

A New Electroreceptive Teleost: *Xenomystus nigri* (Osteoglossiformes: Notopteridae)

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Summary. The African knife fish, *Xenomystus nigri*, is found to be sensitive to weak electric fields by the method of averaged evoked potentials from the brain. Slow waves and spikes were recorded in or near the lateral line area of the medulla and the torus semicircularis of the mesencephalon in response to long pulses (best >50 ms) and low frequency sine waves (best ca. 10 Hz) of voltage gradients down to <10 μ V/cm. Evoked waves in the lateral line area are a sequence of negative and positive deflections beginning with a first peak at ca. 24 ms; in the torus semicircularis the first peak is at ca. 37 ms. Spikes are most likely in the torus between 50 and 80 ms after ON. At each recording locus there is a best axis of the homogeneous electric field and a better polarity. Effects of stimulus intensity, duration and repetition are described. The physiological properties are similar to those of ampullary receptor systems in mormyriiforms, gymnotiforms and siluriforms.

Confirming Braford (1982), *Xenomystus* has a large medullary nucleus resembling the nucleus otherwise peculiar to mormyriiforms, gymnotiforms and siluriforms and now called the electrosensory lateral line lobe (ELLL; formerly the posterior lateral line lobe). We describe the projections of anterior and posterior lateral line nerves by HRP applied to the proximal stump of a cut nerve. A descending central ramus of the anterior lateral line nerve and a lateral component of the ascending ramus of the posterior lateral line nerve end in part in the ELLL.

Electroreception, including the system of discrete central structures mediating it, is for the first time found to be less than an ordinal or even a family character, but apparently a characteristic

of the subfamily Xenomystinae. Species of the other subfamily, Notopterinae as well as of the other families of osteoglossiforms (Osteoglossidae, Hiodontidae and Pantodontidae), lack the ELLL. *Notopterus* and *Pantodon* are found to lack the evoked potential.

The positive finding of evoked activity to feeble electric field is found to be the most practical method for searching widely among fishes for the presence of the electrosense modality and its central pathways. The anatomical criterion of an ELLL can now be taken to be a good criterion for the presence of this sensory system. The absence of evoked response correlates well with the absence of an ELLL.

Introduction

Behavioral evidence has long indicated that three orders of teleost fishes are electroreceptive: Siluriformes, Gymnotiformes and Mormyriiformes (Bennett 1965, 1967, 1970; Kalmijn 1974; Scheich and Bullock 1974; Bullock 1982). The evidence has further suggested that this sensory modality is an ordinal characteristic, i.e. that all members of these orders are electroreceptive and that no other teleosts are. This conclusion derives from intensive study of only a few species, however, and data clearly establishing non-electroreception are particularly rare. Until the advent of a new technique (Bullock et al. 1982), studies of electroreception proceeded in much the same way as studies of echolocation; without good reason to suspect the presence of electroreception, it was assumed to be lacking. The criteria for electroreception, the definition of this sense, and the curious scarcity of intermediate species are discussed by Bullock et al. (1982).

Abbreviations: ELLL electrosensory lateral line lobe; HRP horseradish peroxidase; TS torus semicircularis

A few taxa have now been examined by electrophysiological techniques and found to lack any sign of specialized reception of weak electric fields. Among these is *Notopterus*, chosen because of its superficial resemblance in tapering body form and long undulating anal fin to the gymnotiforms.

Physiological re-examination of the family Notopteridae was suggested to us by M.R. Bradford, who noted (1982) that a nucleus of the lateral line area appears to be anatomically specialized in this family, in a way reminiscent of siluriforms and gymnotiforms. One of us (RGN) saw the same thing in a notopterid whereas no such specialization was found in representatives of several other families of Osteoglossiformes (nomenclature following Nelson 1976). Physiological re-examination of *Notopterus* showed no evidence of electroreception; however another genus of the same family, *Xenomystus* was found to be sensitive to extremely weak electric fields and to be the basis of the anatomical findings of a specialized lateral line area. The present paper reports these results.

