Peripheral Organization and Central Projections of the Electrosensory Nerves in Gymnotiform Fish

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ABSTRACT

The electrosensory system of weakly electric gymnotiform fish is described from the receptor distribution on the body surface to the termination of the primary afferents in the posterior lateral line lobe (PLLL). There are two types of electroreceptor(ampullary and tuberous) and a single type of lateral line mechanoreceptor (neuromast). Receptor counts in *Apteronotus albifrons* show that (1) neuromasts are distributed as in other teleosts; (2) ampullary receptors number 151 on one side of the head and 208 on one side of the body; (3) tuberous receptors were estimated to number 3,000-3,500 on one side of the head and 3,500-5,000 on one side of the body. The distribution of each receptor type is described.

Each receptor is innervated by a single primary afferent. Electrosensory afferents have myelinated cell bodies in the ganglion of the anterior lateral line nerve (ALLN). The distribution of these ganglion cell diameters is strongly bimodal in *Apteronotus* and *Eigenmannia:* The smaller-diameter cells may be those which innervate ampullary electroreceptors, the larger-diameter tuberous electroreceptors.

Transganglionic HRP transport techniques were used to determine the first-order connections of the anterior lateral line nerve in six species of gymnotiform fish. Small branches of the ALLN were labeled so as to determine the somatotopic organization in the PLLL. The PLLL is divided into four segments from medial to lateral, termed medial, centromedial, centrolateral, and lateral segments (Heiligenberg and Dye, '81). Representations of the head are found rostrally in each zone, and the trunk is mapped caudally in each zone. Thus there are four body maps in the PLLL. The medial segment receives ampullary input (Heiligenberg and Dye, '82) and maps the dorsoventral body axis mediolaterally, as does the tuberous centrolateral segment. The tuberous centromedial and lateral segments map the dorsoventral axis lateromedially. Thus the medial and centromedial segments meet belly to belly, the centromedial and centrolateral segments meet back to back, and the centrolateral and lateral segments meet belly to belly. Adjacent electrosensory maps within the PLLL are therefore always mirror images.

The octavolateralis system of teleosts is composed of the lateral line, auditory, and vestibular systems. In teleosts with electrosensory capabilities, the lateral line includes both mechanosensory and electrosensory modalities. In the weakly electric teleosts of South America (Gymnotiformes), electroreceptors and mechanoreceptors are distributed over the body surface and are innervated by the primary afferent fibers of the octavolateralis system. These fibers enter the brain via the anterior lateral line nerve (electrosensory and mechanosensory primary afferents) and the posterior lateral line nerve (mechanosensory primary afferents only). Vestibular and auditory receptors in the ear are innervated by the various rami of the eighth nerve. The first-order termination sites of the octavolateralis system are segregated within the medulla on the basis of

modality. The electroreceptive input projects to the posterior lateral line lobe (PLLL); mechanosensory input projects to nucleus medialis (formerly termed the anterior lateral line lobe) and the caudal octavolateralis nucleus; and the VIII nerve projects to a column of five octaval nuclei (Maler et al., '74; Carr and Matsubara, '81).

The subject of this paper is the peripheral electrosensory system, from the distribution of electroreceptors on the body surface to the projections of the electrosensory portions of the anterior lateral line nerve. Electroreception is a second-order sense (Bennett, '67) with receptor cells which are innervated by primary afferents whose cell bodies are localized in the anterior lateral line ganglion (Szabo, '74; Bullock, '82; Viancour, '79). The electrosense has two major classes of receptors, termed ampullary and tuberous electroreceptors, which can be distinguished on the basis of both morphology and physiology.

Members of the orders Siluriformes, Gymnotiformes, and Mormyriformes all possess electroreceptors, although their electrosensory systems are not believed to be homologous, but to be three separate inventions (McCormick, '82), possibly from common lateral line origins (Bullock, '82; Bullock et al., '82). The similarities in receptor type observed among the three orders are due to convergent evolution. The Siluriformes (catfish) possess only ampullary receptors, which are very sensitive to low-frequency AC fields and are useful in differentiating living from nonliving material in the substrate (for review, see Kalmijn, '74). Ampullary receptors are also found in both orders of the weakly electric fish, the Mormyriformes and the Gymnotiformes. In addition, these orders both possess electroreceptors of the tuberous type, which respond to high-frequency signals and are generally tuned to the animals' own electric organ discharge (EOD) (Scheich and Bullock, '74; Hopkins, '76; Bastian, '76b).

Tuberous electroreceptors monitor the transepidermal current flow of the EOD and are thus responsible for the fishes' powers of electrolocation and communication with conspecifics (see review in Heiligenberg, '77). These receptors are densely distributed over the body and are best suited to provide an electric image of the fish's immediate surroundings. Both gymnotiform and mormyriform fish possess two major types of tuberous electroreceptors which serve analogous functions in both orders. The one type, termed Knollenorgan units in Mormyriformes and T-units or phase coders in wave-type Gymnotiformes, marks the occurrence of an EOD in a yes or no manner and thus does not give much information about local EOD intensity. The projections of these systems are characterized as "fast" in both orders because they have a short-latency pathway up to the midbrain, large-diameter axons, and electronic synapses (Szabo, '74; Réthelyi and Szabo, '73). The other type of tuberous receptor produces a graded response to changes in the local intensity of the EOD and thus plays an important role in electrolocation. In this case, these receptors are termed mormyromasts in Mormyriformes and P-units or probability coders in Gymnotiformes (see review in Heiligenberg, '77).

The distribution and morphology of the electroreceptors has been qualitatively described in all three orders of electroreceptive teleosts (Szabo, '65; '74; Wachtel and Szamier, '66, '69a,b). Quantitative descriptions of the electric images of simple objects are now available (Heiligenberg, '75; Bastian, '81a,b; Hoshimiya et al., '80). The circuitry of the PLLL has also been analyzed in great detail (Maler, '79;

Maler et al., '81). A quantitative description of the numbers and distribution of electroreceptors over the body surface and the precise mapping of these receptors onto the PLLL is a prerequisite to more detailed physiological studies of the PLLL. The following anatomical study should serve to provide some bounds on the convergence and divergence of electroreceptive input to the PLLL.

METHODS
Analysis of receptor organization

The distribution of receptors has been evaluated in the same fashion for all three classes of receptors: neuromasts of the ordinary lateral line, ampullary receptors, and tuberous electroreceptors. In each case the receptor type has been identified by the nature of the pore which overlies the receptor organ. There is ample evidence that this is sufficient measure (Szabo, '65; Szamier and Wachtel, '69, '70; Wachtel and Szamier, '66, '69b; Bennett, '67). Neuromast pores have the greatest diameter (100 μm in *Eigenmannia*) and ampullary receptors the smallest (25 μm). Ampullary receptor pores occur in characteristic clusters. Tuberous electroreceptor pores are intermediate in size (50 μm as measured from a figure) and may or may not be clustered (Bennett, '67).

Neuromasts. The "ordinary lateral line" is entirely separate from the electrosensory system, and its receptors (neuromasts) display typical mechanosensory responses (Szabo, '65, '74).

Receptor organ counts were done on five *Apteronotus* ranging from 10 to 17 cm in length. All neuromasts and ampullary receptor organs of one side of the body were counted and their positions mapped on a drawing of the fish's body. Tuberous receptor organ density was measured at selected points on the head and trunk (see below). The area of the fish's body was estimated by tightly wrapping a plastic sheet over the body, cutting it to fit, and then measuring the area of the unfolded sheet with a Zeiss MOP Image Analyzer.

Analysis of anterior lateral line ganglion

Serial sections (2 μm thick) were made through one NLLa ganglion of *Eigenmannia virescens* and one of *Apteronotus albifrons*. Adjacent sections were examined for evidence of split nucleoli. They were rarely encountered. Nucleoli were counted in every eighth section of the *Eigenmannia* material and every tenth section of the Apteronotid material. A filar micrometer was used to measure the diameter of each counted cell.

Electron microscopy was performed on NLLa ganglia of these two species using procedures described in a previous publication (Maler et al., '81).

Tracing of the ALLN

Thirty fish of the order Gymnotiformes were used. These included six *Eigenmannia virescens*, one *E. limbatus* (Mago-Lecchia, personal communication), and three *Sternopygus dariensis* (family Sternopygidae); six *Apteronotus albifrons* and ten *Leptorhynchus* spp., commonly called brown ghosts (family Apteronotidae); and four *Gymnotus carapo* (family Gymnotidae). The fish were anesthetized with dilute solutions of tricaine methanesulphonate (1:20,000) and ventilated during surgery. Four branches of the ALLN were injected with HRP. These were the supraorbital, the maxillary, and the mandibular branches of the anterior lateral line nerve (head) and the recurrent branch (trunk).

The recurrent branch was labeled at various points along its rostrocaudal extent so as to determine the rostrocaudal topography within the PLLL. Injections of the three nerves on the head enabled us to determine the dorsoventral distribution of the cranial electroreceptors in the PLLL.

