Electroreceptors and Direction Specific Arrangement in the Lateral Line System of Salamanders?

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The arrangement of the lateral line afferents of salamanders as revealed by transganglionic staining with horseradish peroxidase is described. Each lateral line organ is supplied by two fibers only. In the medulla these two afferent fibers run in separate fiber bundles. It is suggested, that only those fibers contacting lateral line sensory cells with the same polarity form together one bundle. Bundles formed by anterior or posterior lateral line afferents are also clearly separated. Beside the lateral line organs smaller pit organs are described. These organs are supplied by one afferent only which reveals an arrangement in the medulla different from that of the lateral line afferents. Based on anatomical facts, these small pit organs are considered to be electroreceptors. Centrifugally projecting neurons, most probably efferents, are described in the medulla.

All amphibian larvae and many adult salamanders as well as some adult frogs have a well developed lateral line system. The sense organs of this systems are arranged in lines along the body and head comparable to the arrangements in fishes [1, 2]. The trunk lateral line organs are supplied by afferents originating from the posterior lateral line ganglion and enter the brain together with the nervus glossopharyngeus. The head lateral line organs are supplied by fibers from the anterior lateral line ganglion and enter the brain dorsal to the nervus statoacusticus. Based on Golgi-studys, the posterior lateral line afferents seem to form two fiber bundles running along the dorso-lateral part of the medulla. The anterior lateral line afferents, however, are assumed to possess three fascicles with the most dorsally located fascicle restricted to the dorsal island of Kingsbury [3] and the other two fascicles running together with the posterior lateral line bundles along the medullary side wall thus forming a medial octavolateralis nucleus [4].

In an experimental study with horseradish peroxidase (HRP) as a transganglionic marker, we have tried to prove this early assumptions for *Triturus cristatus, Triturus alpestris,* larvae of *Salamandra salamandra,* and the axolotl (*Ambystoma mexicanum*). One or several lateral line nerves were exposed under MS 222 anaesthesia, cut and HRP (Böhringer Grade I) was applied to the distal and proximal nerve stumps. The brains were further processed after various survival times as described [5].

The results confirm the assumptions of Herrick [3] and show the arrangement of the afferents into distinct ascending and descending fascicles (Fig. 1). Only in adult animals some collaterals leave the unbranched fibers and course deeper into the neuropil. The projection of the anterior lateral line system to the dorsal island of Kingsbury is composed of thinner fibers which are more coiled around each other (Fig. 1).

Almost all preparations showed label in centrifugal neurons. Since only the posterior lateral line nerve is a pure lateral line nerve [1], only centrifugal neurons of this nerve may be considered as lateral line efferents. No difference in numbers was obtained after labelling one or two of the four posterior lateral line branches. This seems to indicate, that one efferent neuron supplies collaterals to several or all lateral line nerves like in bonyfish [6]. Only few efferent neurons are usually labelled (about 3 to 6) and they seem to be equally distributed both ipsi- and contralateral. The fibers of these cells can be followed from the entrance in the brain to the cells of origin near the nucleus motorius nervi facialis [7]. The bilateral arrangement of efferent neurons is similar to the distribution of efferents of the vestibular system [8] but contrasts to the purely ipsilateral distribution described in bonyfish [6].

In *Xenopus laevis* it is well known, that only two afferents enter each lateral line organ and each afferent fiber innervates only hair cells with one polarity [9]. The arrangement of the lateral line afferents into distinct fascicles may therefore be indicative for a direction specific organization of the afferents. In order to test this assumption, single lateral line organs have been removed and the exposed afferents have been stained with HRP as described above. Both posterior (N = 6) and anterior (N = 6) lateral line organs project via two clearly separated afferents in the medulla. Only in two cases of anterior lateral line organs was a projection to the dorsal island of Kingsbury obtained beside the ventral projection.

