

**Electroreception and Electrogenesis in Fishes**

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## **Introduction**

The aquatic environment has elicited the evolution of sensory systems in fishes and other aquatic vertebrates not represented in terrestrial organisms. The acoustico-lateral line system, external gustation, and electroreception, including electrogenesis, are all sensory mechanisms unique to aquatic vertebrates (Helfman *et al.*, 1997). Such sensory systems may be necessary in environments where vision and audition are not sufficient to survive such as the turbid waters of many coastal and riverine habitats (von der Emde, 1998), where sensing the movements of other organisms by vibration and/or electric impulses produced by muscle movements may allow for avoidance of predation, and successful capture of prey. Water is highly conducive to electrical potentials and, to a lesser extent, sound waves, and allows for these forms of energy to propagate relatively unimpeded through the environment (Moller, 1980; Bullock & Heiligenberg, 1986).

Indeed, electrogenesis in fishes has been known for thousands of years as is evidenced by the inscriptions of the electric catfish (Malapteruridae) on the pyramids of Egypt, and the electric eel (Electrophoridae) in the folklore of the native tribes of South America (Heiligenberg, 1993). The electroreceptive abilities (i.e. the ability to sense electrical impulses in the environment) of elasmobranchs and weakly electric fishes of Africa and South America were not discovered by scientists, however, until the later half of the 20<sup>th</sup> century (von der Emde, 1998). For example, early investigations of the ampullae of Lorenzini (sensory pores in the epidermis of elasmobranchs) proposed pressure as a function of the ampullae as pressing down on them provided a stimulus that sent a signal through the afferent nerve fibers innervating the cells of the ampullary organ (Parker, 1909, in Bullock & Heiligenberg, 1986). Subsequent studies showed that the

ampullae responded to temperature (Sand, 1938, in Bullock & Heiligenberg, 1986), salinity and pressure (Murray, 1960b), and electrical potentials (Murray, 1960a). It wasn't until Dijkgraaf and Kalmijn (1962, in Bullock & Heiligenberg, 1986) performed hunting experiments with sharks that electroreception was confirmed as the biological role of the ampullae of Lorenzini. Since this discovery, a vast body of research has been produced about the physiology, phylogeny, evolution, and ecology of electrogenic and electroreceptive organs of fishes. The focus of this paper will be on reviewing the phylogeny of electroreception and on comparing weakly electric fishes with strongly electric fishes and electroreceptive fishes, such as the elasmobranchs, that inhabit waters all over the world. By understanding the physiological and biochemical mechanisms of this unique sensory system, and comparing how they are different among fish taxa, I hope to elucidate its importance in the environment of fishes, as well as examine some deeper questions of convergent evolution and the loss of the electroreceptive ability in many higher Teleost fishes.

### **Evolution of Electroreception**

In order to be considered electroreceptive, fishes need to display the sensory organs that allow for such perception (ampullary organs or something similar) and the portions of the brain necessary to process the information gathered from the electroreceptors (Bass, 1986). Electroreception appears to have evolved twice in non-Teleost fishes (Fig. 1). The first appearance may have been approximately 350 million years ago as the first Petromyzontiforms (today represented by the lampreys) evolved. This is currently accepted due to the fact that lampreys possess electroreceptive abilities, whereas Myxiniiforms (Hagfish) do not, and the groups separating them (the