Exposed nerves were cut and injected with a 30% solution of HRP (Sigma VI). The cut end was then soaked in a 30% HRP solution in a gelatin sponge and the skin glued shut (Braun-Melsungen Histoacryl Blue tissue glue). In some cases the HRP solution was made up in 3% DMSO in an attempt to enhance terminal filling (Keefer et al., '76; Bell and Russell, '78). The animals were killed after a survival time of 3–8 days. They were first anesthetized in tricaine methanesulphonate (1:10,000) and then perfused through the heart with pH 7.4 phosphate buffer, followed by 2% glutaraldehyde, 2% paraformaldehyde in phosphate buffer, then by 30% sucrose plus 4% glutaraldehyde-paraformaldehyde in phosphate buffer. The brains were then processed in the conventional manner, following the protocols of Mesulam ('78) and Hanker-Yates, modified by Finger (Finger et al., '81).

RESULTS

Distribution of lateral line and electrosensory system receptors

Head (Fig. 1). As in other teleosts (Disler, '71; Szabo, '65), the neuromasts of the head region of *Apteronotus* can be placed in four lines: the supraorbital (five neuromasts), infraorbital (seven neuromasts), preoperculomandibular (seven neuromasts), and temporal (five neuromasts). A small number of neuromasts are not readily assigned to any of these lines and the total number of neuromasts on one side of the head is 32.

We need well-defined rostrocaudal and dorsoventral axes for the fish's body in order to analyze the distribution of tuberous receptors. The supraorbital, infraorbital, and preoperculomandibular lines are excellent rostrocaudal axes for the complexly curved surface of the fish's head since (1) they "follow" the dorsal and ventral edges of the head (Fig. 1) and (2) they are always identical even in fish of very disparate sizes.
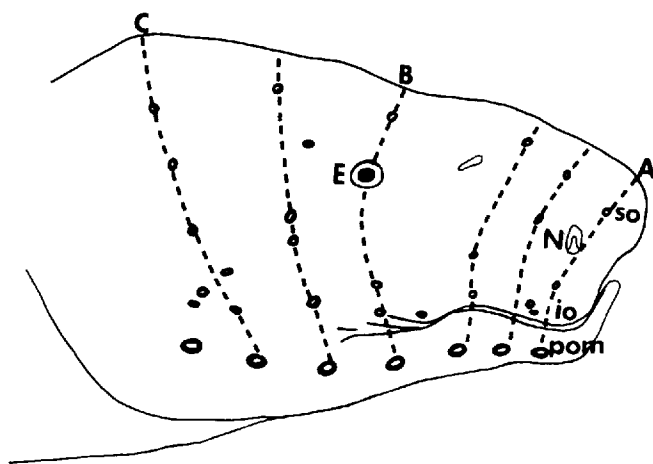

Fig. 1. Distribution of neuromasts on head of *Apteronotus albifrons*. Note that the neuromasts are grouped in supraorbital (so), infraorbital or maxillary (io) and preopercular-mandibular lines (pom). Dashed lines are at right angles to these lines; measurements of tuberous receptor density along the dorsoventral axis were at A, B, and C. E, eyes; N, nares.

Lines drawn through equivalent neuromasts of the supraorbital, infraorbital, and preoperculomandibular lateral lines will intersect both dorsal and ventral surfaces of the fish at about 90° (Fig. 1, dashed lines). These lines are always at right angles to the previously defined rostrocaudal axes and thus serve as arbitrary but consistent dorsoventral axes of the fish's head.

Since the number and distribution of neuromasts on the head is almost entirely constant in fish of various sizes these longitudinal and vertical axes provide a suitable framework for examining the spatial density variations of tuberous electroreceptors in fish of various body lengths.

Trunk. Most neuromasts of the trunk occur in the well-defined lateral line (70). As for the head, the lateral line can define a rostrocaudal axis for the trunk, and lines perpendicular to it are considered as lying on the dorsoventral axis of the trunk. A small number of free neuromasts (ie, not confined to the lateral line) are found along the dorsum of the fish (ten), scattered along the dorsolateral body wall (46) and scattered on the ventrolateral body surface (four to six). The total number of neuromasts on one side of the trunk is thus about 130.

The number of neuromasts does not vary with the size of the fish, within the size range which we have examined (10–17 cm). There is a small degree of variations in the number of neuromasts in the lateral line (67–72) but this seems to depend only on whether a few extra neuromasts are present in the region above the pectoral fin.

Ampullary receptors

The distribution of ampullary receptor organs is remarkably similar in both the Siluriformes and the Gymnotiformes (Szabo, '65; Szamier and Wachtel, '69, '70; Wachtel and Szamier, '69b; Peters et al., '74).

Generally, an ampullary receptor organ is a unit consisting of an ampulla which contains sensory and supporting cells and has a jelly-filled duct which opens to the outside. However, a receptor organ can also be formed from clusters of two to 12 of these receptor units. Each organ is innervated by a single myelinated fiber (Szabo, '65; Szamier and Wachtel, '69).

Head (Fig. 2A,B). Ampullary receptor organs are fairly randomly scattered over the head although there is some tendency for them to cluster near the mouth, nares, eye, and over the operculum.

The total number on one side of the head is 151 and this number remains constant in fish of varying lengths.

Trunk (Fig. 3). Ampullary receptor organs of the trunk are found in four groups: (1) just ventral to the pectoral fin (17), (2) along the dorsum of the fish (100), (3) along the lateral line (44), and (4) along the ventral surface of the fish (47). The total number of ampullary receptor organs on the trunk is 208 and this does not vary with the length of the fish.

Tuberous receptors (probability coders plus phase coders)

Tuberous receptors are much more densely distributed over the body surface than were either of the two preceding types. Tuberous electroreceptors do not have a duct to the surface but an epithelial plug below a pore. Each receptor organ contains a number of receptor cells which are characteristic of the receptor type, although considerable variation exists between various species of Gymnotiformes (Szabo, '65, '74; Bennett, '67).
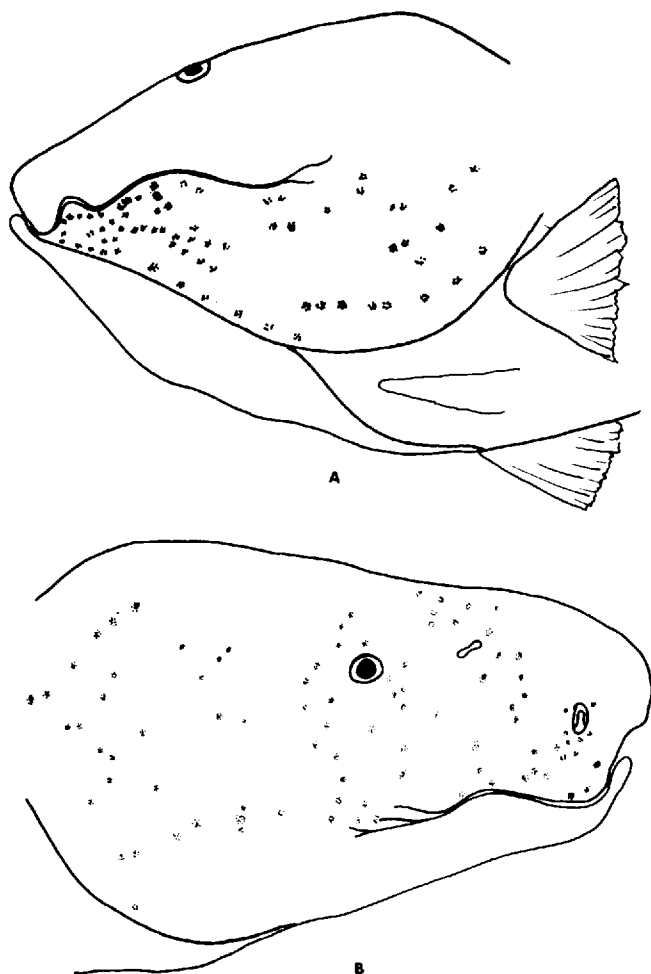
Fig. 2. A. Distribution of ampullary receptors on the dorsal aspect of the head. B. Distribution of ampullary receptors on the ventral aspect of the head. Note somewhat greater density near mouth, nares, and eye.
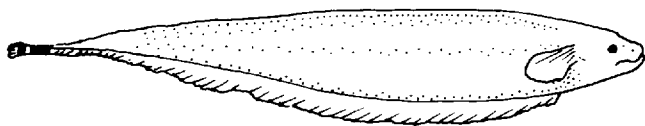

Fig. 3. Distribution of ampullary receptors on the trunk. Note that receptors are present only at the dorsal and ventral asepcts of the body and along the lateral line.

Head. The rostrocaudal distribution of tuberous electroreceptor pores was measured along the supraorbital, infraorbital, and preoperculomandibular lines. The dorsoventral distribution was measured along the arbitrary dorsoventral axes previously defined (Fig. 1) at three positions (Fig. 1): just rostral to the nares (A), just caudal to eye (B), and in the middle of the operculum (C). In the rostrocaudal direction there is a fairly linear decline in tuberous receptor pore density. This is graphically illus-

trated for a 15-cm fish (Fig. 4a) where the density rostrally ranges from nine to 15 receptor organs/mm² and falls to seven to nine receptor organs/mm² over the operculum region; it should be noted that a somewhat higher density (20–25 receptor ogans/mm²) is present at the very rostralmost surface of the snout.

