

Interspecific Variation in the Projection of Primary Afferents Onto the Electrosensory Lateral Line Lobe of Weakly Electric Teleosts: Different Solutions to the Same Mapping Problem

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ABSTRACT

We demonstrate that preterminal axons composing the primary afferent projection onto the four somatotopically organized electrosensory lateral line lobe (ELL) segments in weakly electric gymnotiform teleosts course in fundamentally different directions in the most commonly studied species. Afferents enter the deep fiber layer (dff) of the ELL and course in variable, but species-specific, directions within a horizontal plane before turning dorsally to terminate within the deep neuropil layer of the ELL (dnl). Among the species considered here, apteronotids exhibit the tightest projection pattern. Afferents enter the rostral ELL from the anterior lateral line nerve ganglion (ALLNG) in a nonsomatotopic fashion. As they course horizontally, these fibers undergo a rostrocaudal somatotopic sorting along the ventrolateral border of the dff, then turn within a horizontal plane to course medially across the ELL segments. These medially coursing horizontal fibers are sorted: they form sublaminae according to the nerve branch containing their peripheral axon. Horizontal axons then turn dorsally, form fascicles, and terminate within the dnl. Within the dorsal fascicles, axons run directly into the dnl with little deviation, and their terminal fields exhibit no appreciable spread.

In sternopygids, dff horizontal fibers course in directions orthogonal to those in apteronotids. Fibers enter the rostral ELL and course *medially* across segments before turning *caudally* within segments. Unlike apteronotids, sternopygid horizontal fibers do not sort tightly by nerve branch. As horizontal axons turn dorsally they also form tight fascicles. But rather than terminating directly and without spreading, as in apteronotids, sternopygid fibers disperse from these fascicles and become sorted horizontally a second time prior to terminating in the dnl. Gymnotids show a third pattern: their primary afferents course into the rostral ELL without an obvious organization, they form no tight laminae of horizontal fibers and no fascicles of dorsal fibers. Unlike the other gymnotiforms examined, afferents coursing to the gymnotid MS can take one of two routes, ventrally through the dff in the manner of all other gymnotiforms, or, uniquely, dorsally through the plexiform layer of the ELL (pl), which is typically the location of ELL efferents. These afferents then turn *ventrally* to terminate.

Variations in axonal trajectories do not appear to reflect major functional differences in the processing of electrosensory information, but instead may reflect the phylogenetic relationships of the developmental processes involved in guiding axons. We propose a simple model for the development of these dif-

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ferent trajectories based on the assumption that among species similar guidance cues are expressed at different times as the projection develops.

Key words: sensory maps, somatotopic projections, fasciculation, axonal trajectories, *Gymnotiformes*

A key question in developmental neurobiology concerns the mechanisms underlying the formation of ordered connections (e.g., Easter et al., '85; and others). The most useful preparations for examining this problem are experimentally accessible systems where both the projecting neurons and their targets are highly ordered, an arrangement that facilitates the examination of axonal trajectories and their final connectivities (Cowan and Hunt, '85). With this in mind we have begun to study the pathways of primary electrosensory afferents onto the electrosensory lateral line lobe (ELL) of weakly electric gymnotiform teleosts (Lannoo et al., '89a,b).

In the periphery, electrosensory afferents run subepidermally and are easily accessed. The ipsilateral ELL—their target—consists of four segments (from medial to lateral termed medial segment of the ELL (MS), centromedial segment of the ELL (CMS), centrolateral segment of the ELL (CLS), and lateral segment of the ELL (LS), each forming a map that is somatotopically and functionally organized (Carr et al., '82; Heiligenberg and Dye, '82; Lannoo et al., '89a,b). In terms of somatotomy, within each map the rostrocaudal fish axis is represented rostrocaudally in the ELL, but the dorsoventral fish axis varies: the fish is mapped as if lying on one side or the other, with adjacent maps oriented oppositely. MS and CMS meet ventral to ventral, CMS and CLS meet dorsal to dorsal, and CLS and LS meet ventral to ventral, making adjacent somatotopic maps mirror images of each other (Heiligenberg and Dye, '82; Carr et al., '82). Maps can be grouped on the basis of the type of electrosensory information they receive. Afferents innervating ampullary electroreceptors terminate in the MS, afferents innervating tuberous electroreceptors trifurcate and send collaterals to terminate in each of the three lateral maps (CMS, CLS, and LS; Heiligenberg and Dye, '82).