Pteraspidiformes and Thelodontiformes) are extinct, and, therefore, it is difficult to discern whether or not they possessed electroreceptive abilities (Bass, 1986). All non-teleost groups following the lampreys possess electroreception including all Elasmobranchs and Holocephalans, all Sarcopterygians, including lower amphibians (Tetrapoda), Polypteriforms, and Chondrosteans (Moller, 1980; Bass, 1986; Bullock & Heiligenberg, 1986; Hill & Wyse, 1989; Feng, 1991; Withers, 1992; Bleckmann, 1993; Heiligenberg, 1993; Helfman *et al.*, 1997; von der Emde, 1998). The ability was lost, however, in the Lepisosteiforms (gars) and Amiiforms (bowfins), only to be regained by some early Teleosts, namely Osteoglossomorphs and Ostariophysans, two unrelated, primarily freshwater subdivisions highly represented in South America and Africa (Fig. 2). Even within these subdivisions, only select orders have electroreceptive abilities. All Teleosts after the Ostariophysans have lost electroreceptive abilities. There is one family of Perciform fishes, members of the family Uranoscopidae (star gazers), that do possess the ability to generate moderately strong electrical impulses, but this ability seems unrelated to electroreception as is represented in non-Teleost and early Teleost groups. Since electroreception was lost in both the gars and bowfins, it appears that it re-evolved in the Osteoglossimorphs, along with electrogenesis. It further appears that electroreception was lost in the two subdivisions, Elopomorpha and Clupeomorpha, which separate the Osteoglossomorphs and Ostariophysans (Fig. 2).

Probably the best example of convergent evolution in electroreceptive fishes is the comparison of the Osteoglossomorphs and Ostariophysans. In the Osteoglossomorphs, one order (Osteoglossiformes) has members that have evolved electrogenesis and electroreception. The families Mormyridae (elephant fishes),

Notopteridae, Gymnarchidae, and one subfamily (Xenomystinae, the Old World knifefishes) of family Osteoglossidae all have independently (except the notopterids, which are basal to the mormyrids indicating that they may have evolved electroreception first) evolved their electrical abilities. Similar to these fishes, two major orders of subdivision Ostariophysi, Siluriformes (catfishes) and Gymnotiformes (knifefishes), have evolved electrogenesis and electroreception. The Siluriforms appear to have evolved electroreception and electrogenesis first, as they are basal to the Gymnotiforms in the Ostariophysan clade (Alves-Gomes *et al.*, 1995). Including these groups, electroreception evolved a total of five separate times in fishes. The Osteoglossiform fishes are primarily found in Africa, whereas the Gymnotiforms and Siluriforms are found primarily in South America. Since these Teleost groups evolved independently from one another, and independently from the non-Teleost groups, there are some differences in the morphology and physiology of their electric organs, but these differences are relatively small, and may be more environmental than phylogenetically based (Bass, 1986). Nevertheless, it is important to examine at least a few different electroreceptive and electrogenic organs to appreciate how these organisms utilize the electric sense to perceive their environment.

### **Detection of electric potentials**

Two categories have been established within which electroreceptive and electrogenic fishes are placed: Passive and Active electrosensory. Passive electrosensory refers to fishes that possess only ampullary receptors that sense the electrical potentials created by muscle movements and metabolic processes of organisms in their environment. This group encompasses all of the non-Teleost fishes, including elasmobranchs (with a few exceptions, of course). Active electrosensory, on the other

hand, refers to fishes that literally produce an electrical field around themselves as a mode of electrolocation (to sense their environment based on the resistance and capacitance of objects around them) and electrocommunication. This group encompasses the Osteoglossomorph and Ostariophysan electric fishes (Bass, 1986). Actively electric fishes possess an electric organ that produces an electric organ discharge (EOD) and another type of sensory organ, tuberous organs, that can encode the EOD as it interacts with objects in their environment, and have ampullary organs as well. Ampullary and Tuberous organs are displayed in figure 3.

Ampullary organs are characterized by a long canal leading from a pore in the epidermis to sensory cells at the base of the canal that respond to voltage gradients. The canal is filled with a conductive jelly, produced by support cells, that, when combined with the high resistance of the epidermis of the fish, acts as a cable to conduct any electric potential coming in contact with the fish through the canal to the receptor cells (Bass, 1986; Heiligenberg, 1993; von der Emde, 1998). In elasmobranchs, the ampullary receptor cells respond to outside (i.e. outside of the body of the fish) negative gradients. The negative stimulus causes a depolarization of the receptor cell membrane potentials, which in turn depolarizes the afferent nerve fiber innervating the receptor cells. This causes an increase in the amount of acetylcholine released and, therefore, a strong signal is sent to the electrosensory lateral line lobe (ELL) in the medullary complex of the brain (Obara & Sugawara, 1984, in von der Emde, 1998). If a positive stimulus is presented, the receptor membranes hyperpolarize and less acetylcholine is released and less of a signal is sent to the ELL. The afferent nerve fibers are, therefore, tonically active and can detect the difference between a positive and negative signal. This is important as