Materials and Methods

The electrophysiological results are based on studies of eleven specimens of *Xenomystus nigri*, an African knife fish, three specimens each of *Notopterus chitala* and *N. notopterus*, Asiatic knife fishes and three of *Pantodon* sp., the African butterfly fish. Specimens ranged from 11–20 cm in length. The anatomical data are based on transverse serial sections, stained with cresyl violet, from one or more individuals of *X. nigri*, *N. chitala*, *N. notopterus*, *Osteoglossum bicirrhosum*, *Pantodon buchholzi*, and *Hiodon tergisus*.

For recording evoked potentials, the fish were first anesthetized either with MS 222 (tricaine methane sulfonate, 1:7,000) or by cooling in ice water. The dorsal surface of the midbrain, cerebellum and anterior medulla was exposed for a length of 7.5 mm. Flaxedil was injected intramuscularly (0.06–0.1 ml of a 2 mg/ml solution), the temperature brought back to 22 °C, and the fish mounted in a large bath with a tube in its mouth carrying a respiratory stream of water. The water conductivity was held at 3–5 kohm-cm. Semimicroelectrodes of tungsten or glass micropipettes were used; the reference electrode was in the saline pool over the brain, the roving electrode typically explored a dozen or more loci – chiefly in the midbrain – from the tectal surface to a depth of 3.5 mm. Amplifier filters passed 3–3,000 Hz. 16–64 responses were summed by a Nicolet 1170 signal processor. Homogeneous fields, created by long carbon rods at the ends or sides of the bath, constituted the electric stimuli; high series resistances assured constant current, and an isolation unit kept the stimulus far from ground. Other stimuli are described below. Selected electrode sites were marked by electrolytic lesion.

The anatomical material was prepared as follows. Six false featherfins (*X. nigri*) were anesthetized by immersion in 0.1% methane sulfonate solution and an anterior or posterior lateral line nerve exposed and transected. A small pledget of Gelfoam saturated with 20–40% HRP was applied to the proximal stump of the cut nerve and the incision was closed. The fish were allowed to survive 4–30 days postoperatively at 25–27 °C before being reanesthetized and perfused with cold 0.1 mol/l

phosphate buffer followed by 2% glutaraldehyde in 0.1 mol/l phosphate buffer. The brains were removed, washed in 10% sucrose phosphate buffer, and embedded in gelatin blocks. The gelatin blocks were fixed for an additional four hours in 2% glutaraldehyde, sectioned at 35 µm, and processed by the tetramethylbenzidine protocol (Mesulam 1979) to visualize the HRP. Brain sections were mounted and counterstained with 1% neutral red to identify cell groups.

Results

A. Physiology

1. Xenomystus

Midbrain. Evoked potentials to weak electric fields were found, essentially without searching in every specimen of this genus except three which appeared to be injured in preparation because their light flash evoked potentials in the tectum were small and failed prematurely. In nearly all cases, the first penetration revealed responses to weak electric fields, not at the surface or at loci in the first half millimeter traversing the tectum, but strongly at 1.0–1.5 mm of depth. This subtectal area of response lies under somewhat more than the posterolateral quadrant of the optic tectum. From its depth and position we believe the responsive area lies in the torus semicircularis (TS), but have not verified the midbrain recording loci.

As shown in Fig. 1A, a feeble electric pulse (20 µV/cm) evokes a series of deflections in the torus semicircularis (TS) beginning with a small N25 (negativity of the rove at 25 ms after the ON) and continuing with a larger P37 and N57, smaller P75 and N95. In this experiment the stimulus pulse was 110 ms long; thus it was not clear whether the P45, N70, P85 sequence following the OFF was influenced in some degree by still later components of the ON response. From other evidence we know there is little to be seen later than 100 ms. The recording site of Fig. 1A was at the depth of maximum response, 2.5 mm below the tectal surface within the TS. At the locus of Fig. 1A the response is somewhat different according to stimulus polarity, slightly favoring the ipsilateral positive transverse current. Besides polarity there is also a preferred axis of orientation; longitudinal current at this locus was slightly less effective. Some preference for orientation and polarity was found at all loci; it is particularly pronounced in Fig. 1B. There was no reversal of sign of the evoked waves at any depth, for electric field stimuli. However there was a reversal at 2.25 mm for acoustic stimuli (very faint clicks from a loud speaker in the air above the bath) which evoked a different