Previously, we have investigated the trajectory of primary electrosensory afferents in adult *Apteronotus leptorhynchus*, first to compare with larvae in our developmental studies (Lannoo, et al., in press), and second to determine the extent of the effects of experimental perturbation (Lannoo and Maler, '88). In these afferents, receptor somatotomy is lost as fibers course from the electroreceptor organs, through the ganglion, and up to the ELL border (Lannoo et al., '89a,b). Upon entering the rostral ELL, fibers form the deep fiber layer of the ELL (df), and within the df become organized by segment and somatotopically within segment. As somatotomy is becoming reestablished within the df, horizontal fibers form sublaminae based on nerve branch: posterior division of the anterior lateral line nerve (pALLN) fibers that innervate the trunk occur most dorsally, followed progressively more ventrally by supraorbital branch of the anterior division of the anterior lateral line nerve (so), infraorbital branch of the anterior division of the anterior lateral line nerve (io), and mandibular branch of the anterior division of the anterior lateral line nerve (mn) fibers that innervate the head. Fibers from these horizontal laminae form fascicles, then turn dorsally within each segment

to terminate in the correct segment and in the somatotopically correct position. To generalize, the two main morphological features of the *Apteronotus* df are superficial horizontal fibers and dorsal vertical fibers (Fig. 1; Lannoo et al., '89a).

Here, we report on the interspecific differences in components of the trajectory of these primary electrosensory afferents. These differences fall out along taxonomic lines according to family; they do not correlate with known functional differences within the ELL. We view these variations as different solutions to a common problem—obtaining precise somatotopic projections—and discuss the relative roles of fiber lamination, fasciculation, and fiber sorting towards this end. The variation in components of the electroreceptive projection within this single teleost order appears to encompass most of the reported variation in the well-studied retinotectal projection across fish and amphibian classes.

MATERIALS AND METHODS

Five species of weakly electric gymnotiform teleosts were examined and are listed in Table 1. Fish were usually obtained from local suppliers. The *Apteronotus* brain sections that we observed were prepared as a part of previous studies (Lannoo et al., '89a,b). In addition we examined at least 12 individuals each of *Eigenmannia* and *Sternopygus*, and 3 *Gymnotus*. Both species of *Apteronotus* (see Table 1) showed identical primary afferent projection patterns and will be considered together.

To label primary electrosensory afferent nerves, two techniques were employed. Either single nerve branches were cut and 30% HRP (horseradish peroxidase; Sigma, St. Louis, MO) soaked gel foam was applied to the proximal end, or HRP was applied to one branch and cobalt chloride applied to a second branch according to the double-labelling technique of Ebbesson and Bazer ('87). Animals were allowed to survive 48 hours, then perfused through the heart with either 4% paraformaldehyde (HRP fills), or 3% glutaraldehyde (double label) according to Ebbesson and Bazer ('87). Brains were blocked and cut in the true transverse plane of the ELL (Carr et al., '82) at 30 μ m on a cryostat. HRP was visualized by using TMB (Mesulam, '78); cobalt was visualized by using the intensification technique of Ebbesson and Bazer ('87).

HRP alone usually resulted in a better resolution of single axons. The double-labelling technique was important in determining the relationships between populations of axons from different nerve branches.

RESULTS

The primary electrosensory afferents of *Apteronotus* show a tighter organization than those of *Sternopygus*, *Eigenmannia*, and *Gymnotus* and will be considered first.