different objects in the environment may emit different DC currents. For example, a wounded crustacean may release a strong positive stimulus, whereas the earth's electromagnetic field may be either positive or negative depending on location (Kalmijn, 1978, 1982; Heiligenberg, 1993). The ampullary organs of other non-Teleost fishes as well as Teleosts respond in an opposite manner to elasmobranchs in that it is an outside positive stimulus that causes a strong signal to the ELL (von der Emde, 1998).

Elasmobranch ampullary receptors respond to electric potentials as small as  $0.1 \mu\text{V}/\text{cm}$  and frequencies of 1-8 Hz, whereas Teleosts respond to slightly stronger potentials ( $1 \text{ mV}/\text{cm}$ ) and frequencies of 6-12 Hz (von der Emde, 1998). Further, all marine electroreceptive fishes, including some siluriforms, have longer ampullary canals than the freshwater representatives. This is due to the low resistance of seawater, which therefore, makes the epidermis of the fish have a relatively low resistance in comparison to the freshwater fishes, a difference that requires a longer "cable" to transmit the signal to the receptors at the base of the organ (Heiligenberg, 1993).

Tuberous organs are characterized by a chamber filled with loosely packed epidermal cells, of which the loose arrangement allows for the conductance of the electrical potential through the extra-cellular spaces to the receptor cells at the base of the canal (Fig. 3). Tuberous organs are further divided into categories based on their function. Some tuberous organs are specialized to encode the timing of an EOD as it returns to the fish, whereas others are specialized for encoding the amplitude of the EOD (Moller, 1980; Feng, 1991; Heiligenberg, 1993; von der Emde, 1998). This is especially important in considering how electrical signals interact with objects in the environment.

Objects that have a high resistance tend to leave an EOD unchanged as it returns to the fish, but a capacitive object, on the other hand, distorts the amplitude of the EOD (Fig. 4).

A good example of a tuberous organ and its function are the mormyromasts of mormyrid fishes of Africa (Fig. 5). These organs are characterized by having an upper chamber and lower chamber that house A and B receptor cells, respectively. The A cells are almost completely embedded in the epithelium of the upper chamber and are highly innervated with 2-3 afferent nerve fibers per organ, whereas the B cells are almost completely free in the lower chamber and only one afferent nerve fiber innervates the organ (von der Emde, 1998). The two afferent nerves end at two different portions of the ELL showing that they are processed independently. Further, these cells respond differently to the EOD of a fish as it interacts with objects in the environment (Fig. 6). The A cells tend to respond to the EOD returning from a capacitive object (a distorted signal) by a decrease in the number action potentials (spikes) generated, and an increase in spike latency, and oppositely to a resistive object, generating more spikes and shorter spike latencies. B cells respond oppositely to A cells as they are more reactive to a distorted signal, generating more spikes and shorter spike latencies (Fig. 6). This suggests that the A and B cells are used to encode different portions of the EOD as it returns from the environment and, therefore, help the fish perceive the objects in the environment based on electrical conductance. Gymnotid fishes from South America also exhibit an ability to encode electrical potentials and sense differences between resistive objects from capacitive objects (Fig. 7). The resistive object (on the right) caused a different signal to return to the fish than the capacitive object (on the left), allowing the fish to imprint its environment on its body (von der Emde, 1998). Another behavior

electrogenic fishes will exhibit that supports “imprinting” are called probing motor acts. During probing motor acts the fishes will swim back and forth in front of an object and do tail bends, and even swim backwards at an object to get a good electric “picture” of the object (von der Emde, 1998). One of the most impressive experiments performed showed that a mormyrid fish in a tank completely void of light was able to locate a hole in the false bottom even though the hole was plugged with an electrically transparent agar, indicating that the electrical sense was used to locate the hole (Bass, 1986; Hopkins, 1986; von der Emde, 1998). When the hole was plugged with an electrically non-transparent substance, or the afferent nerves of the tuberous organs were severed, the hole was not located. All of the above experiments point to the preciseness with which the fishes can detect their environment solely based on their electric sense.