These results are supported by the observations of Szabo ('65), who found similar densities of electroreceptors in an *Apteronotus albifrons* of 13 cm length.

In the dorsoventral plane a similar pattern emerges at positions A, B, and C: The tuberous receptor density is highest at the dorsal and ventral edges and somewhat less in between (Fig. 4b). The increase of tuberous receptor density at the ventral surface has not been previously reported for gymnotiform fish (Szabo, '65; Westby, '75).

Trunk. The rostrocaudal distribution of tuberous electroreceptor organs was measured along the dorsum of the fish, along the lateral line, and just above the anal fin. The dorsoventral distribution was measured at three positions: just behind the gills (R), in the middle of the trunk (M), and just in front of a white band found in the tail region. The results for the same 15-cm fish are graphically presented in Fig. 5a,b. The same pattern is present on the trunk as on the head: The rostrocaudal electroreceptor density shows a simple decline while the dorsoventral distribution has peaks at the dorsal and ventral edges of the fish. The absolute densities are far lower on the trunk than on the head, ranging between 0.6 and 3.4 tuberous electroreceptor organs/mm².

When equivalent regions of the head and trunk are compared among fish of different lengths the smaller fish has a greater density of tuberous electroreceptors. This indicates that the number of tuberous electroreceptors does not increase substantially as the fish grows from 10 to 17 cm. In order to verify this point we picked a 13-cm and a 17-cm fish and counted all the tuberous receptor organs in two strips of skin: between the eye and the caudal nares, and between the caudal and rostral nares. These regions were clearly larger in the larger fish and we assume that the growth has been a simple linear expansion so that the regions remain precisely homologous in fish of different lengths. In the region between eye and nares the smaller fish has 25 receptor organs while the larger had 26; the region between the nares contained 47 receptor organs in both fish. Thus over the size range of fish which we have examined the number of neuromasts and ampullary and tuberous receptors all apparently remain constant.

For a fish 15 cm in length we estimate that one side of the head has a area of 391 mm² and, assuming an average receptor density between 8 and 9/mm², contains 3,000–3,500 tuberous electroreceptor organs. One side of the trunk is about 2,500 mm², and, assuming an average density between 1.4 and 2/mm², contains approximately 3,500–5,000 tuberous electroreceptor organs; the total number of tuberous receptor organs on one side of the body is thus 6,500–8,500. These numbers represent mostly the probability coders, since phase coders may be rare in Apteronotids (Scheich and Bullock, '74; Bastian, personal communication).

Anterior lateral line ganglion

The anterior lateral line nerve ganglion consists of compact strands of spherical ganglion cells separated by bundles of myelinated nerve fibers. At the light microscopic level (Fig. 6A), the ganglion cells appear strongly baso-
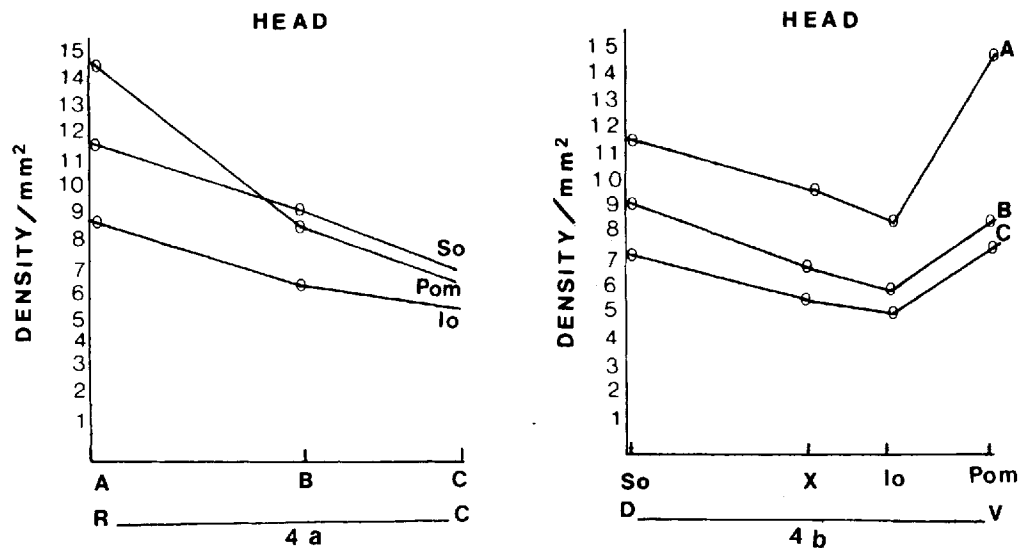
Fig. 4. Tuberous receptor density (number per mm²) on head. a. Rostrocaudal (R–C) distribution along supraorbital (so), infraorbital (io), and mandibular (pom) neuromast lines. Measurements were made at A, B, and C of Fig. 1 (A–B, 6.5 mm; B–C, 8.5 mm). b. Dorsoventral (D–v) distribution along dotted lines A, B, C (Fig. 1). Measurements were made at supraorbital neuromast (so), just below nares (x), infraorbital neuromast (io), and mandibular neuromast (pom). Note increased density at dorsal and ventral aspects of head.
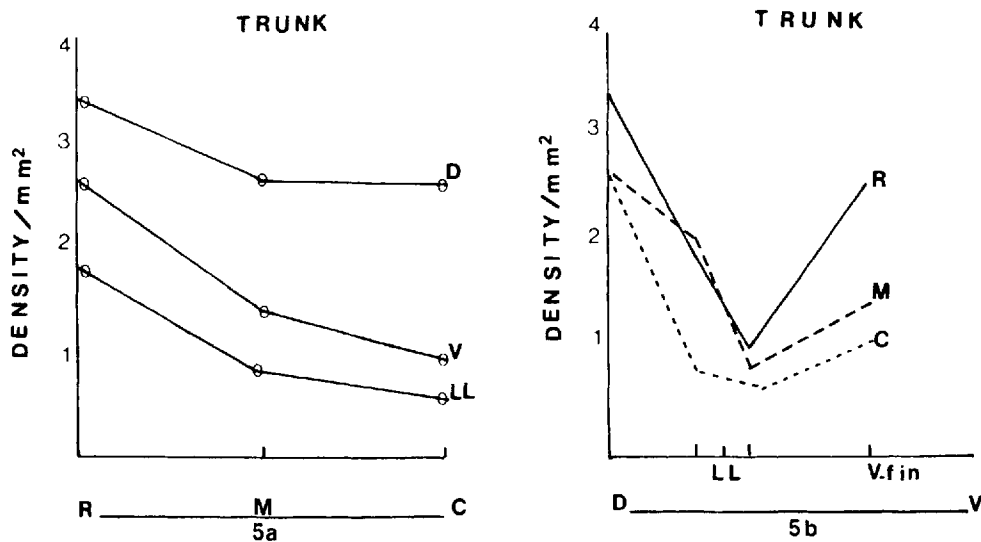

Fig. 5. Tuberous receptor density on trunk. a. Rostrocaudal distribution along dorsal (D) and ventral (V) aspect of the trunk and along lateral line (LL). Measurements were taken just behind operculum (R), at the midpoint of the trunk (M), and just in front of the first white stripe on the tail (C). b. Dorsoventral distribution at points R, M, and C. Measurements were taken at dorsally and ventrally (V-fin, ventral fin) as well as just above and below the lateral line (LL). Note increased density at dorsal and ventral aspects of the trunk.

philic; their nucleus is centrally located and round; it contains dispersed chromatin and a well-developed nucleolus; In about 10% of the cells, two nucleoli are present. At the electron microscopic level (Fig. 6B) ganglion cells contain large amounts of rough endoplasmic reticulum and numerous mitochondria. Fascicles of neurofilaments are also prominent, as are dense bodies occasionally containing granular (Fig. 6C) or paracrystalline inclusions. All ganglion cells are surrounded by myelin. The smaller cells are wrapped by loose myelin while the larger ones have six to 12 lamellae of loose myelin surrounded by a few lamellae of compact myelin. The existence of myelinated cell bodies has previously been demonstrated in the VIII nerve ganglia of both teleosts and mammals (Adams and Daignault, '70; Rosenbluth, '62; Rosenbluth and Palay, '61) and their presence in a lateral line ganglia is consistent with the proposed evolutionary link between lateral line and VIII nerve systems (van Bergejik, '67).