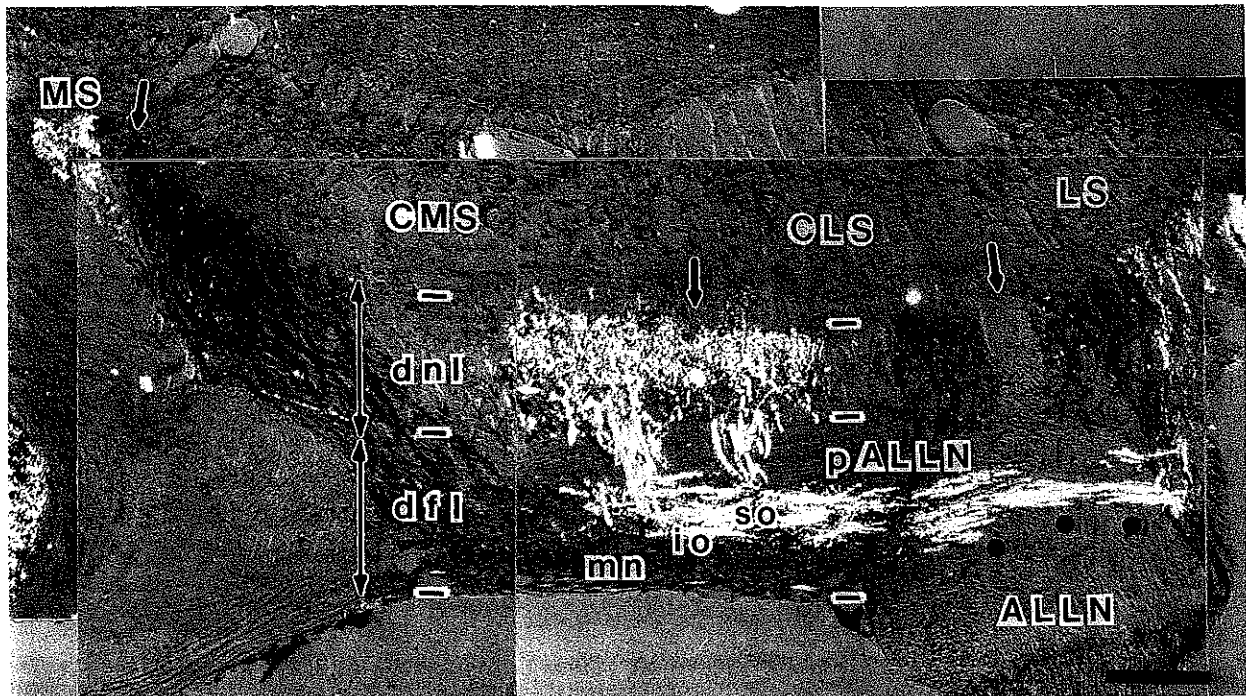


Fig. 1. Fiber pathways within the ELL of *Aptereronotus*. Dorsal is up, lateral is to the right. The so nerve branch is labelled with HRP and appears white because of birefringence, the mn branch is labelled with cobalt chloride and appears black; adjacent segments are mirror-image oriented. The anterior lateral line nerve (ALLN) enters the ELL from the bottom right; labelled fibers enter from a more rostral level (not shown) and course caudally along the ventrolateral border of the ELL

(in the area of the filled circles). After coursing caudally, fibers turn medially to run across segments (LS, CLS, CMS, MS; map boundaries located at ventrally pointed arrows). Fibers course medially within the dfI in sublaminae, sorted by nerve branch (mn, io, so, pALLN). At the somatotopically correct position fibers then form fascicles and turn dorsally, where they enter the dnl to terminate. Observe the tendency for fibers to change directions at right angles. Scale bar = 200 μ m.

TABLE 1. A List of Gymnotiform Species, by Family, Examined in the Present Study

Aptereronotidae
<i>Aptereronotus leptorhynchus</i>
<i>Aptereronotus albifrons</i>
Sternopygidae
<i>Sternopygus macrurus</i>
<i>Eigenmannia virescens</i>
Gymnotidae
<i>Gymnotus carapo</i>

Abbreviations

CLS, cls	centrolateral segment of the ELL
CMS, cms	centromedial segment of the ELL
dfI	deep fiber layer of the ELL
dnl	deep neuropil layer of the ELL
ELL, ell	electrosensory lateral line lobe
io	infraorbital branch of the anterior division of the anterior lateral line nerve
LS, ls	lateral segment of the ELL
MS, ms	medial segment of the ELL
mn	mandibular branch of the anterior division of the anterior lateral line nerve
pALLN	posterior division of the anterior lateral line nerve
pl	plexiform layer of the ELL
so	supraorbital branch of the anterior division of the anterior lateral line nerve

In *Aptereronotus*, horizontal fibers enter the ELL and course caudally along the ventrolateral border of the dfI. Axons run caudally until they reach the somatotopically correct rostro-caudal level (which varies slightly but is at about the same level in each of the four segments), then turn medially within the horizontal plane to course across segments (Fig. 1). Within each segment, at the correct mediolateral position, afferents turn dorsally at nearly right angles, form fascicles, and run into the dnl, where they terminate (Fig. 1). Individual fibers coursing dorsally meander slightly, and their terminal fields spread a small amount, less than the diameter of a fascicle, from the fascicular boundaries. However, these deviations are minor compared to the amplitude of sinusoidal extremes in the horizontally coursing fibers, and in the spread of terminal fields of other species (Fig. 2). Therefore, in *Aptereronotus*, once preterminal axons are within a dorsal fascicle they are committed to terminating within a restricted area of a specific map.

Sternopygid primary afferents enter the rostral ELL and course horizontally in directions orthogonal to those in apteronotids. As sternopygid primary afferents enter the ELL they first course *medially* across segments, then turn *caudally* within segments until they reach their correct somatotopic position (Fig. 3). This difference in fiber direction is obvious in transverse sections through the ELL. In *Aptereronotus*, true transverse sections of the ELL cut dfI horizontal fibers longitudinally and often reveal their full