Another type of tuberous organ, a knollenorgan, is also found in the mormyrids. The knollenorgans are used only for electrocommunication with other fishes, and can also encode amplitude and timing of an electrical potential. During electrocommunication, fishes emit different signals under different circumstances such as during feeding bouts, predator avoidance, courtship, mating, or in aggressive actions between males (Black-Cleworth, 1970; Moller, 1980; Hopkins, 1986; Feng, 1991; Heiligenberg, 1993; von der Emde, 1998). While the knollenorgans respond well to other fishes EOD’s, they are turned off during electrolocation. Knollenorgans have been shown to respond fervently to a fish’s own EOD, but the nerve impulses from the knollenorgan to the brain are blocked and, therefore, are not allowed to interfere with the mormyromast function as the EOD is interpreted (von der Emde, 1998).

Actively electric fishes are categorized into two groups based on the electric signals that they emit into their environment. Waveform fishes emit a constant signal that takes on an almost sinusoidal form, whereas pulse type fishes send out quick pulse signals separated by a length of time (Fig. 8). For the waveform fishes, the frequency of their EOD is very important, as is maintaining an individual frequency (Black-Cleworth, 1970; Hopkins, 1986; Feng, 1991; Heiligenberg, 1993; von der Emde, 1998). If a frequency of one fish overlaps with that of another in its immediate environment, then both frequencies will be distorted and, therefore, difficult for the fishes to encode the impulse. To avoid this, waveform fishes undergo what is called the jamming avoidance response (JAR) where they adjust the frequency of their EOD such that there is approximately a 10 Hz difference between fishes in close proximity to one another (Bass, 1986). Maintaining autonomy is important during complex social interactions, especially when schooling in large numbers requires the fishes to be almost touching one another (Black-Cleworth, 1970). Pulse type fishes will merely adjust the timing between pulses (Hopkins, 1986).

### **Electric Organ Structure and Function**

In general, the electric organs of electrogenic fishes resemble and function like batteries. Electrogenic cells (electroplaques) are usually connected in series by nerve fibers (Fig. 9). Since the electroplaques are connected in series, then as each cell depolarizes generating an electric potential, the total potential produced by the organ is the overall sum of the cells in series (Feng, 1991; Heiligenberg, 1993; von der Emde, 1998). Further, if a column of cells in series is connected in parallel to another column, the current is additive. At this point it is important to remember that the power (watts) of

an electrical impulse is the quotient of the current (amps) and the potential (volts), and that this physical law also governs impulses produced by electrogenic fishes. Under this premise, a comparison of the electric organs of strongly electric fishes with weakly electric fishes is very interesting. The differences come down to how many cells are in series and how many cell columns are in parallel in each fish. For example, in the weakly electric mormyrids of Africa, the electric organ has 10-100 cells in series and produces a weak (1-1000 mV) electric potential and weak current (von der Emde, 1998). Recall that weakly electric fishes only use their EOD for electrolocation and electrocommunication. The strongly electric fishes, however, utilize their strong EOD for prey capture and predator avoidance (Kalmijn, 1978; Fox *et al.*, 1985; Feng, 1991; Heiligenberg, 1993; Lowe *et al.*, 1994; von der Emde, 1998). The elasmobranch family Torpedinidae have electric organs derived from branchial musculature that are characterized by columns of 500-800 electroplaques and also have many columns in parallel (Fox *et al.*, 1985; Feng, 1991; Lowe *et al.*, 1994; von der Emde, 1998). They can produce a potential of 60 V and a power of 1 kW, certainly enough to knock a man unconscious and stun passing prey items, coastal fishes (Lowe *et al.*, 1994; von der Emde, 1998). The electric catfishes of family Malapteruridae in Africa have electric organs derived from pectoral musculature that, in other catfishes, is used to generate sound for communication (von der Emde, 1998). These organs are generally more spread out and are characterized by millions of cells in the epidermis all connected in series, and can generate potentials of 300-500 V (Bass, 1986). The current is inversely proportional the resistance of the medium ( $I=V/R$ ), and the resistance of freshwater is much higher

than seawater (von der Emde, 1998). The power then, is still comparable to the torpedo rays mentioned above.