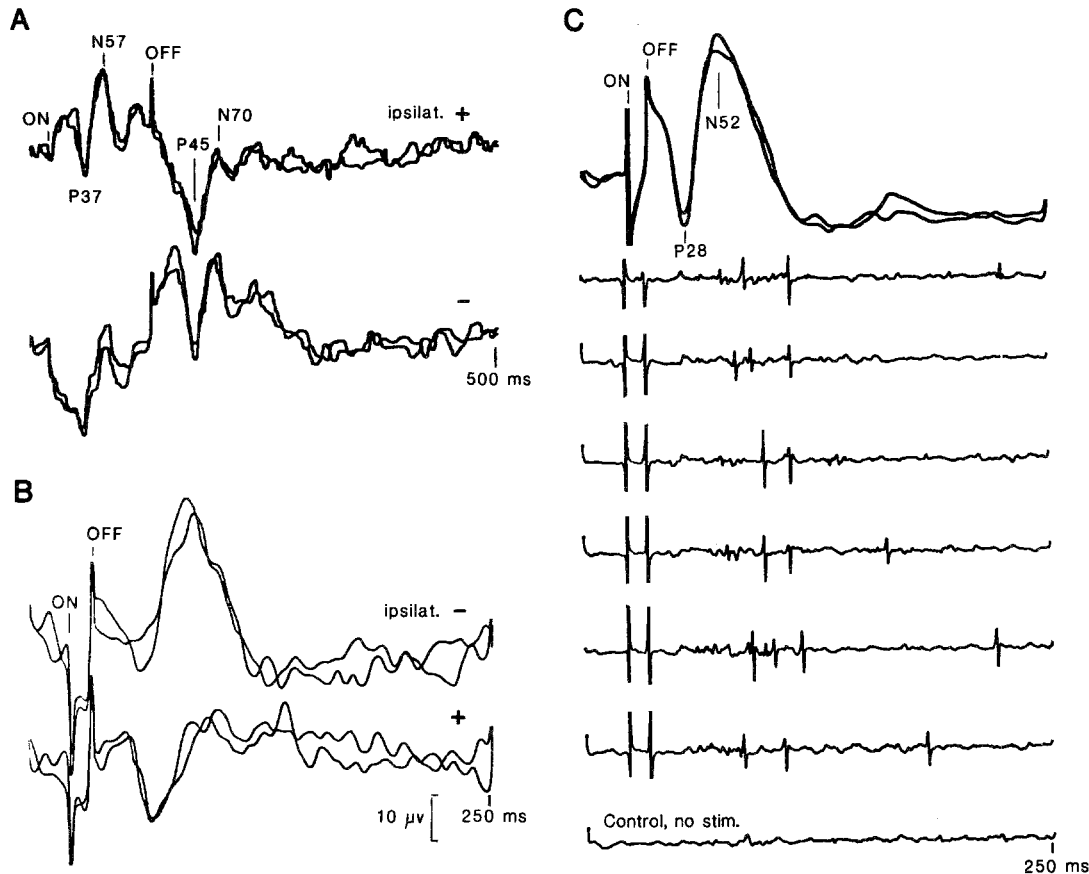


Fig. 1A–C. Responses of *Xenomystus* to homogeneous electric fields, recording in or near the torus semicircularis. **A** Long pulse, transverse field stimulation (110 ms) at 20 $\mu\text{V}/\text{cm}$, 2/s, summing 128 responses, in each of the two polarities. Amplifier filters 3–3,000 Hz. Nomenclature of waves: N=negativity of the brain at the stated number of ms (upwards deflection); P=positivity. Smaller peaks and valleys are not labelled. The polarity makes only a small difference at this locus. **B** Another fish and locus where polarity has a strong effect with transverse stimulation; short pulse (12 ms) at 50 $\mu\text{V}/\text{cm}$, 1/s, summing 64 responses. The large negative (upwards) wave with the ipsilateral negative stimulus is close to the same latency as N57 in **A**. Calib. applies only to **B**. **C** Same as the preceding but longitudinal, 500 $\mu\text{V}/\text{cm}$; ON and OFF artifacts are labelled. Top pair of traces filtered at 3–3,000 Hz are averages of 64 sweeps; next 6 traces taken after a small advance of the electrode were filtered for spikes (300–3,000 Hz) and are single sweeps. Last trace is a control, without stimulation; a series of such sweeps shows that there is no spontaneous firing of these few units. Note that the spikes tend to occur during the falling phase of the large negative slow wave. This locus is much more sensitive to transverse fields