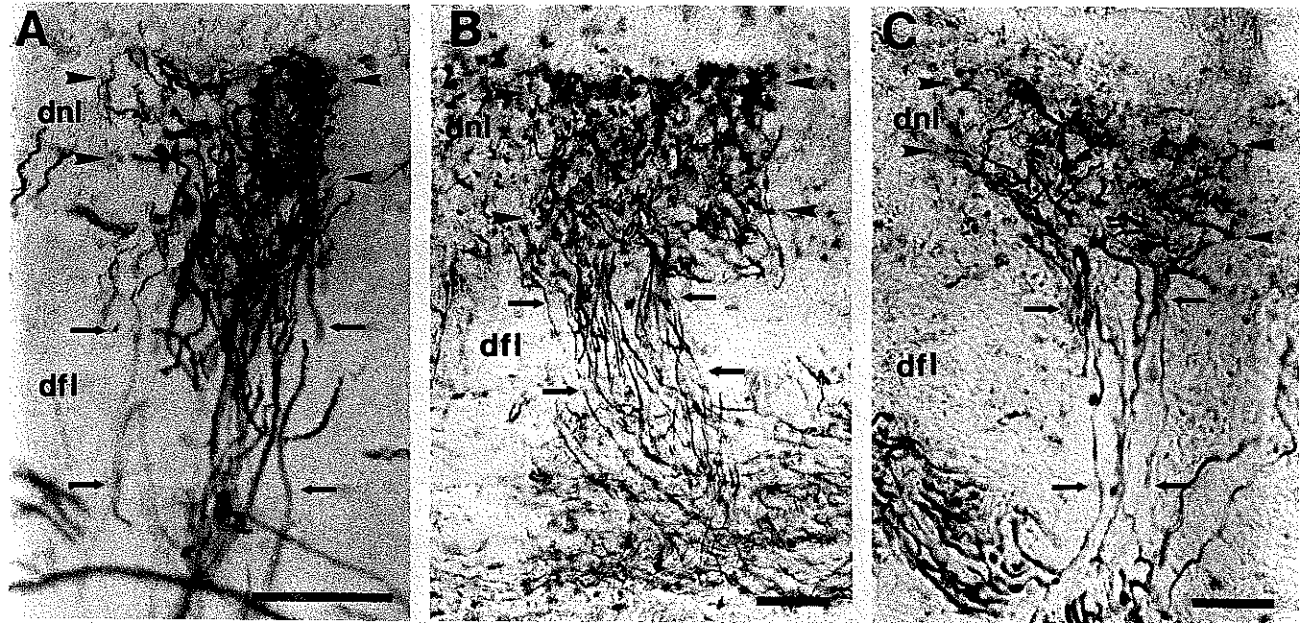


Fig. 2. The preterminal axon fascicles and terminal fields of primary electrosensory afferents in the CMS of A) *Apteronotus* (Apteronotidae), B) *Eigenmannia* (Sternopygidae), and C) *Sternopygus* (Sternopygidae) following an HRP fill of the io nerve branch, seen in same orientation as

Figure 1. Note that the sternopygid dfl terminal fields (arrowheads) spread laterally beyond the boundaries of their dfl fascicles (arrows) to a much greater extent than in the apteronotid. Scale bars = 25 μ m.

mediolateral course (Fig. 1), while in sternopygids horizontal fibers are cut in cross section, and gaps are visible between bundles (Fig. 3).

In sternopygids, preterminal fibers course dorsally in tight, evenly spaced fascicles (Figs. 2b,c, 3). Up to six fascicles project dorsally into the dnl for each nerve branch in each segment (Fig. 3b). But unlike apteronotids, as axons reach the dnl they are not committed to terminate according to the somatotopic order imposed by the fascicle, instead fibers disperse horizontally once more before terminating (Fig. 2b,c, Fig. 3), and terminal fields from axons originating in adjacent fascicles overlap (Fig. 3). This intermingling, which occurs over a distance of two to six fascicular diameters, produces a final somatotopic adjustment within the ELL, fibers shift their mediolateral position immediately prior to terminating. The result of this shifting may be a somatotopic fine tuning along the dorsoventral axis of each map (shown schematically in Fig. 4).

There is variation in the degree of overlap of dnl fibers that characterizes the two genera of sternopygids that we observed. Fiber overlap is greater in *Eigenmannia* (up to six fascicular diameters) than in *Sternopygus* (usually 2-3 fascicular diameters; Fig. 2b,c). In fact, *Eigenmannia* axons can course from almost one edge of the segment to the other prior to terminating (Fig. 2b), a distance not observed in *Sternopygus*, or in species within any of the other gymnotiform families. Within the sternopygids then, the genera *Eigenmannia* and *Sternopygus* can be distinguished solely on the basis of their primary afferent projection patterns.

Primary electrosensory afferents in the ELL of the gymnotid *Gymnotus* lack the linear orientation and right-angle directional shifts characteristic of apteronotids and sternopygids (shown schematically in Fig. 5). In the dfl, afferents

arising from one nerve branch become intermingled with fibers from the other branches and do not show the lamination apparent in apteronotids. Likewise, the horizontal fibers of *Gymnotus* are not oriented either mediolaterally, as in apteronotids, or rostrocaudally, as in sternopygids, but are obliquely oriented (not shown).

The most unusual feature of the *Gymnotus* ELL is that fibers coursing to the MS (presumably ampullary afferents, see Heiligenberg and Dye, '82) accomplish this in one of two ways, either 1) by running ventrally in the dfl then turning dorsally into the dnl, or 2) by running dorsally within the pl then turning ventrally into the dnl to terminate (Fig. 6). This latter pattern appears to be unique to this taxa, it has never been described in gymnotiforms and we have never seen it in other species. To detail this pathway, fibers that course through the pl to the MS run dorsally through the CMS (Fig. 3a) into the pl, where they turn medially, run within the pl to the MS, then turn ventrally into the dnl to terminate. What makes this trajectory unusual is that the pl typically contains ELL efferents, not afferents (Maler, '79; Carr et al., '82).