The electric eel of family Electrophoridae, found in South America, has electric organs derived from trunk musculature characterized by 1000 electroplaques in series, and possesses several electric organs all over the body (von der Emde, 1998). These fishes are the strongest electrogenic fishes, generating electrical potentials of 500-700 V, but again because of the resistance of freshwater, generate power approximately comparable to the torpedinids (>1kW), but slightly greater. One final group of fishes that are, phylogenetically, completely removed from the other strongly electric fishes, and considered moderately electric, is the genus *Astroscopus* of the family Uranoscopidae (see above, "Evolution of Electroreception"). These fishes have an electric organ derived from ocular musculature with 150-200 electroplaques in series and can generate a potential of 5-25 V (Bass, 1986; Feng, 1991; Heiligenberg, 1993; von der Emde, 1998). Since the overall power is moderate, and little is known of this completely marine, cryptic group of fishes, it is difficult to confirm the main function of the electrical impulse of the fishes of the genus *Astroscopus* (von der Emde, 1998). It may be primarily predator avoidance as the main predators of astroscopoids are rajioids (elasmobranchs), and therefore, the strong EOD may confuse the predator while the fish swims away.

## **Discussion**

In general, fishes have exploited all possible avenues of sensory in order to perceive their environment. As the largest vertebrate group with approximately 26,000 extant species (Helfman *et al.*, 1997), they have been very successful. What is interesting

about electrosensory, both passive and active, is that it can be used in environments where vision and audition may not be enough to survive. Electrical impulses can travel through turbid waters, and allow fishes to “see” what is on the other side of dense objects (e.g. a rock or log), whereas vision would fail to provide such abilities (Moller, 1980). Further, active electrosensory is a mode of communication that allows conspecifics to interact with one another completely independent of other organisms in their environment.

The phylogeny of electroreception provides terrific examples of convergent evolution, and displays that whenever a mode of sensory is needed, organisms find a way to express it. The overall similarity in the environments and subsequent similarities of the electroreceptive and electrogenic organs of the Osteoglossomorphs and Ostariophysans supports the statement of evolution based on need. Further studies into the ecology and use of electrogenesis in *Atrioscopus* may also provide support. Biochemically speaking, the use of muscle cells to generate electrical potentials to be released into the environment may be a unique use of these cells, which indicates that this modification is an adaptation explicitly for the purpose of electrogenesis. Modification of any process or anything, whether it is a protein or membrane potentials, for use in one circumstance that is not ultimately exploited by another is rare in biochemical evolution, making electrogenesis all the more interesting.