pattern of deflections (first peak at 5–8 ms) with a maximum at 3 mm depth. In other experiments the depth of maximum electric evoked potential was 1.5 mm, still without reversal, and the click reversal point was also 1.5 mm.

The electric evoked potential is attenuated but usually only slightly delayed by decreasing the stimulus intensity, especially in the range from 100 to 10 $\mu\text{V}/\text{cm}$. In a higher intensity range there is more influence of voltage upon latency. The attenuation of amplitude can be approximately proportional to the stimulus over a 20 dB or greater range but is nonlinear near threshold and near saturation – which are >40 dB apart (<10 $\mu\text{V}/\text{cm}$ and >1.2 mV/cm). Sensitivity is lower for pulses

<20 ms in duration, and it is difficult to get a response with pulses of <2.5 ms, if we limit the voltage to a few mV/cm.

Figure 1C, representing a different specimen and locus of recording, shows a few unit spikes that fire between 50 and 80 ms after ON of a shorter stimulus pulse (12 ms), during the falling phase of a large evoked wave that peaks at N52. These units have no spontaneous discharge.

Repetition of brief (10 ms) stimulus pulses generally leads to depression of evoked potentials, seen as early as the second response if the interval is only 100 ms, but also seen in a cumulative average even at 500 ms. However, at a stimulus interval of 150 ms facilitation can be seen in certain loci,

affecting especially the first positive and second negative waves.

To stimulation by a single sine wave the response is best at ca. 10 Hz. It is an N-P-N sequence of peaks about 10–15 ms apart during one half of the sine wave, depending on the polarity selectivity of the particular recording locus.

Medulla. We did not usually look for electric evoked potentials in the medulla, after noting that the responsive area is easier to find in the midbrain. However, in three specimens of *Xenomystus* we exposed the lateral aspect of the rostral medulla from the side and placed a microelectrode in the electro-sensory lateral line lobe (equivalent to posterior lateral line lobe of some authors). At horizontal depths of 0.4–0.8 mm multiunit hash was heard following weak electric pulses (25 μ V/cm, 10 ms duration); an evoked wave was maximal at 0.8 mm and still visible at 2.5 mm. The best position for spikes was lesioned and histologically found to be within the boundaries of the ELLL (Fig. 2).

2. *Notopterus*

No evoked potential was found in any specimen of this genus, in any electrode track. Up to 12 electrode tracks were examined in each fish, at depths to at least 3.5 mm, in steps varying from 0.1 to 0.3 mm. The most likely areas of the mid-brain and medulla were searched. Stimulus intensities up to 6 mV/cm were used, in various orientations, pulse durations and repetition rates, especially those most suitable for *Xenomystus*. Good responses to light flash, to acoustic clicks and tone bursts, and to local water movement, each in appropriate loci, indicated that the preparations were in good condition.

3. *Pantodon*

The same result as in *Notopterus* was seen in the three specimens tested.