DISCUSSION

The projection patterns of primary electrosensory afferents onto the ELL vary along family lines within the order Gymnotiformes (shown schematically in Figs. 4, 5). We first address this variation by discussing the interspecific differences in fiber lamination, trajectories, and fasciculation. Secondly, we propose a model of axonal guidance mechanisms, based on parsimony, that accounts for these differences by suggesting that among species, axons follow the

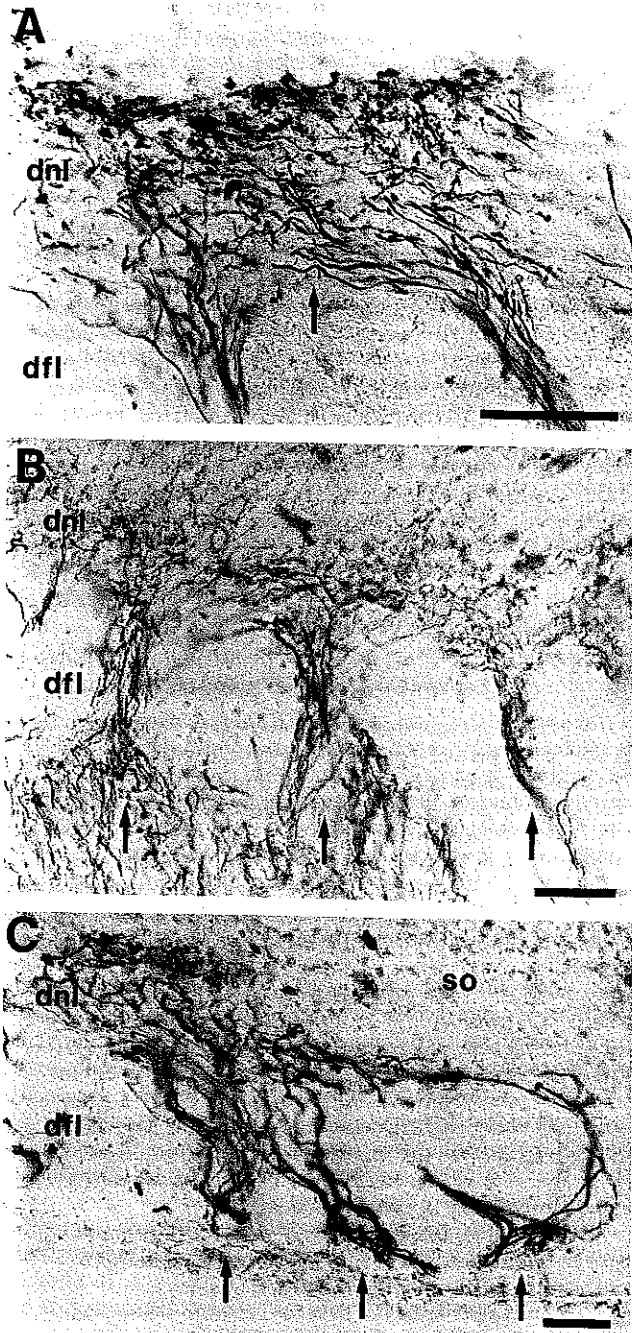


Fig. 3. The terminal fields and axon fascicles of the sternopygids, *Sternopygus* (A,B) and *Eigenmannia* (C) following an io nerve branch fill, further illustrating the features of these projections; orientation the same as Figure 1. A: Note the dorsal spread of axons in the dnl after they emerge from their df fascicles, and the overlap (arrow) between fibers from adjacent df fascicles. B: Observe the absence of mediolateral fibers in the ventral df (arrows, compare to Fig. 1); instead fibers run rostrocaudally. Axons then turn dorsally to form tight fascicles before dispersing again upon entering the dnl (seen more clearly in A). C: Again note the rostrocaudally running fibers within the ventral df (arrows). Observe that despite terminating close together, fibers take dramatically different pathways as they course dorsally; in particular the fiber on the right initially courses to the right before turning left, and runs across the so terminal field before terminating in the neuropil to the left. Scale bars = 25 μ m.