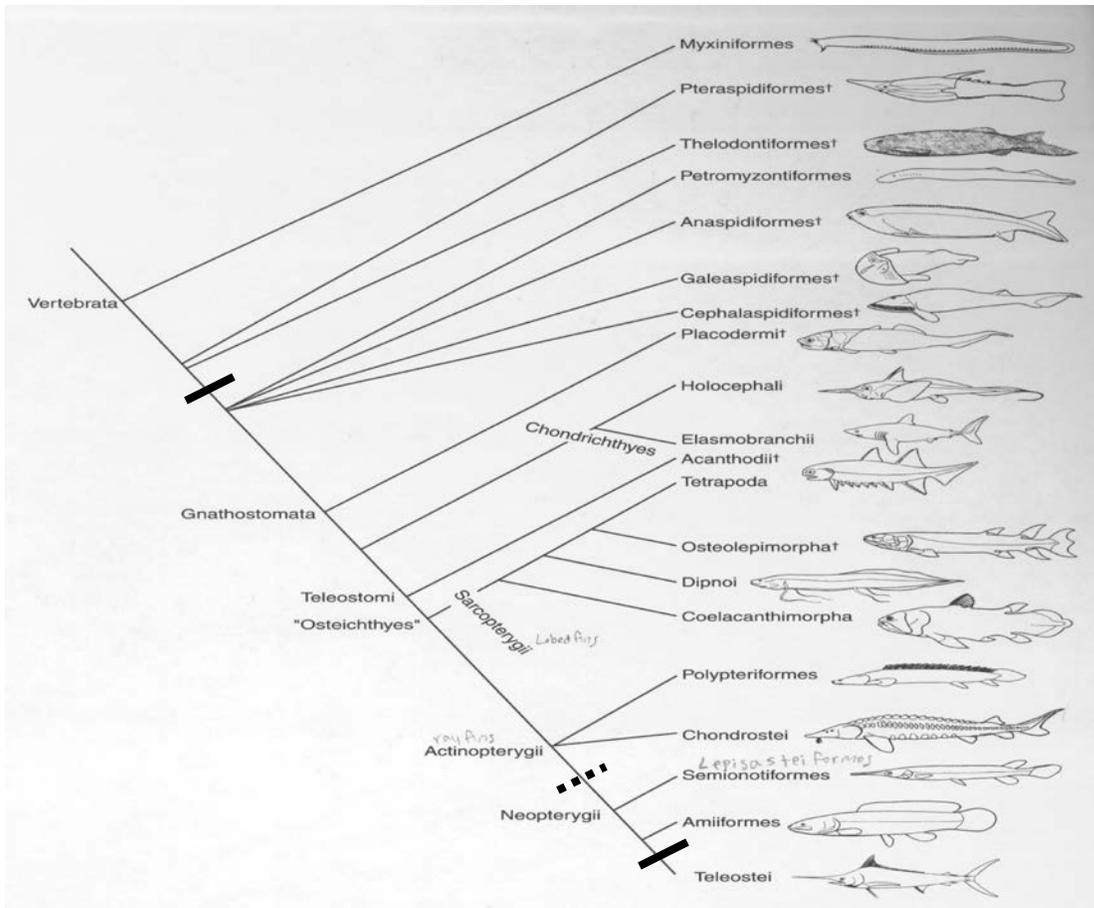
A troubling factor in the story of the evolution of electroreception and electrogenesis is the loss of the ability in the Holosteans (gars and bowfins) and higher Teleosts. These fishes certainly inhabit some of the same waters as many of the groups of fishes that have electric abilities, and are highly successful. Why and how these

groups can be successful in environments where electrosensory is touted as essential is puzzling. There are, potentially, a number of behavioral and ecological factors involved in the success of these non-electric groups that await discovery. Further, the examination of Teleosts that have lost their eyes (e.g. cavefishes, family Amblyopsidae; and blind gobies, family Gobiidae) has shown that they have increased lateral line and chemosensory, but not electroreception (Helfman *et al.*, 1997). Perhaps caves, or the intertidal (the habitat of the blind gobie) are not habitats that elicit a need of electroreception. Nevertheless, electroreception is an amazing mode of sensory and communication in fishes, and attests to the fact that fishes are truly amazingly well adapted organisms in the aquatic environment. Further study and characterization of electroreception may lead to discoveries of this ability in other groups of fishes, and perhaps invertebrates. If electroreception were to be discovered in invertebrates, that would open a new realm of research into the evolution of this sensory mechanism. Already it has been discovered that electrogenic fishes have abilities to regenerate flesh, bone and even neuronal tissue (Nigel Marvin Electric Eel special, Discovery Channel). At this time, it appears that this regenerative ability is limited to electrogenic fishes, prompting investigation into the why's and how's that only these fishes have this ability, and how it is tied to their electrogenic capabilities.