B. Anatomy

1. Organization and Variation of the Osteoglossiform Lateralis Column in the Medulla

Many osteoglossiform fishes possess a lateral column comparable to that in other nonelectroreceptive teleosts in that the column consists of a large, anteriorly situated medial octavolateralis nucleus capped by a cerebellar crest and a smaller, more posteriorly located caudal octavolateralis nucleus

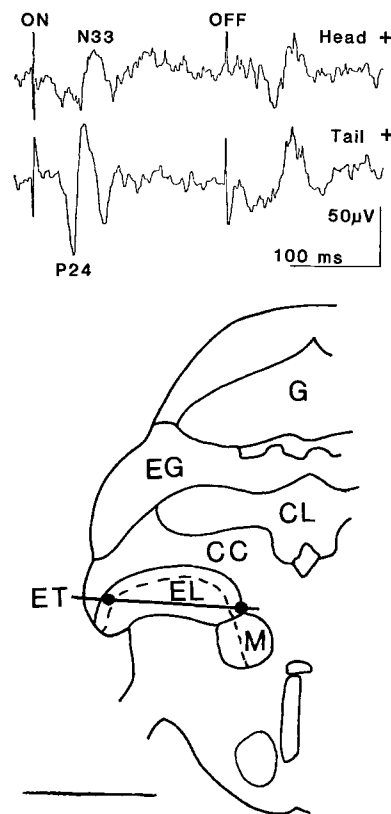


Fig. 2. Responses in the electro-sensory lateral line lobe of *Xenomystus*. Above, averaged evoked potentials to electric field stimuli (200 ms, 25 μ V/cm, 2/s) in the longitudinal axis, in each of the two polarities, as shown; each trace = 64 sweeps. Some of the evoked peaks are labelled with the sign of the potential in the medulla relative to a remote reference, and the latency from the recent ON or OFF. Below, a transverse section of the medulla of the same fish, showing the electrode track (ET) and loci of lesions (dots). The record above, at the depth of maximum amplitude was taken about half way between the dots. CC, cerebellar crest; CL, caudal lobe of cerebellum; EL, electro-sensory lateral line lobe; ET, electrode track; G, granular layer of cerebellar corpus; M, medial octavolateralis nucleus. Bar scale equals 1 mm

(Figs. 3, 4) (Bass 1982). In all osteoglossiforms that we have examined the cerebellar crest and medial octavolateralis nucleus fuse medially across the midline (except in *Hiodon*) and the medial nucleus is divided into a pars lateralis and pars medialis along much of its rostrocaudal length (Pearson 1936). These divisions of the medial nucleus are easily recognized, based on differences in cell size and density. However, the two divisions of the medial nucleus are similar in that the bulk of the cells in each division is located dorsally, overlying a dense neuropil that contains a few scattered cells (Fig. 3 B–C).

The lateral column of *Xenomystus* (Figs. 3 A, 4) and apparently *Papyrocranus* (M.