The total number of ganglion cells on one side in *Eigenmannia* is 7,608 and in *Apteronotus* is 7,290; these figures are not corrected for split nucleoli since we find few of them in our material (see Konigsmark et al., '69,
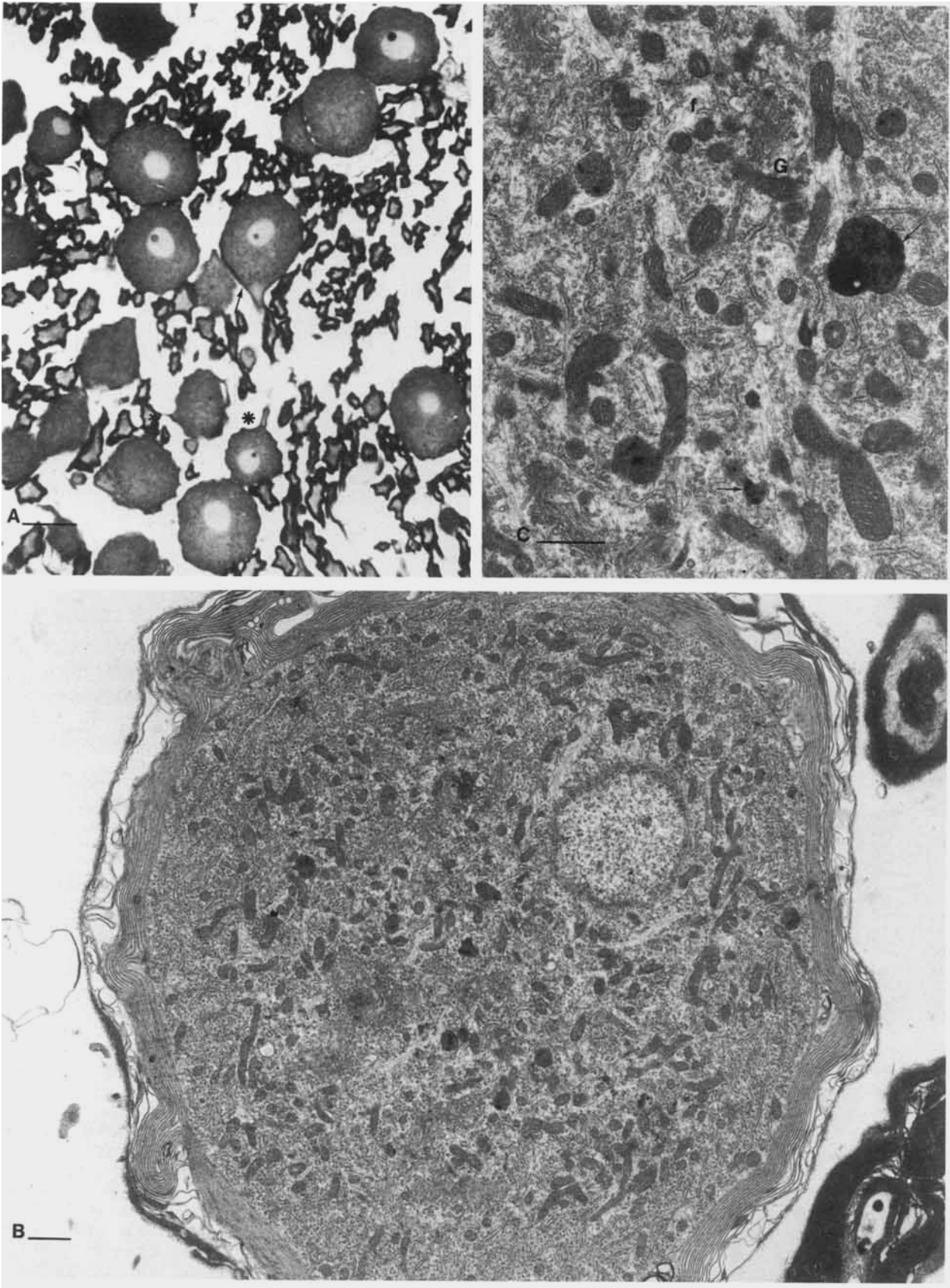
Figure 6

for discussion). At least for *Apteronotus* the number of ganglion cells is within the estimated range of tuberous plus ampullary receptors (7,000–9,000). These results imply that one ganglion cell usually innervates one tuberous receptor organ; this is an important conclusion since it determines the limits of convergence from primary afferents onto neurons of the PLLL (see Discussion). The number of ampullary receptors is so small that no conclusion can be drawn as to whether a ganglion cell innervates one or several clusters of these receptor organs.

For both *Eigenmannia* and *Apteronotus* the distribution of ganglion cell diameters is strongly bimodal with major peaks *(Eigenmannia)* at 25 μm and 31 μm; the peaks for *Apteronotus* are merely shifted 1.6 μm higher than *Eigenmannia* (Fig. 7A,B). The probability of a normal distribution fitting this curve is only 0.001% (chi-square test) indicating that the bimodality is not a statistical artifact. In the *Apteronotus* ganglion there may be additional small peaks at 21 μm and 41 μm; the peak at 41 μm might represent phase coders since these are innervated by very thick, rapidly conducting axons (Type I tuberous receptor, Szabo, '74), while the peak at 21 μm may consist of ganglion cells innervating the rather slowly responding ampullary system (Bennett, '67). The number of cells in each major peak (26.6 μm and 32.6 μm) is large and most of these cells must innervate the probability coders. The two size classes may represent ganglion cells innervating head (smaller cells) or trunk (larger cells) electroreceptor organs. Alternatively these size classes may correspond to the P-unit functional subtypes recently described (Bastian, '81a). The observations of Heiligenberg and Dye (1982) support the former explanation. Intracellular HRP fills of phase coder electroreceptors in the ALLG of *Eigenmannia* show that the largest cell bodies belong to those phase coders which innervate the most caudal electroreceptors. Phase coders with smaller cell bodies innervated head and rostral trunk electroreceptors. The same may be true for probability coders in *Apteronotus*.

Distribution of electroreceptor afferents in the posterior lateral line lobe

The anterior lateral line nerve of gymnotiform fish consists of anterior (ALLN) and recurrent rami (RALLN). In the periphery, branches of the anterior ramus contain afferent fibers which innervate neuromasts as well as fibers to ampullary and tuberous electroreceptors. These branches are also associated with the trigeminal and facial nerves. The ALLN does not anastomose with either of these nerves, although all three ganglia (ALLN, V, and VII) are found
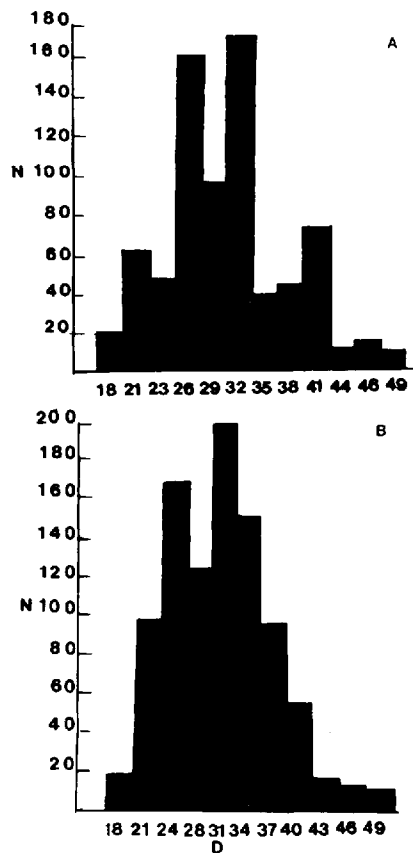

Fig. 7. Distribution of soma diameters within *Apteronotus* (A) and *Eigenmannia* (B) ganglia. Note major peaks at 26.6 μm and 32.6 μm and minor at 21 μm and 41 μm in *Apteronotus*. *Eigenmannia* has just two major peaks shifted about 1.6 μm down from *Apteronotus*.

Fig. 6. A. Toluidine blue-stained plastic section through anterior lateral line nerve ganglion showing a strand of ganglion cells containing prominent nuclei and nucleoli. Most cells are similar in size but a smaller one is also seen (asterisk). Arrow points to myelin surrounding soma. Bar maker is 15 μm.

B. Electron micrograph of a smaller ganglion cell. Note presence of loose myelin. The periphery of the cytoplasm contains dense rough endoplasmic reticulum while the interior has numerous mitochondria and lysosomes. Bar marker is 1 μm.

C. High-power view of ganglion cell cytoplasm. Golgi apparatus (G) and fascicles of filaments (f) are seen. Note dense inclusions within lysosomes (arrows). Bar maker is 1 μm.

within the same bony cavity of the cranium. The ganglia of nerves V and VII are found anterior and ventral to the ALLN ganglion, but are contained within separate connective tissue sheaths. We have not determined whether the neuromasts of the ordinary lateral line occupy a separate region of the anterior lateral line ganglion. However, degeneration and HRP studies suggest that the central termination of the neuromasts is separate from that of the electroreceptors. The posterior lateral line nerve contains a pure population of mechanoreceptors which terminate in nucleus medialis (formerly anterior lateral line lobe), the eminentia granularis, the caudal lobe of the cerebellum, in portions of the octaval cell column, and in the caudal octavolateralis nucleus (Carr and Matsubara, '81; Maler et al., '74). It appears likely that the mechanoreceptors of the head in the anterior lateral line nerve also terminate in these same nuclei: HRP fills of the mixed anterior branch of the anterior lateral line nerve produce terminal fields in these nuclei, as well as in the PLLL. In addition, no mechanoreceptive units have been recorded in numerous single unit studies of the PLLL (Bastian and Heiligenberg, '80; Bullock et al.; '72a,b; Heiligenberg, '77), although mechanoreceptive responses have been recorded from the nucleus medialis (Matsubara, personal communication). A single mechanoreceptive primary afferent in the anterior lateral line ganglion was injected with HRP

and was observed to terminate within the ALLL, but not within the PLLL (Heiligenberg and Dye, '82).