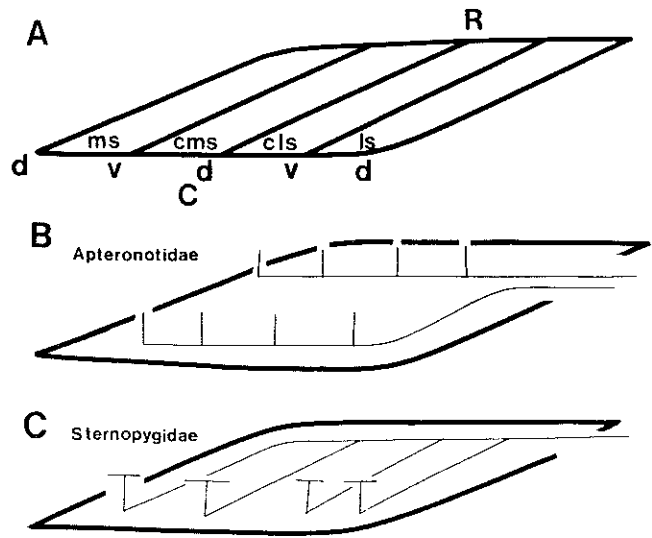


Fig. 4. Schematic diagrams illustrating the differences between the primary electrosensory afferent projection pathways of apteronotids and sternopygids. A: The ELL in oblique horizontal plane showing the four segments and their orientations to each other (R = rostral; C = caudal; d = dorsal; v = ventral; letters at the boundaries of adjacent segments hold for both segments). B: In apteronotids, fibers enter the ELL and course rostrocaudally before coursing medially across segments; axons course straight dorsally prior to terminating in each segment. C: In sternopygids, axons sort first by segment, then rostrocaudally within segments before coursing dorsally. In the dorsal dfl, fibers disperse mediolaterally (somatotopically dorsoventral) prior to terminating. The magnitude of this dorsal dispersion is greater in *Eigenmannia* than *Sternopygus* (see Fig. 3).

same guidance cues which are expressed at variable rates or times during development, or at different positions along the pathway. Then we compare the phylogenetic patterns of primary afferents to the functional and cytoarchitectural patterns of the ELL. Finally, we compare the variation in electrosensory axonal trajectories within this single teleost order to variation in the well studied retinotectal projection across three vertebrate classes.

Horizontal fiber lamination

Of the families examined here, apteronotid horizontal fibers are the most tightly laminated, laminae are defined by the nerve branch of the peripheral neurite (Fig. 1). Unlike apteronotids, fibers in sternopygids exhibit moderate lamination; gymnotid fibers do not appear laminated. Lannoo et al. ('89a) suggested that in apteronotids, lamination could aid in fiber sorting. As fibers enter the ELL they are not ordered, but prior to terminating become tightly somatotopically ordered and sorted by segment (this re-specification occurs over a distance of about 2 mm in adults). We felt that lamination could facilitate somatotopic ordering by sorting axons by nerve branch (Lannoo et al., '89a). Clearly, if this mechanism does hold for apteronotids, it cannot operate to the same degree for sternopygids and gymnotids—their fibers are not similarly laminated—and therefore cannot be generalizable within the gymnotiforms.

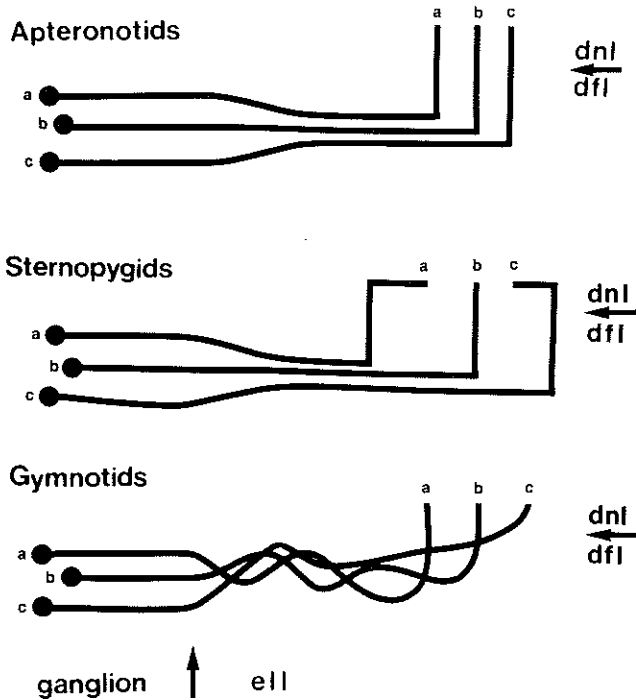


Fig. 5. Schematic diagrams illustrating the patterns of primary afferent fasciculation observed here. Apteronotids form fascicles as axons course dorsally prior to terminating. Sternopygids also form fascicles as they ascend to terminate, but in the dorsal dfl, axons undergo a further mediolateral shift prior to terminating. Note that axons in all three families terminate in the somatotopically correct position (indicated by the letters a, b, c in both the peripheral and central processes) independent of the pathways fibers take to reach the dnl.

Horizontal fiber direction

Horizontal fibers course in orthogonal directions in apteronotids and sternopygids. In apteronotids incoming afferents enter the ELL rostrally, course caudally, then course medially within the horizontal plane across segments. Apterontids, therefore, appear to sort fibers first on the basis of rostrocaudal somatotopic position (as they course from rostral to caudal) and secondly on the basis of segment (as they course medially). In contrast, sternopygid afferents enter the ELL and first course medially across segments prior to coursing caudally to the correct rostrocaudal position within segments. It appears that sternopygids sort electrosensory afferents first on the basis of segment (medially directed fibers) and secondly on the basis of rostrocaudal somatotopic position (as fibers course caudally).