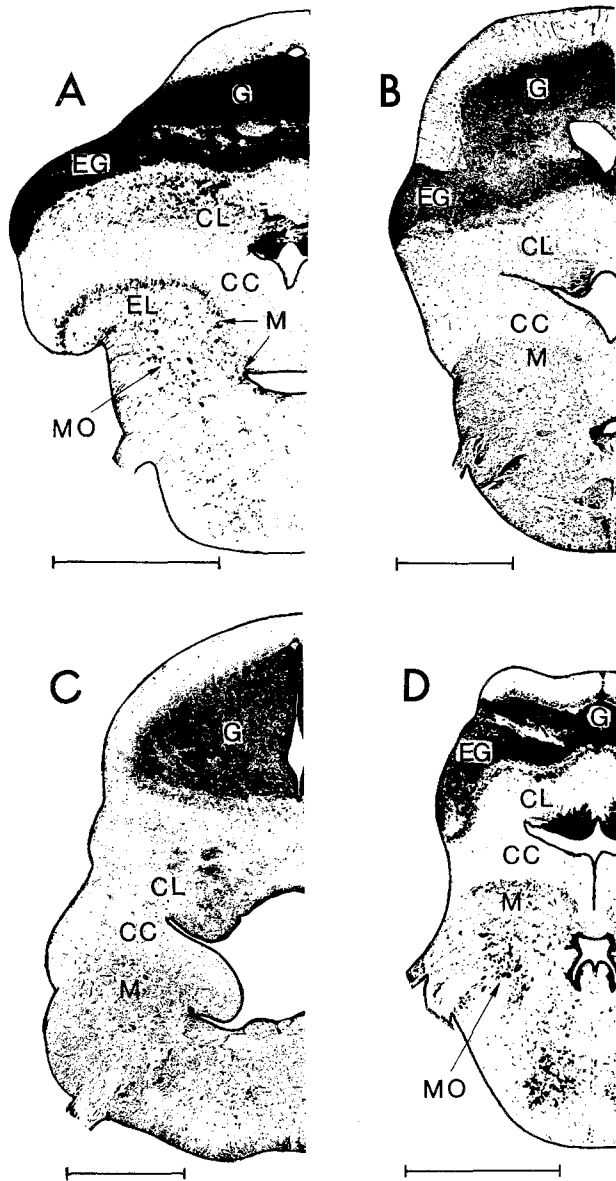


Fig. 3A–D. Photomicrographs of transverse sections through comparative levels of the medulla of a number of osteoglossiform fishes illustrating organization of the lateral line areas. **A** *Xenomystus nigri*; **B** *Notopterus notopterus*; **C** *Hiodon tergisus*; **D** *Osteoglossum bicirrhosum*. CC, cerebellar crest; CL, caudal lobe of cerebellum; EG, eminentia granularis; EL, electrosensory lateral line lobe; G, granular layer of cerebellar corpus; M, medial octavolateral nucleus; MO, magnocellular octaval nucleus. Bar scales equal 1 mm

Braford 1982 and personal communication) is characterized by the same nuclei as other nonelectroreceptive osteoglossiforms but also possesses an additional highly organized cell and neuropil mass corresponding to the electrosensory lateral line lobe (ELLL; Figs. 3A, 4) of gymnotiforms, mormyriiforms and siluriforms. This lobe has been

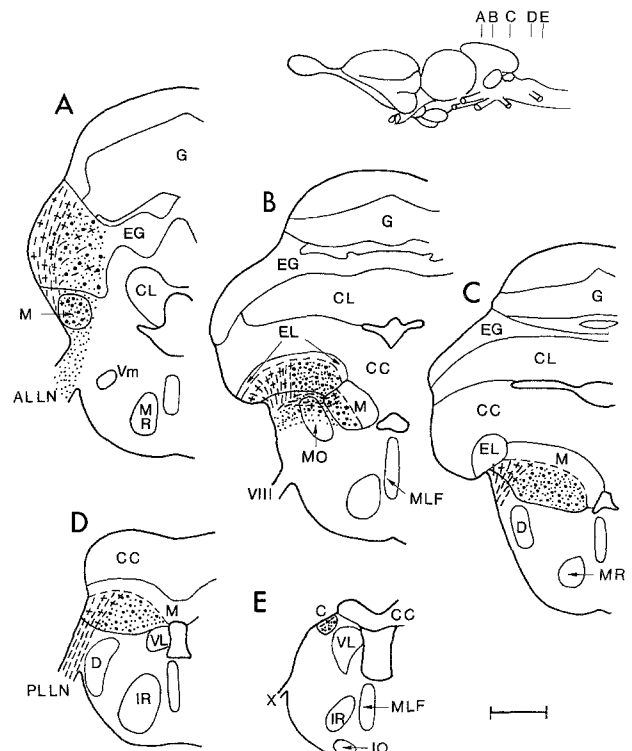


Fig. 4A–E. Chartings of the primary projections of the anterior (stipling) and the posterior (dashes) lateral line nerves of *Xenomystus* as revealed by application of HRP to the transected nerves. Terminal fields of the anterior and posterior lateral line nerves are indicated by crosses and larger dots respectively. The dashed lines within the boundaries of the ELLL and medial nucleus denote the ventral edge of the cellular plates of these nuclei. ALLN, anterior lateral line nerve; C, caudal octavolateral nucleus; CC, cerebellar crest; CL, caudal lobe; D, descending octaval nucleus; EG, eminentia granularis; ELLL, electrosensory lateral line lobe; G, granular layer of cerebellar corpus; IO, inferior olive; IR, inferior reticular formation; M, medial octavolateral nucleus; MLF, medial longitudinal fasciculus; MO, magnocellular octaval nucleus; MR, medial reticular formation; PLLN, posterior lateral line nerve; VL, vagal lobe; Vm, trigeminal motor nucleus; VIII, octaval nerve; X, vagal nerve. Bar scale equals 0.5 mm