The electroreceptors of the ALLN terminate exclusively in the ipsilateral PLLL. The gymnotiform PLLL is a large dorsal expansion of the medulla, and it has been described previously by Maler et al. ('74) and by Rethelyi and Szabo ('73). It has a complex laminar structure which has been analyzed by Maler ('79) and Maler et al. ('81). The primary afferents enter as a deep fiber lamina ventral to the cellular laminae. Three discontinuities or breaks in these laminae serve to divide the PLLL into four roughly equal areas which run from medial to lateral (Fig. 8). Only two breaks have previously been described. A third has recently been identified by Heiligenberg and Dye ('81, '82). The most medial segment is also the most caudal, as the PLLL is oriented at a 45° angle to the rostrocaudal axis

of the brainstem. In this paper, as in previous reports of Maler ('79), the terms "transverse" and "longitudinal" will be used to describe the intrinsic axes of the PLLL, rather than the axes of the rest of the brainstem. The medial segment is the smallest and its medial surface is adjacent to the mechanosensory nucleus medialis. The centromedial segment is the largest and is divided from the centrolateral segment by the central break. The lateral break divides the centrolateral segment from the lateral segment. The lateral segment turns upward to fuse with the caudal lobe of the cerebellum. Consequently the laminar organization of the lateral segment is not as distinct as that of the central segments.

We made injections of HRP into the various rami of the ALLN in order to determine the topography of the primary afferent input into the four segments of the PLLL. The
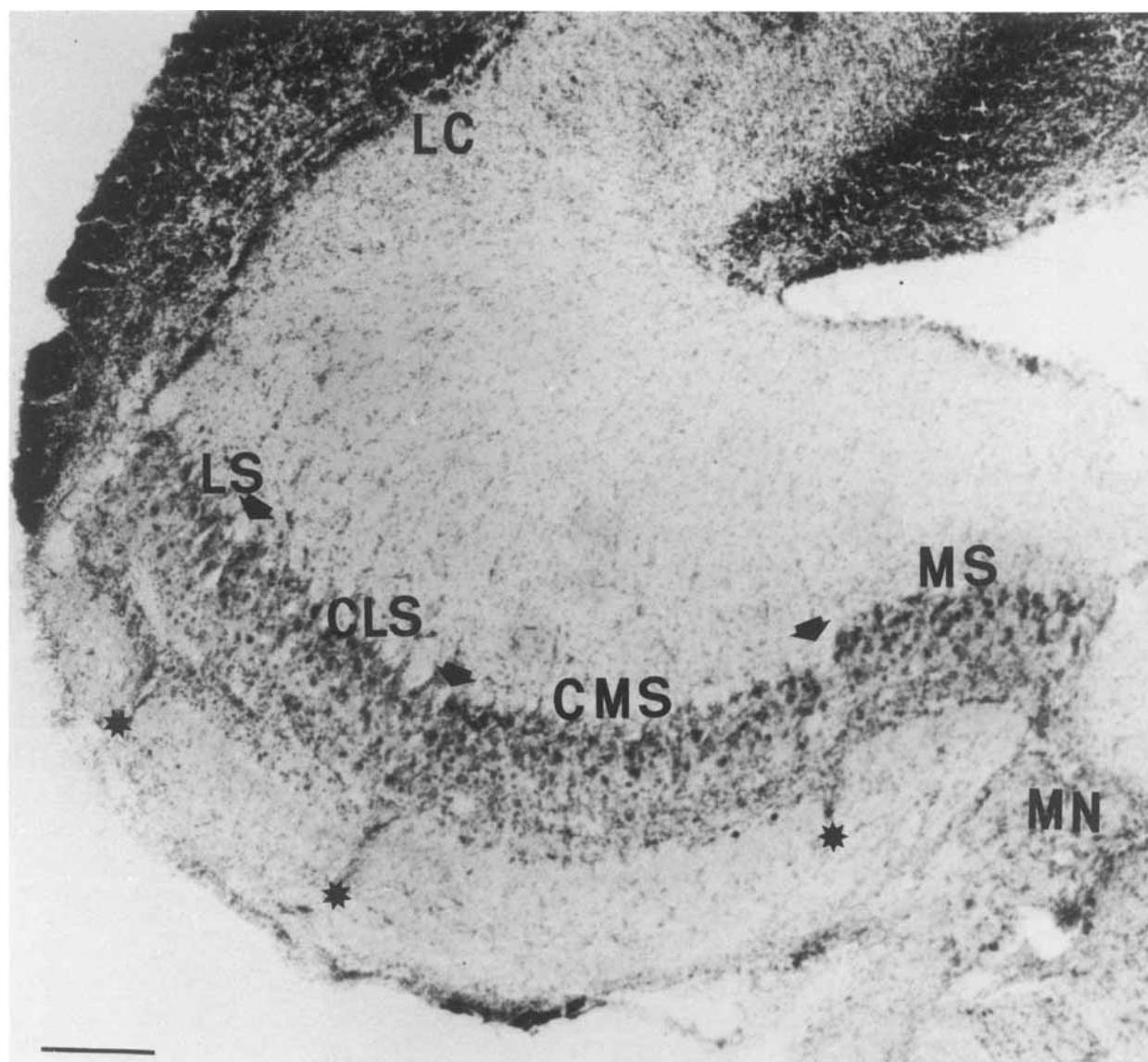

Fig. 8. Divisions within the posterior lateral line lobe: Low-power photomicrograph of an oblique section through the medulla of *Apteronotus albifrons* shows the discontinuities or breaks in the cellular laminae of the PLLL which divide it into four segments. Each break is marked with an arrowhead in the molecular layer; an asterisk indicates an increased glial density which often marks the breaks in the deep neuropil layer. Bar = 200 μm.

anterior ramus of the ALLN has three major divisions: The supraoptic branch runs over the orbit and presumably innervates the dorsalmost electroreceptors; the maxillary branch runs ventrally from the ALLN ganglion and then travels along the upper jaw and the mandibular branch innervates the ventral portion of the head and lower jaw.

Labeling of the RALLN (trunk) provided information as to the rostrocaudal axis of the primary afferent organizatwon of the PLLL. Labeling of the entire RALLN demonstrated that the trunk electroreceptors mapped onto the caudal portions of the PLLL and produced uniformly dense filling throughout the caudal portions of all four segments with the exception of gaps in the labeling found at each break (Fig. 9A,B).

Injection of HRP into any ramus of the ALLN produced labeling within the rostral portion of all four segments of the PLLL, and each ramus projected to a distinct region of each segment. Thus we can conclude that the rostrocaudal body axis maps rostrocaudally upon all four segments of the PLLL.

Labeling of the three cranial branches of the ALLN enabled us to distinguish dorsal from ventral topography. The dorsal supraoptic branch projects to the medial third of the medial segment (Fig. 10A), to the lateral third of the centrolateral segment, the adjoining medial third of the centrolateral segment, and the lateral third of the lateral third of the lateral segment (Fig. 10A,B). Similarly, the ventral mandibular branch projects to the lateral portion of the medial segment and the medial portions of the centromedial and lateral segments and the lateral portion of the centrolateral segment (Fig. 12a). Thus the map of the ventral body in the medial segment is closely apposed to the map of the ventral body in the centromedial segment (Fig. 12A). However, they can be clearly distinguished as two separate maps of the same body region, as the break between the laminae of the two segments is distinct, and the centromedial map is mostly rostral to the medial map. Similarly, maps of the dorsal body meet at the centromedial and centrolateral segment boundary and maps of the ventral body meet at the centrolateral and lateral segment boundary (Fig. 12B). The electroreceptors of the maxillary branch terminate in the center of each segment, filling in the midportion of the body map in each segment (Fig. 11). These four separate termination sites, one to each segment, offer convincing support for the existence of four separate somatotopic maps in the PLLL (Fig. 11A–C).

The somatotopy within the four segments is similar for the centromedial and lateral segments. The dorsal surface of the body maps laterally in each segment, the ventral surface medially, and the rostrocaudal axis is the same as that of the body. The maps in the medial and centrolateral segments have an inverted somatotopic organization compared to that of the other two segments, as the dorsum is mapped medially, while the lateral portion represents the ventral body. Table 1 and Figure 13 summarize the topographic representation of the four somatotopic maps within the PLLL. Note that adjacent maps in the gymnotiform PLLL are always mirror images with respect to the orientation of the dorsoventral body axis.