Tosney and Landmesser ('85) have suggested that in the chick hindlimb, motor neurons experience "decision" regions that actively guide growth cones during axon outgrowth. Decision regions are separated by areas of "non-decision" regions, where axon trajectories are regulated by general pathway constraints. This concept may apply to ELL afferents as well. The presence of localized decision regions is suggested by the right-angle changes in axonal trajectories, both within the horizontal fibers and as these fibers turn dorsally prior to terminating.

Fiber fasciculation

In apteronotids and sternopygids, preterminal axons are arranged into fascicles as they leave the horizontal laminae of the dfl to course dorsally. These fascicles may form in the horizontal laminae, or perhaps at some point earlier in the pathway. In apteronotids, axons in fascicles terminate next to each other and must innervate neighboring electroreceptors if they are to achieve their tight somatotopic projection. Therefore, in apteronotids, axonal decisions necessary for somatotopy must be made by the time axons form fascicles; once axons enter dorsal fascicles they are committed.

In sternopygids, preterminal fibers from adjacent fascicles overlap in the dnl, suggesting that fibers within a fascicle do not necessarily innervate adjacent electroreceptors, and that decisions involving fine-tuned somatotopic terminations continue after fibers have dispersed from their fascicles. If fasciculation does play a role in sorting fibers in apteronotids (as suggested by Lannoo et al., '89a), it almost certainly cannot—at least to the same degree of somatotopic resolution—in sternopygids, and therefore cannot be generalized to gymnotiforms. The functional result of this final mediolateral "adjustment" of fibers prior to terminating in the ELL is that fibers shift their location in the somatotopic dorsoventral plane of the animal.

Axonal guidance model

To explain the interspecific differences we observe in the trajectories of primary electrosensory afferents in the ELL, we propose a model of axonal guidance based on varying three parameters during development. We suggest that as the ELL projection forms there is 1) a global rostrocaudal somatotopic gradient; 2) a mediolateral segment specification; and 3) an intrasegmental mediolateral somatotopic gradient. Perhaps these gradients are chemical, as has been proposed for the retinotectal system (Schmidt, '85; Easter, et al., '85).

In apteronotids we propose that the global rostrocaudal gradient is expressed first, followed by the mediolateral segment specification, followed by the fine-tuned mediolateral gradient. Fibers enter the ELL, course caudally following the rostrocaudal gradient, then course medially across segments until the correct segment is specified. Within this segment, fibers follow the mediolateral gradient, and when their position is appropriate turn dorsally to terminate in the somatotopically appropriate position.

In this scenario, fibers in sternopygids follow the mediolateral segment first, then the global rostrocaudal gradient, then the intrasegmental mediolateral gradient. In addition to switching the order of the first two cues, sternopygids differ from apteronotids in the positioning of the presumptive interspecific mediolateral gradient. In apteronotids this presumptive gradient appears prior to the formation of dorsal fascicles, so that once fibers are fasciculated, their somatotopic position has been specified. In sternopygids the gradient is located more dorsally, at the base of the dnl, and therefore accounts for the preterminal mediolateral spread of axons that we observe in this lamina.

Gymnotid primary electrosensory afferents do not appear to form laminae, do not form distinct fascicles, and do not change directions at right angles. We propose that rather than following separate gradients one at a time, that incoming fibers follow the rostrocaudal and segmental gradients simultaneously, producing an oblique, perhaps diffuse,