called the posterior lateral line lobe by some authors (Maler et al. 1973; Bell 1981; Carr et al. 1982) and the lateral line lobe by others (McCormick 1981; Braford 1982; Bass 1982; Bass and Hopkins 1982). At a recent conference of most of the current workers the new name (ELLL) was recommended. This lobe occupies the rostral one third of the lateralis column (Figs. 3A, 4) and like the medial octavolateralis nucleus is capped by a cerebellar crest; the lobe consists dorsally of cells and ventrally of neuropil. However, the ELLL is easily distinguished from the medial nucleus as its cells are larger, on the average, and tightly packed into a cellular plate some two to three cells thick

and the neuropil of the ELLL contains fewer cells than that of the medial nucleus (Fig. 3).

We examined Nissl stained sections of species of each of the other osteoglossiform families: *Osteoglossum bicirrhosum* (Osteoglossidae), *Hiodon tergisus* (Hiodontidae) and *Pantodon buchholzi* (Pantodontidae) (Fig. 3). All resemble *Notopterus* in respect to the absence of an ELLL. Bass (1982) shows sections of the medulla of these genera and of *Xenomystus*, and others, as examples of nonelectroreceptive fishes, without commenting on specialization in this nucleus.

2. Primary Projections of the Lateral Line Nerves in *Xenomystus*

The anterior lateral line nerve of *Xenomystus* divides into ascending and descending rami as it enters the medulla (Fig. 4A). The ascending ramus terminates in the medial two thirds of the medial octavolateralis nucleus rostrally as well as in a more medial segment of the eminentia granularis. Although the main target of the entering anterior lateral line nerve fibers is the more medial eminentia granularis there does appear to be some overlap with the termination of posterior lateral line nerve fibers (Fig. 4A).

The descending ramus of the anterior lateral line nerve courses caudally where it terminates in the medial half of the neuropil of the ELLL and in the medial two thirds of the neuropil of the medial octavolateralis nucleus (Fig. 4B–D). At this same level, fibers of the anterior lateral line nerve also appear to terminate upon the dendrites and cell bodies of the magnocellular octaval nucleus (Fig. 4B). Finally, the caudalmost coursing fibers of the descending ramus terminate in the medial half of the caudal octavolateralis nucleus (Fig. 4E).

The fibers of the posterior lateral line nerve enter the medulla far caudally (Fig. 4D) where they form a short descending ramus that terminates in the lateral half of the caudal octavolateralis nucleus (Fig. 4E) and a long ascending ramus. The ascending ramus runs in the ventrolateral margin of the medial octavolateralis nucleus where it gives off terminals to the lateral one-third of the ventrally situated neuropil of the medial octavolateralis nucleus (Fig. 4B). The fibers of the ascending ramus split into lateral and medial components. The lateral component courses into and terminates within the lateral half of the neuropil of the ELLL whereas the medial component courses through and probably terminates, in part, in the magnocellular octaval nucleus and the ventrolateral one third of the neuropil of the medial octavolateralis

nucleus. Some fibers of the medial component of the ascending ramus of the posterior lateral line nerve continue anteriorly to terminate in the rostralmost portion of the medial octavolateralis nucleus and in a lateral portion of the eminentia granularis (Fig. 4A). Although most ascending posterior lateral line nerve fibers terminate in the lateral eminentia granularis, some fibers course more medially and end within the terminal zone of the entering anterior lateral line nerve fibers.

Discussion

The physiological findings confirm with quasi-normal electric stimuli Braford's (1982) suggestion based on anatomy, that some osteoglossiforms, namely notopterids might be specialized for electroreception. The demonstration that some are functionally electroreceptive is a striking case of serendipity. We had earlier tested several *Notopterus*, with clearly negative results. The suggestion that motivated a re-examination specified only a notopterid and it was chance that included both *Xenomystus* and *Notopterus* in the shipment received from a dealer. We have not yet tested *Papyrocranus afer*, of the same subfamily as *Xenomystus* (Nelson 1976) and found by Braford to exhibit the same anatomical specialization of the lateral line area.