Maler ('79) and Maler et al. ('81) have described the termination of the primary afferents in the PLLL at both light and electron microscopic levels. An additional feature demonstrated by HRP fills of the ALLN is that when filling is sparse, the terminal branching of a single afferent fiber can be measured. In *Apteronotus albifrons* the max-
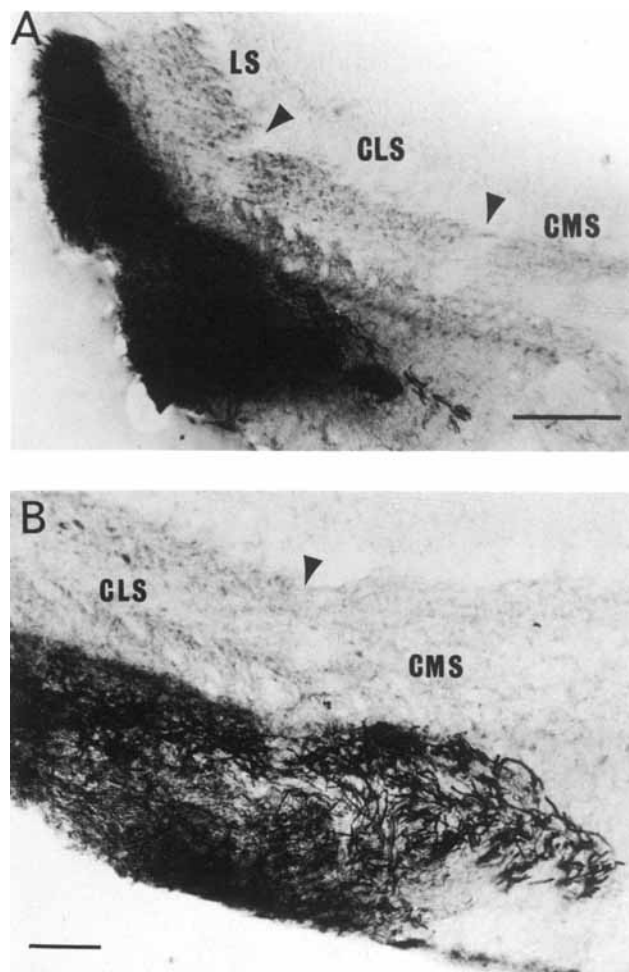

Fig. 9. Photomicrographs of transverse sections through the PLLL showing the distribution of electroreceptive primary afferent fibers from the recurrent branch of the ALLN, which innervates electroreceptors on the trunk. Note that these sections are cut on a true transverse plane through the medulla, while the orientation of the PLLL itself is approximately at a 45° angle to the longitudinal axis of the medulla. The consequence of this is that only an oblique section will contain all four segments of the PLLL. A transverse section will contain at most three out of the four segments, with only caudal portions of the most lateral segment and rostral portions of the most medial segment. Arrowheads mark the zones.

A. HRP-filled fibers from the RALLN terminate in the lateral and centrolateral segments of the PLLL. RALLN fibers only terminate in the caudal portions of each segment and thus would not be observed in the rostral portions of the centromedial segment. Bar = 200 μm.

B. HRP-filled fibers from the RALLN at a more caudal level showing primary afferent terminations in the centrolateral and centromedial segments. Bar = 100 μm.

Abbreviations

|	
ALLN	Anterior lateral line nerve
CMS	Centromedial segment of the PLLL
CLS	Centrolateral segment of the PLLL
LC	Lobus caudalis of the cerebellum
LS	Lateral segment of the PLLL
MN	Medial octavolateralis nucleus
MON	Magnocellular octaval nucleus
MS	Medial segment of the PLLL
PLLL	Posterior lateral line lobe
PLLN	Posterior lateral line nerve
RALLN	Recurrent branch of the anterior lateral line nerve
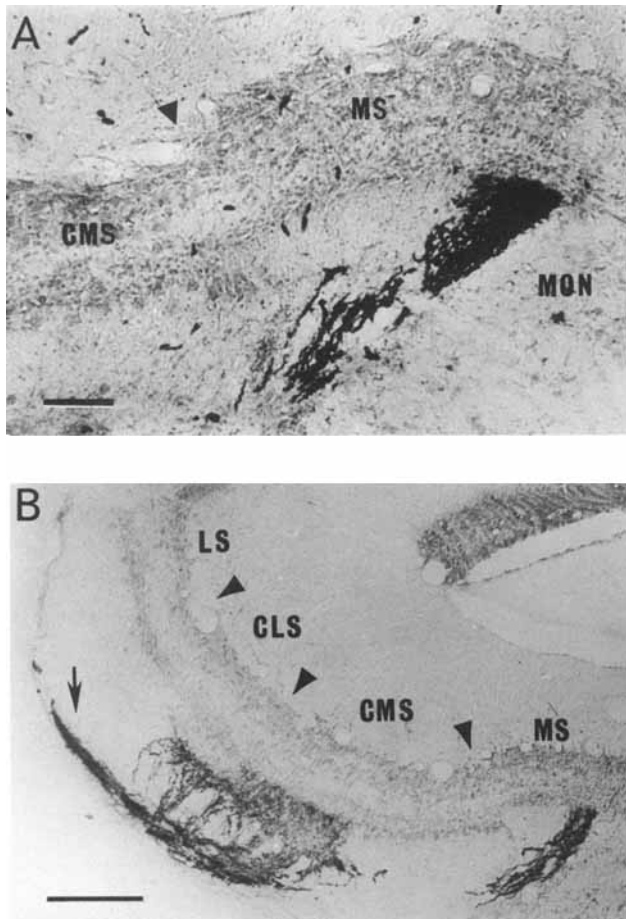
Fig. 10. Photomicrographs of oblique sections through the PLLL following labeling of the supraoptic branch of the ALLN. Arrowheads mark the breaks between each segment.

A. HRP-filled fibers occupy the most medial portion of the medial segment, adjacent to the mechanoreceptive nucleus medialis (MN). Bar = 50 μm.

B. Low-power view of the PLLL showing HRP-filled primary afferent fibers terminating in the medial portion of the medial segment, in the lateral portion of the centromedial segment, and in the adjoining medial portion of the controlateral segment. Arrow points to fibers which will terminate in the lateral segment in a more rostral section. Note that the supraoptic branch innervates the most dorsal electroreceptors on the head and thus these termination sites are the PLLL representation of the dorsal body. Bar = 200 μm.

imum measured spread of a single fiber was 100 μm in the mediolateral direction and 200 μm rostrocaudally.

HRP injections into any of the cranial branches of the ALLN results in labeled fibers within the caudal lobe of the cerebellum, whereas the RALLN does not project to the caudal lobe. Since the RALLN contains no ordinary lateral line afferents (Bennett, '67; Suga, '67; Szabo, '65), this indicates that the ALLN input to the caudal lobe may be from neuromasts rather than electroreceptors. Details of this projection are provided elsewhere (Carr and Matsubara, '81).

Both mechanoreceptive and eighth nerve afferents send collaterals to the eminentia granularis (Carr and Matsubara, '81). In the light of the presumed common origins of the electroreceptive and mechanoreceptive lateral line systems it is surprising that no such primary afferent elec-
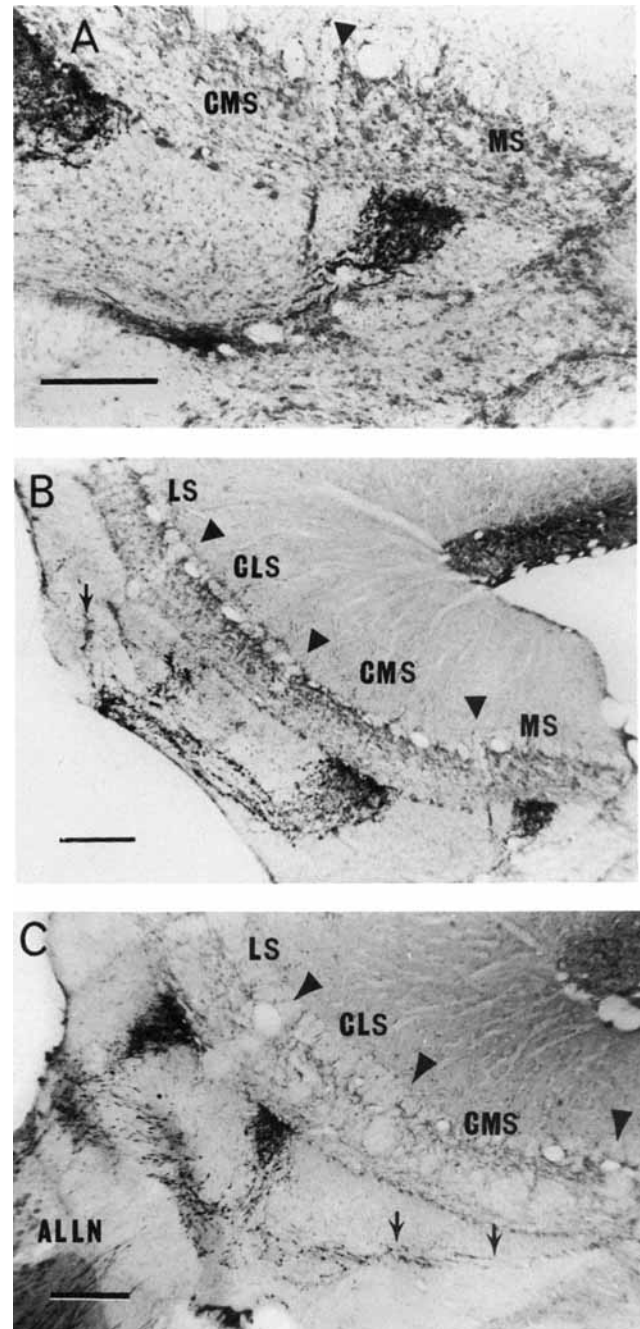