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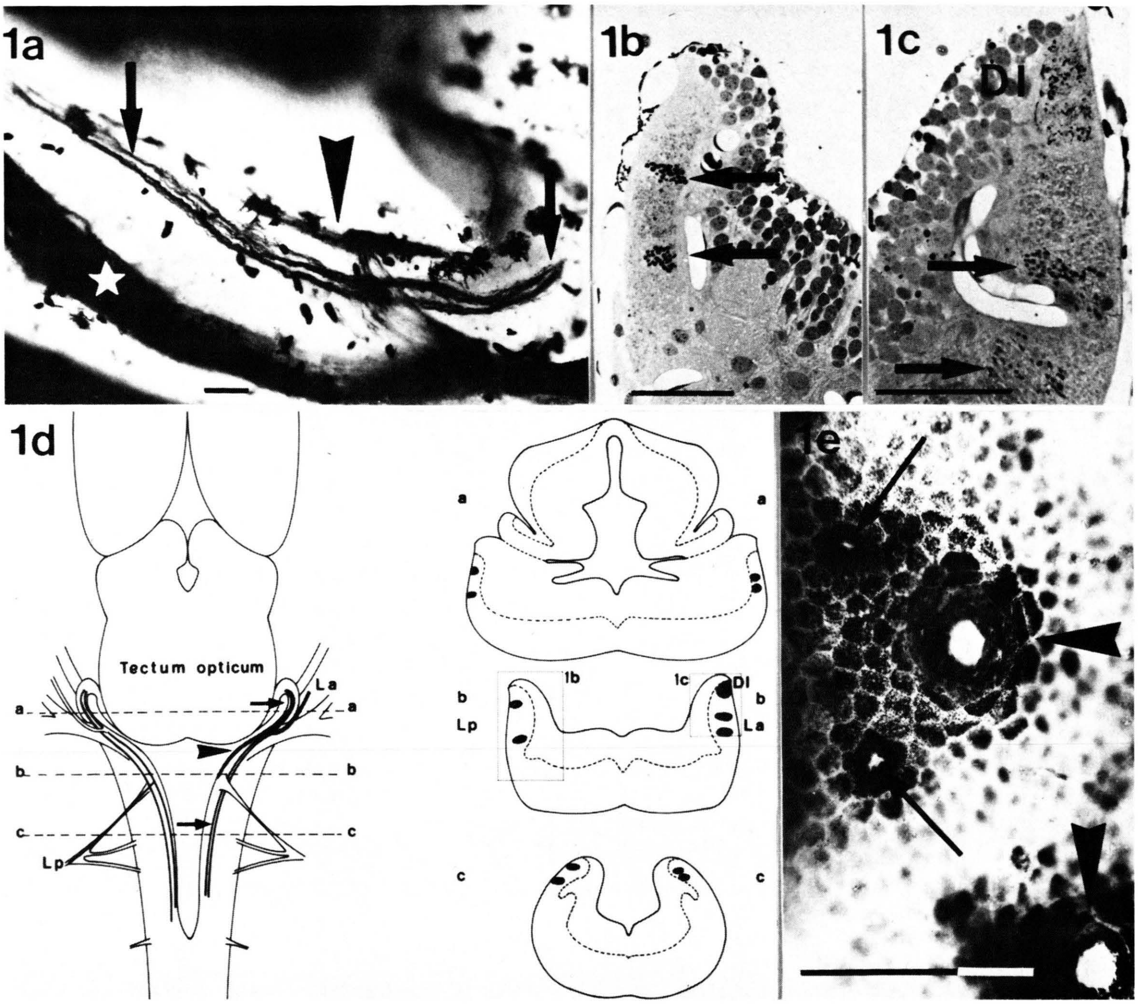

Fig. 1 a. Dorsolateral aspect of the medulla of a larval *Salamandra sal.* The central course of the anterior lateral line afferents (arrows and arrowhead) and the trigeminal afferents (star) are visible in this whole mount preparation. Notice the much shorter dorsal island projection (arrowhead) and the separation into two bundles of the more ventral lateral line nerve projection (arrows).

Figs. 1 b, c. Cross sections of the medulla of a larval *Salamandra sal.* at the level indicated in Fig. 1 d, showing the arrangement of the posterior lateral line afferents into two bundles (1 b, arrows) and of the anterior lateral line afferents into three bundles (DI, Arrows). Afferents of the dorsal island (DI) are thinner and originate at pit organs (Fig. 1 e, arrows) of the head.

Fig. 1 d. Schematic drawing of the medulla and the midbrain of a salamander showing the course of the posterior (Lp) and the anterior (La) lateral line afferents. Like in Fig. 1 a the dorsal island (DI) is indicated by an arrowhead and the separate bundles from the ordinary neuromasts of the anterior lateral line nerve by arrows.

Fig. 1 e. Dorsal view of the head of a larval *Salamandra sal.* showing two lateral line organs (arrowheads) and two presumably electroreceptive pit organs (arrows) in the skin of the head. Differences in size, skin cell arrangement, and pigmentation are visible.
Bars indicate 100 μm in all photomicrographs.

This data implicate a direction specific organization of lateral line afferents in the medulla of salamanders in some respect comparable to the retinotopic organization of the visual and the tonotopic projection of the acustic system. The lateral line afferent organization may prove to be "directotopic". Opposite to the visual and acustic system and the lateral line system in fishes and frogs, the simple arrangement of the described system seems to make it particularly usefull for an analysis of its information processing.

The dorsal island projection of the anterior lateral line nerve of the salamanders seems to be comparable to the dorsal projection of the electroreceptor afferents of electroreceptive fishes like sharks, rays, primitive bonyfish, electric fish, and lungfish. Electroreception is assumed for *Latimeria* and early amphibians [10]. Ampullary organs comparable to the ampullae of Lorenzini of sharks or the organs of Fahrenholz of lungfish [11] have been described for caecilians [1] but not for salamanders. We have therefore reexamined the skin of larvae and we have found, next to many anterior lateral line organs, small organs with a pit instead of a cupula (Fig. 1 e), which closely resemble the sunken lateral line organs of caecilians [12]. However, the distribution of these organs is similar to the distribution of ampullary and not of the sunken lateral line organs of caecilians. Cutting out single pit organs revealed projections only to the dorsal island of Kingsbury. This strongly supports the view of [13], that the electroreceptive ampullary organs developed out of sunken neuromasts and that at least the tested salamanders, like some caecilians, may be electroreceptive.

Frogs, like nonelectric bonyfish, seem to have no dorsally projecting part of the anterior lateral line nerve [4]. However, frogs have a dorsal auditory nucleus in that area. The old hypothesis of [14], that the dorsal lateral line nucleus of fishes becomes the auditory nucleus of frogs and amniots may be wrong only insofar, as it is not the lateral line nucleus but the dorsal electroreceptive nucleus that becomes the auditory nucleus. This readily explains why some frogs have a lateral line nucleus beside an acustic nucleus [15], and why salamanders show only a very weak dorsal projection of the vestibular nerve [16].

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