Our anatomical findings also fully confirm Braford's descriptions. We add a few details on the nature of the specialization and describe the terminations of the entering primary fibers of the lateral line nerve rami. We also add some species, representing other families of osteoglossiform fishes, to the list of presumptively nonelectroreceptive taxa.

Electroreception is known to have evolved at least three times (Bullock et al. 1982), – once in primitive vertebrates from which lampreys, elasmobranchs, holocephalans, dipnoans, crossopterygians, polypteriforms and chondrosteans inherited it, once in a mormyriiform stem and at least once in ostariophysans which include the siluriforms and gymnotiforms (Fink and Fink 1981). It is not too surprising that yet another taxon is found to have this sensory modality, as well as the specialized central structures to process it. The new case is remarkable in that electroreception is not an ordinal or even a family character, but apparently that of a subfamily (*Xenomystinae*). This makes it problematical whether the appearance of the character here can be attributed to the same evolutionary invention of electroreception that took place in some ancestor of the Mormyriiformes. Al-

though that order and the Osteoglossiformes are generally considered to be closely related, the Xenomystinae are not supposed, as far as we know, to be closer to that stem than other notopterids, although notopterids are closer to mormyriforms than are hiodontids, pantodontids or osteoglossids (Greenwood 1973).

The anatomical and physiological data on *Xenomystus* suggest that, as in other electroreceptive fishes, both teleosts and nonteleosts, central structures mediating electroreception are discrete and to a large extent distinct from those mediating other octavolateral modalities. More precise physiological localization is needed to show whether they are more distinct or more overlapping.

The dynamic properties of the evoked potentials are like those of ampullary systems in siluriforms (Knudsen 1976; Bullock 1979). No responses were noted that suggest the high frequency sensitive, tuberous systems of mormyriforms and gymnotiforms i.e. pulses <2.5 ms in duration or sine waves > 50 Hz had very high or unattainable thresholds. We have yet to find the receptors in xenomystines and to compare them, as well as central units at different levels with those of the other three orders. Further data on the anatomy of medullary, midbrain and cerebellar pathways should also yield significant comparisons with the well studied forms. Behavioral studies of electrosensory ability in xenomystines are also needed.

Electroreception presents a particular kind of problem in its distribution. A whole set of organs of special sense in the periphery and a system of electrosensory processing structures in the brain are known to be well developed in 10 orders and one subfamily of another order of fishes, not known in the majority of that order or in the other 30 orders of fishes. Zoology is familiar with bats and dolphins that enlarge upon existing sensory systems and with blind cave fishes and other scattered taxa of vertebrates and invertebrates that have lost or nearly lost whole sensory systems. But a distribution like that of electrosensory systems is puzzling. It is generally assumed that this modality was invented independently at least three times and lost one or a very few times (Bullock et al. 1982; Bass and Hopkins 1982) because the assumption of a single origin and a series of independent losses in dozens of ordinal stem forms seems more complicated. This problem is discussed in its broader aspects by Bodznick et al. (in prep.). In the present context one special aspect is noteworthy. Most of the 30 orders of fishes not known to have electroreception have probably not been adequately examined. From the findings reported

here, the task is much larger than sampling 30 orders.

Until recently no feasible method was available for revealing the presence or absence of this sensory modality, without inordinate labor. Evoked potentials have emerged as such a method, especially for establishing rapidly the presence of electroreception. The consistent physiological findings among individuals of *Xenomystus* and *Notopterus* and their correlation with the presence or absence of a brain nucleus shown to have the proper connections help on the one hand to validate a new anatomical criterion for electroreception in teleosts – the ELLL, and on the other hand to add weight to the otherwise unconvincing negative physiological result – the failure to find electric evoked potentials. This latter criterion has been the main evidence for claiming the absence of the electroreceptive system in six orders of teleosts and the main hope for further sampling of the majority of orders. Now, however, both anatomical and physiological criteria are available and many more taxa of lower category should be sampled. This may not simplify the zoological problem of a major sensory system with a checkered distribution, but it would delimit it and probably turn up new clues to the possibilities of convergent evolution.

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