Fig. 11. Photomicrographs of oblique sections through the PLLL which show the termination sites of HRP-labeled primary afferents from the maxillary branch of the ALLN. Note that the labeled terminals are all found in the center of each segment, as might be expected from a fill of the maxillary nerve, which innervates the region of the upper jaw, below the region of the eye which is innervated by the supraoptic branch, and above the lower jaw region which is innervated by the mandibular branch of the ALLN. Arrowheads mark the zones. A. HRP-filled fibers occupy the central portion of the medial segment. Bar = 100 μm. B. HRP-filled fibers terminate in the caudal three of the four segments of the PLLL. An arrow marks the fibers which will terminate in the lateral segment in a more rostral section. Bar = 200 μm. C. An oblique section through the rostral PLLL contains terminal fields in the center of the lateral and centrolateral segments. Arrows point to the fibers which will terminate in the centromedial and medial segments. Note that all these figures are from the same case. Bar = 200 μm.
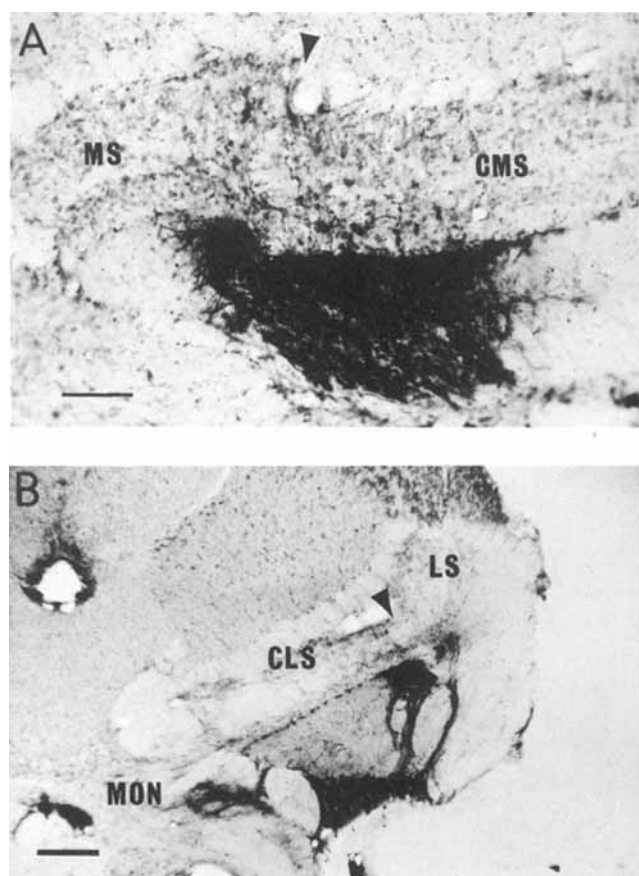
Fig. 12. Photomicrographs of transverse sections through the PLLL following HRP-labeling of the mandibular branch of the ALLN. Arrowheads point to the breaks between the laminae. Note that the HRP filling of the primary afferents in this case was so intense that some HRP has travelled transneuronally and has labeled some of the cells of the PLLL (see Triller and Korn, '81). A. HRP-filled fibers terminate in the lateral portion of the medial segment and the medial portion of the centromedial segment. Bar = 50 μm. B. HRP-filled fibers terminate in the lateral portion of the centrolateral segment and in the adjoining medial segment of the lateral zone, thus mapping the fish's electroreceptors belly to belly at this and the medial-centromedial boundary. Bar = 100 μm.

troreceptive projections to the cerebellum exist in either Gymnotiformes or Mormyrids (Bell and Russell, '78).

The recurrent branch does contain a few fibers which diverge from the bundles entering the PLLL. These fibers turn ventrally and medially to terminate in a nucleus identified as the descending trigeminal nucleus (Carr, unpublished observations). The presence of these fibers destined for the trigeminal nucleus may explain the observations of Feng and Bullock ('77). They found a number of units in the RALLN of *Eigenmannia* which were sensitive to the direction and degree of forced bending of the tail. It would be of comparative interest to determine whether such proprioceptive fibers run within the lateral line nerves of other teleosts or whether this is a special adaptation related to the need for the Gymnotiform fish to sense the position of its electric organ (Heiligenberg, '75).

DISCUSSION
Electroreceptor organization

Electroreceptors are distributed over the body in a nonuniform fashion, the greatest densities being on the head and on the dorsal and ventral surfaces of the body. These greater electroreceptor densities on the head may reflect the increased current density at the anterior end of the fish (Heiligenberg, '75; Hoshimiya et al., '81). Greater sensitivity around the mouth would presumably aid the fish in capturing prey. Further behavioral studies will be necessary to determine why tuberous electroreceptors are especially dense on the ventral surfaces of the fish. One interesting clue may be Bastian and Heiligenberg's ('80) suggestion that the ventral body is usually less contaminated by the electric organ discharge of nearby conspecifics and may therefore provide a reference signal for generating a correct jamming avoidance response.

The highest density of tuberous electroreceptors is about 10–20/mm^2 in the region of the snout (see Results), which would presumably be the area of greatest electroreceptive sensitivity. Electroreceptor density has particular relevance to the electric images perceived by the fish, as electroreception is limited to close ranges, the electric image cannot be focussed, although it can be enhanced by behavioral means such as bending the tail around the object of interest (Heiligenberg, '73, '75). Thus the spatial resolution of the electric image is affected by both the electroreceptor density and secondarily by the degree of convergence of the primary afferents onto the second-order cells of the posterior lateral line lobe.

Estimates of the numbers of tuberous electroreceptor organs on each side of the body of *Apteronotus* range from 6,500 to 8,500 while an earlier count of the number of neurons in the PLLL (Maler, '79) yielded 7,700 pyramidal cells. Approximately half, or 3,800, of these pyramidal cells possess a basilar dendrite which receives primary afferent input (Maler, '79).

The medial segment of the PLLL is the smallest and we may thus estimate the number of basilar pyramids to be 800 in the medial segment and 1,000 in each of the other segments (centromedial, centrolateral, and lateral). Since each ganglion cell innervates one tuberous electroreceptor (Bennett, '67; Watson and Bastian, '79) and each tuberous ganglion cell reaches three segments (Heiligenberg and Dye, '81), there is a minimum convergence of about seven receptors onto one basilar pyramid. This agrees with the estimate (six to 15 receptors →basilar pyramid) made on physiological grounds (Bastian, '81a,b). The maximum spread of a tuberous primary afferent is 100 μm × 200 μm; since the basilar dendrites of basilar pyramids are 50 μm in diameter and nonoverlapping (Maler, '79), a tuberous primary afferent can diverge to contact a potential maximum of eight basilar pyramids. This implies that there is in fact much more convergence of tuberous afferents onto basilar pyramids; the precise amount of convergence depends on the amount of overlap in the terminal fields of neighboring tuberous receptor afferents. The spread and overlap of tuberous afferent terminals may vary with the body region represented; it would be natural to imagine smaller terminal fields and less overlap for afferents from the head than from the trunk.

The spread and overlap of tuberous afferents may be different in the centromedial, centrolateral, and lateral

TABLE 1. Comparison of the Primary Afferent Input and Somatotopic Organization in the Posterior Lateral Line
Lobes of the Mormyridae and the Gymnotiformes[1]

I. Mormyridae				
Structure	n. medialis (anterior nucleus)	Ventrolateral zone	Dorsolateral zone	Medial zone
Somatotopy	?	D—V	D—V	V—D
Input	Ordinary lateral line	Nucleus of PLLL Ampullary D—V Knollenorgan	Mormyromasts	Mormyromasts

II. Gymnotiformes					
Structure	n. medialis (anterior nucleus)	Medial segment	Centromedial segment	Centrolateral segment	Lateral segment
Somatotopy	?	D—V	V—D	D—V	V—D
Input	Ordinary lateral line	Ampullary	Tuberous P- and T-units	Tuberous P- and T-units	Tuberous P- and T-units

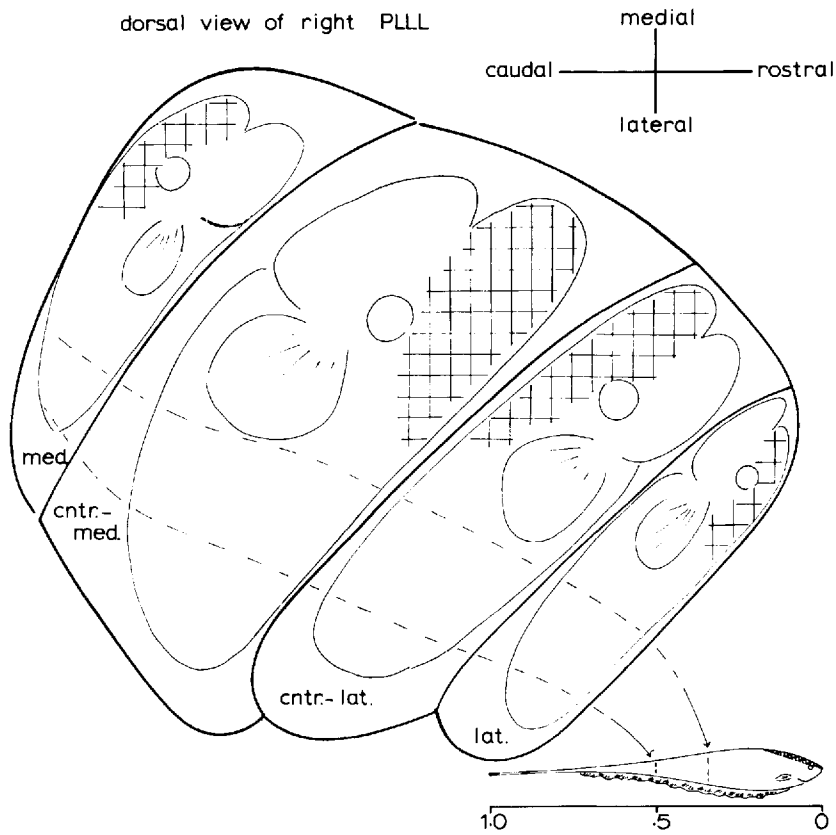[1]Bell and Russell '78, Heiligenberg and Dye, '81, '82.