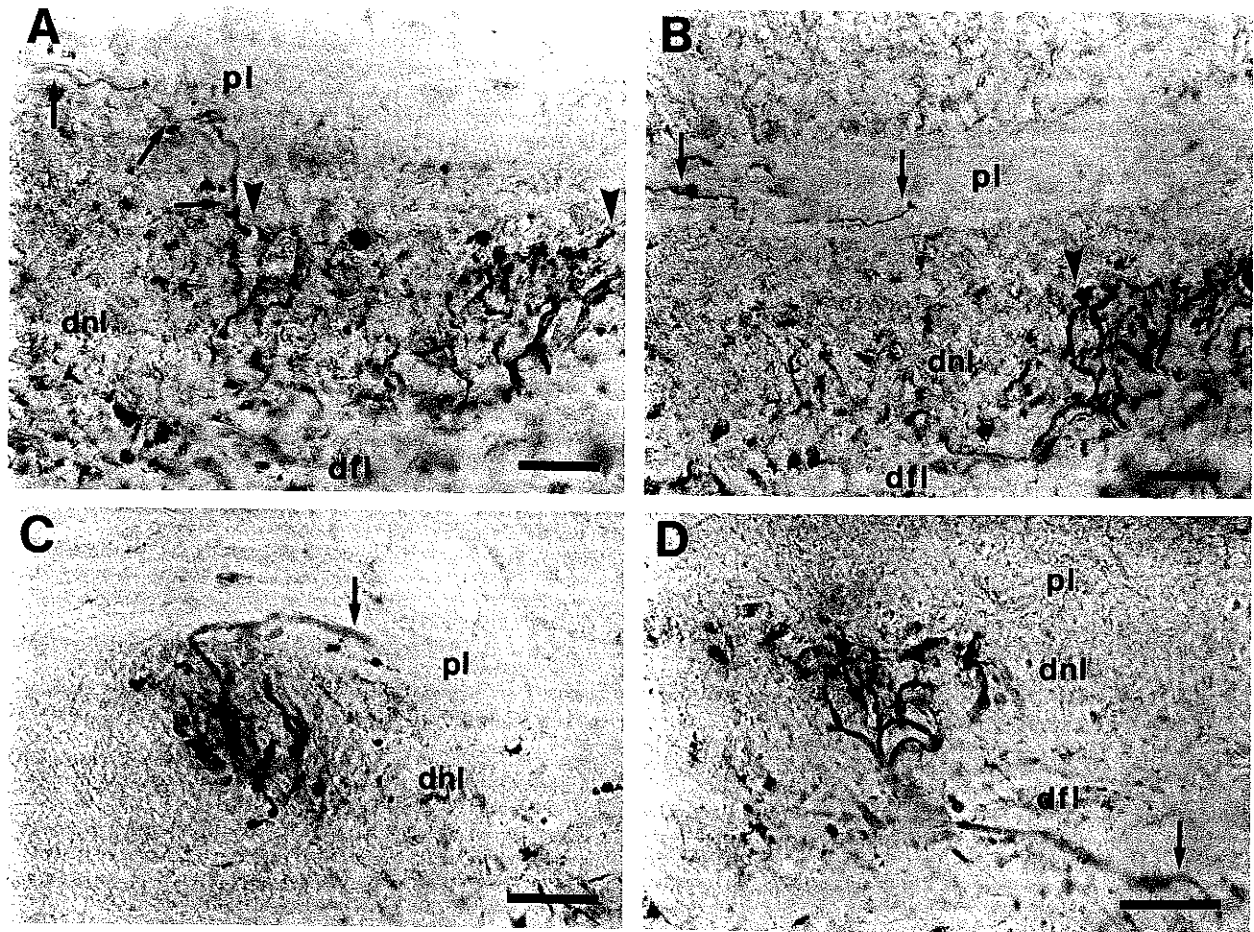


Fig. 6. Axon trajectories and terminal fields of fibers coursing to the MS, following an io nerve branch fill, in *Gymnotus*, visualized in the same plane as Figure 1. A: Axons (arrows) course up to the pl adjacent to the labelled CMS terminal field (located between arrowheads). B: Axons (arrows) farther medially in the pl (CMS to the right of the arrowhead).

C: Axon (arrow) approaching the MS dorsally in the pl and turning ventrally into the dnl to terminate. D: A typical gymnotiform MS projection, also seen here in *Gymnotus*, where the axon (arrow) approaches the dnl ventrally from the dfl. Scale bars = 25 μm.

pathway, rather than one ordered along a given series of directions. The fact that fibers coursing to the MS can get there by taking an extremely aberrant dorsal pathway (Fig. 6) suggests that general, rather than specific cues are guiding axons.

Phylogenetic considerations

Among these three gymnotiform families, patterns of primary afferents are more similar among species within families than they are among families—in the present paper we are able to generalize along family lines. This is true despite the fact that the ELL of *Eigenmannia* is morphologically and functionally more similar to that of *Apteronotus* than to *Sternopygus*. *Eigenmannia* and *Apteronotus*—but not *Sternopygus*—have a lamina of spherical cells that make gap junction contacts with primary afferents and mediate a rapid time coding component of electroreception (Matsubara, '82). Primary afferent trajectories, therefore, correlate best with phylogenetic factors rather than functional and cytoarchitectural features of the ELL. In fact, species can be

accurately identified to genus on the basis of their ELL afferent trajectories alone.

Retinotectal comparison

The variation in axonal trajectories, lamination, and fasciculation exhibited among gymnotiforms, a single teleost order, is similar to the variation observed in the well-studied retinotectal system across at least three vertebrate classes (Chondrichthyes, Amphibia, Teleostei). For example, from the retina to the tectum fibers may or may not maintain their initial order, and fasciculate to varying degrees depending on the taxon being considered (e.g., Constantine-Paton, et al., '83; Taylor, '87; Roussoff and Easter, '80; Easter et al., '81, '85; Bunt, '82; Bunt and Horder, '83; Springer and Mednick, '86). But while various patterns of fasciculation may be a prominent feature of the retinotectal system, precise fasciculation of retinal afferents is not necessary for the establishment of a topographic retinotectal mapping (Stuermer, '88; and references therein). In this regard, our data on gym-

notiform electrosensory mapping is in accord with that from the visual system.

In general, to discover the mechanisms underlying large morphological variations, it is theoretically better to minimize the phylogenetic distance, and therefore confounding factors, between species being compared. In this sense, the large variation in axonal trajectories within this single order of electrosensory teleosts may prove to be ideal for elucidating fundamental rules underlying neuronal guidance and the formation of ordered connections.

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