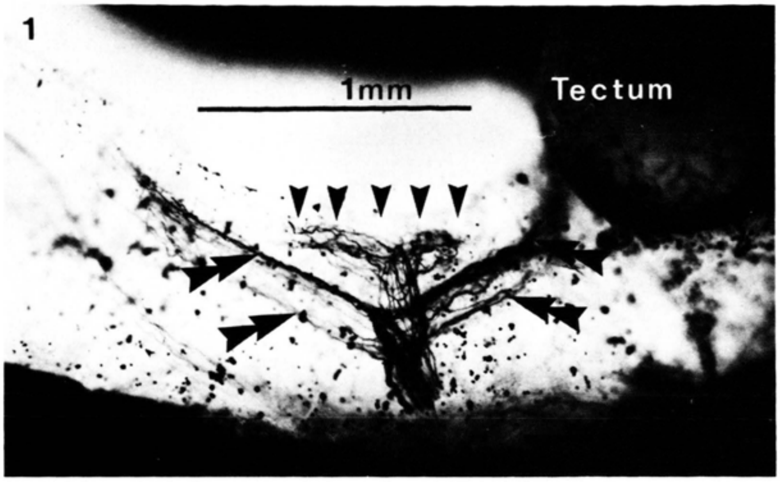
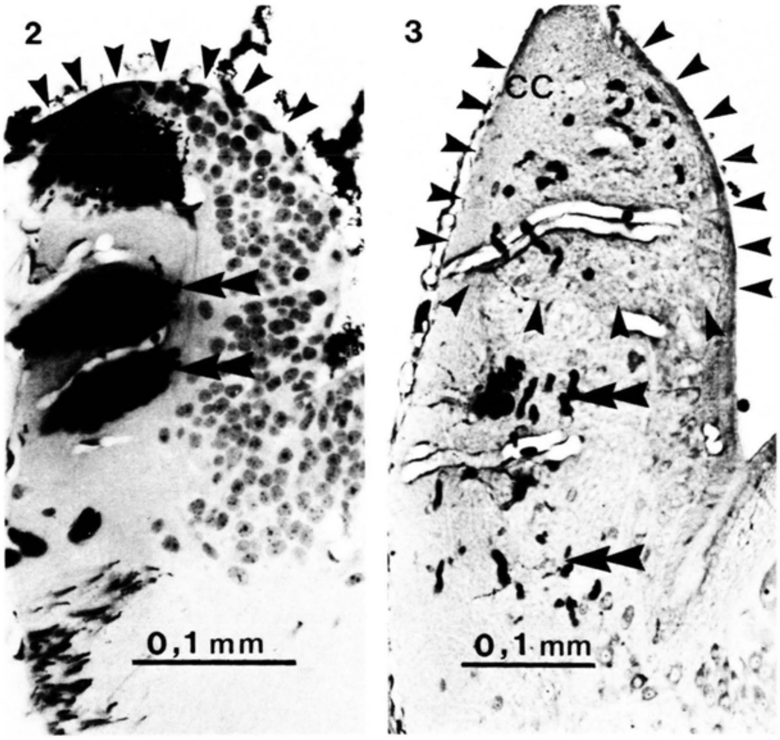


Fig. 1. This lateral view of the hindbrain of *Lampetra fluviatilis* shows the dorsal, short fascicle (arrowheads) and the two longer ventral fascicles (double arrowheads) of the lateral-line afferents of the nervus buccalis. Whereas fibers are interchanged between the two ventral fascicles there is a clearcut separation of the short dorsal fibers.



Figs. 2, 3. Coronal sections (20 μm thickness) of resin-embedded rhombencephalic alar plates of a salamander (*Gyrinophilus porphyriticus*, Fig. 2) and a lamprey (Fig. 3) are shown. In both species the dorsal projections of ampullary organ afferents (arrowheads) are separated by a gap from the ventral bundles (double arrowheads). Whereas the ventral afferents from neuromasts are clearly separated into two fascicles in the salamander (Fig. 2, double arrowheads) the fasciculation in lampreys is blurred due to the scattered ventral fascicle fibers (double arrowheads, Fig. 3). No afferents enter the cerebellar crest (CC).

defined by Larsell [9]). No fibers were found to cross the midline.

Coronal sections clearly support the notion of a distinct dorsal and ventral projection of the anterior lateral-line nerve (Fig. 3). They show in addition that the short dorsal projection is confined to the nucleus dorsalis [10] – no fibers enter the cerebellar crest covering the dorsal nucleus. In particular, the nucleus dorsalis, defined by cytoarchitectonic criteria, is longer than the rostro-caudal extent of the dorsal projection. The long ventral projections show some fasciculation, but the more ventral fibers scatter.

Despite the strong labeling of the afferent fibers, no retrogradely labeled cells were found close to the sulcus limitans, as was described for a number of vertebrates (for a review see [11]). This negative result tends to support the absence of efferent terminals in lateral-line organs [12]. Further, in contrast to earlier description on non-experimental material, there is no overlap of the dorsal and the ventral lateral-line projections [9] and the dorsal and ventral projections are much shorter than previously suggested [9]. In particular, we found no contralateral fibers and the dorsal fibers are virtually all restricted to the short dorsal projection.

The overall organization of the lateral-line projections in urodeles (Fig. 2) and lampreys (Fig. 1, 3) show striking similarities. In urodeles it has been unequivocally shown that the electroreceptive ampullary organs [2, 13] project with their single afferent fiber exclusively to the nucleus dorsalis [14, 15]. Ampullary organs are also found in lampreys (Northcutt, pers. comm.). Our data show that the dorsal projection to the nucleus dorsalis in lampreys is very similar to that found in urodeles, and hence support the electrophysiological evidence of electroreception in this vertebrate class [6]. Taken together, these similarities favour the concept that electroreception represents a primitive or plesiomorphic character found in all craniote vertebrates [1, 5].

The similarities between the ventral fascicles in urodeles and lampreys may presumably represent the two directions of sensitivity of each mechanoreceptive neuromast [14]. Whereas the rostralmost termination of the mechanoreceptive lateral-line afferents in urodeles is the eminentia granularis [15], these ventral fascicles in lampreys extend to the midline of the cerebellum. This difference is related to the unsolved topographic organization of the rostral part of the rhombencephalon in the lamprey [9, 16], and may indicate that the rostrodorsal ridge in this fish should be considered as an extension of the nucleus intermedius [16] rather than as a corpus cerebelli [9].

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