Fig. 13. Summary diagram of a dorsal view of the right PLLL which shows the somatotopic organization of the electroreceptive projections in *Eigenmannia*. Data for this figure were obtained by intracellular recording from electroreceptive primary afferents in the ALLG, accompanied by receptive field localization on the body surface. The crosshatched area represents the portion of the head which was out of the water and thus could not be sampled. The pectoral fin is drawn in only as a landmark, and it carries no electroreceptors itself. In a 10-cm fish the rostrocaudal extent of the PLLL is approximately 1mm. This figure is used courtesy of W.F. Heiligenberg.

segments; this would determine the spatial resolution available in these three maps and might be the raison d'être for such a triplication of electrosensory input. The changes in the electric field produced by objects are now well understood physically (Heiligenberg, '75; Hoshimiya et al., '80) as is the response of tuberous electroreceptors to these changes (Bastian, '81a). Taken together with the results of this paper on distribution of receptors it is now possible to calculate the number of tuberous receptors (in)activated by an object and their degree of (in)activation. When we know the answer to the questions raised above we will be able to reconstruct the primary "image" created by an object in the three tuberous semgents of the PLLL.

PLLL pyramidal cells are responsive to objects moving at various velocities in the electric field: Of particular relevance to this issue is that the total number of electroreceptors on the body does not increase as the animal grows. This would have the effect of increasing the distance between the receptors as the skin grows and thus decreasing the apparent velocity of the object. Compensation may exist for these age-dependent changes in velocity determination. One intriguing possibility is that visual information may be used for calibration of the electrosensory system.

This apparent constancy of electroreceptor number with growth is in marked contrast to the visual and auditory systems of other anamniotes. Johns and Easter ('77) showed an increase in retinal cell number, particularly in the number of rods, with growth in the goldfish, while Corwin ('81) has demonstrated postembryonic hair cell production in the shark ear. In the goldfish eye and the shark ear the increase in receptor number can be presumed to lead to an increase in sensitivity; similar mechanisms may not apply in the electrosensory system.

Termination of electroreceptive afferents in the PLLL

The gymnotiform PLLL is not homologous to the PLLL of the Mormyriformes as both structures are thought to be derived independently from portions of nucleus medialis, the primary sensory nucleus of the ordinary lateral line (Bullock et al., '82; Bullock, '82). However, considerable parallels exist in the organization of the two structures. The gymnotiform PLLL is divided into four segments and the mormyriform PLLL can be subdivided into three cortical zones and a nucleus of the PLLL (Maler et al., '73; Maler, '73). Bell and Russell ('78) discovered a separate somatotopic map in each of the three cortical zones in the mormyrid, and the structural similarities between the two orders led them to suggest that three separate maps might also be found in the gymnotiform PLLL. At that time Heiligenberg and Dye ('81, '82) had not yet identified the central break which divided the central zone into a centromedial and a centrolateral segment. The original descriptions of the PLLL in *Gymnotus carapo* (Rethelyi and Szabo, '73) and *Apteronotus albifrons* (Maler et al., '74; but see Fig. 5, which points to central and lateral breaks) did not identify the central break as it is not as clearly defined by a discontinuity in the laminae as are the lateral and medial breaks. The central break is not clearly defined in high-frequency fish (*Apteronotus* and *Eigenmannia*), although it can be seen clearly in various pulse-type weakly electric fish (Carr, unpublished observations).

Despite the presence of an extra map, the similarity in PLLL organization between the two orders of weakly elec-

tric fish is remarkable, although some differences exist in (1) the somatotopic organization of the central segment of the PLLL, and (2) the segregation of the types of primary afferent. The primary afferent inputs and somatotopic organization of the PLLL's in the two orders are compared in Table 1. The somatotopy of the centrolateral and lateral segments is the same in both orders, while the somatotopy of the centromedial segment is inverted with respect to the mormyrid dorsolateral segment. The reasons for both the inversion and duplication of these electroreceptive maps are not clear: They may either be developmental or functional in nature.

The gymnotiform medial segment and the mormyrid ventrolateral segment are both presumed to be ampullary and are similarly organized in that both are situated adjacent to the midline ordinary lateral line nucleus. The dorsal body surface is mapped closest to the midline while the map of the ventral surface abuts the central segment in Gymnotiformes and the dorsolateral segment in mormyrids. Bell and Russell ('76) used physiological means to demonstrate ampullary input to this segment in mormyrids, while Heiligenberg and Dye ('81) reported in abstract form that intracellular injections of HRP into tuberous electroreceptor ganglion cells produced terminal fields in the centromedial, centrolateral, and lateral segments of the PLLL of Gymnotiformes, while ampullary ganglion cell fills labeled fibers only in the medial segment.

Maler ('79) and Maler et al. ('81) have described the termination of tuberous electroreceptor afferents in the PLLL at both light and electron microscopic levels. Each type of tuberous electroreceptor terminates in different laminae of the PLLL. Primary afferents form the deep fiber layer and terminate dorsally on the dendrites and cell bodies of the deep neuropil layer. Phase-sensitive T-units form electrotonic synapses on the spherical cells of the deep fiber layer, while P-units terminate on basal dendrites of granule cells and basilar pyramidal cells (Maler et al., '81). Thus in the Gymnotiformes, each type of tuberous electroreceptor has a separate termination site, but they are arranged so that each somatotopic map is superimposed.

This is not the case in mormyrids. Bell and Russell ('78) report that the mormyriform analogue of T-units, the Knollenorgan receptors, terminate exclusively in the nucleus of the PLLL which is an area medial to the ventrolateral zone and distinct from the three cortical zones. This nucleus is also somatotopically organized, although the somatotopy is not as precise as in the PLLL cortex (Bell and Russell, '78; Enger et al., '76a,b). Functionally, the phase coders of both orders are kept separate from the probability coders (P-units or mormyromasts). Gymnotiformes may require a more precise somatotopic organization of the phase-coding system and this may be the reason for the superimposition of the P- and T-unit systems in the PLLL. The mormyrid Knollenorgan system is postulated to be involved in electrocommunication (Bennett, '71; Moller and Bauer, '73) and Bell and Russell ('76) have suggested that precise somatotopic information may not be necessary in this case. This segregation of P- and T-unit information appears to be functionally important as it is reflected in the projection to the midbrain torus in both orders (Bell et al., '81; Carr et al., '81; Haugedé-Carré, '79).

Bell and Russell ('78) postulated that the mormyrid dorsolateral and medial segments might each receive a physiologically distinct type of mormyromast input. Since it appears as if this type of functional separation is not the case in the Gymnotiformes (Heiligenberg and Dye, '82),

this question will have to be specifically addressed in mormyrids.

This begs the question of why there might be three tuberous maps in the PLLL of the Gymnotiformes and why they are organized in mirror-image fashion. There are a number of possibilities, all pertaining to the notion of parallel processing of electrosensory input: (1) the processing within the three maps may be different, and/or (2) the descending inputs to each segment may be different.

Maler et al. ('81) have described the circuitry of the two central and the lateral segments of the PLLL at the electron microscopic level. One cell type, the neuron of the ventral molecular layer, is found predominantly in the lateral segment and centrolateral segment of *Apteronotus* (Maler et al., '74: Fig. 5), and may be involved in processing confined to these segments.

There are distinct descending inputs to each segment of the PLLL from different regions of nucleus praeeminentialis (Maler and Sas, in preparation). These connections may provide a substrate for separate feedback control of the electrosensory processing in each segment.

The three tuberous maps may also receive different scale somatotopic maps (see discussion above) as both the spherical and pyramidal cells of the lateral segment are larger than the cells of the two central segments (unpublished observations). Physiological studies to date have concentrated on the two central segments of the PLLL (Bastian, '81; Matsubara, '81 and in press), and no attempt has been made to differentiate the outputs of the triplicated tuberous electroreceptive maps; this is clearly one of the pressing problems in electrosensory research.

Another interesting problem raised by these results is developmental: How do fibers from the anterior lateral line nerve ganglion sort themselves out into four separate topographic maps, such that adjacent maps are always mirror images? Perhaps the PLLL can provide a critical test for developmental theories of topographic maps (e.g., the retinotectal map) which rely on chemical gradients to generate the correct mapping.

ACKNOWLEDGMENTS

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