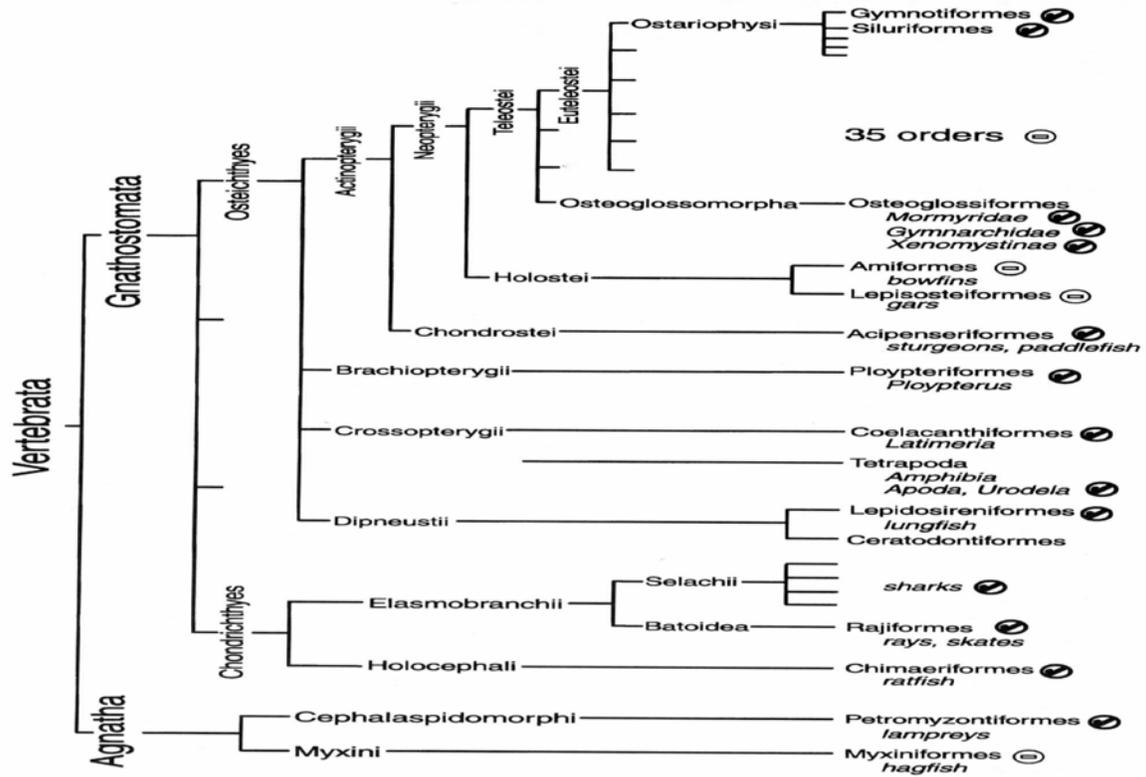
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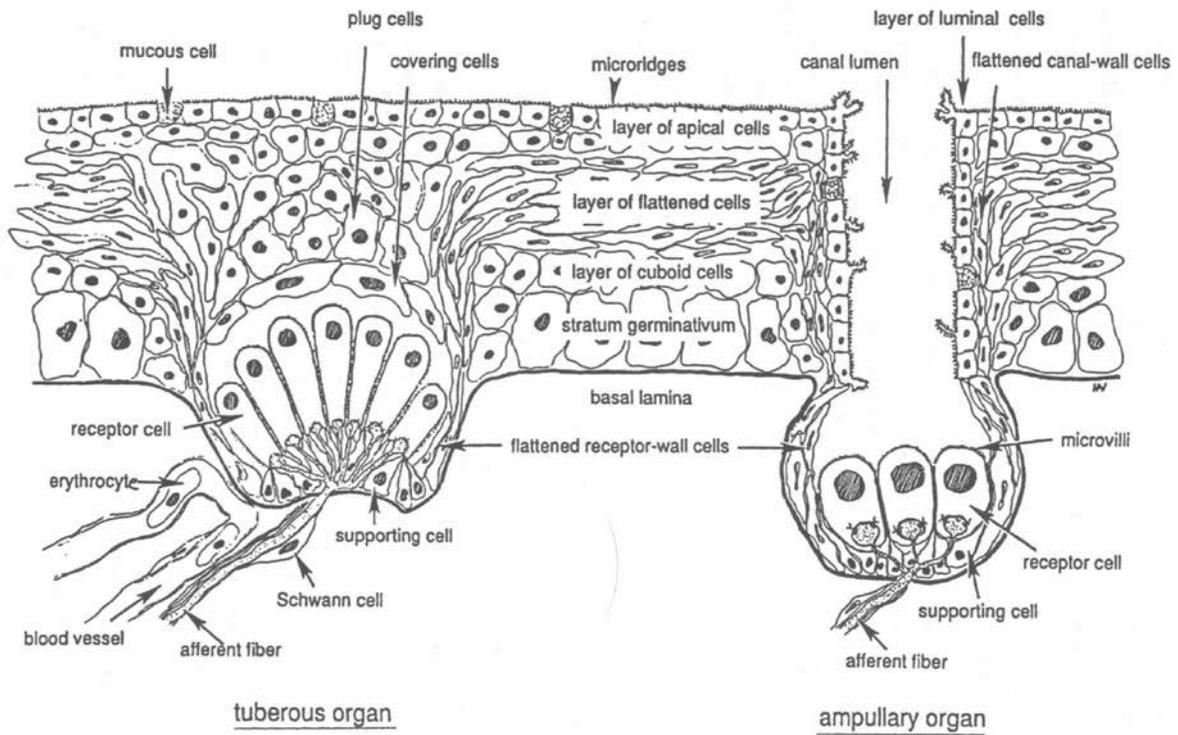
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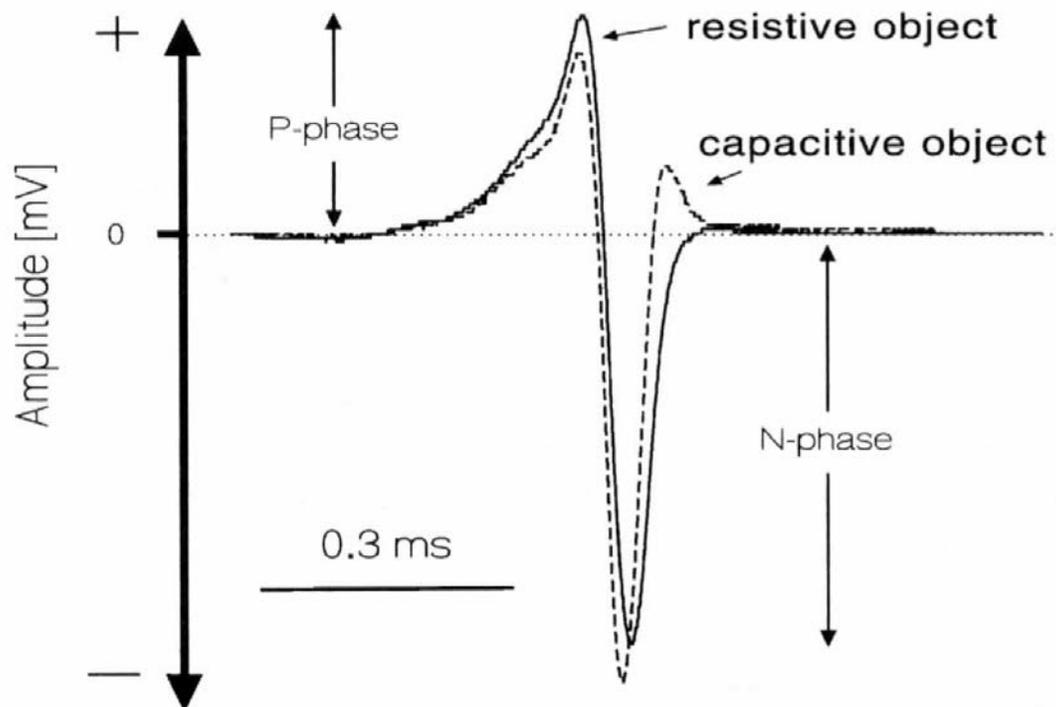
**Figure 1.** Cladogram of fish evolution incorporating evolution of electroreception. Solid bar indicates gain of electroreceptive abilities, dashed bar indicates loss. (From Helfman et al., 1997; used without permission).



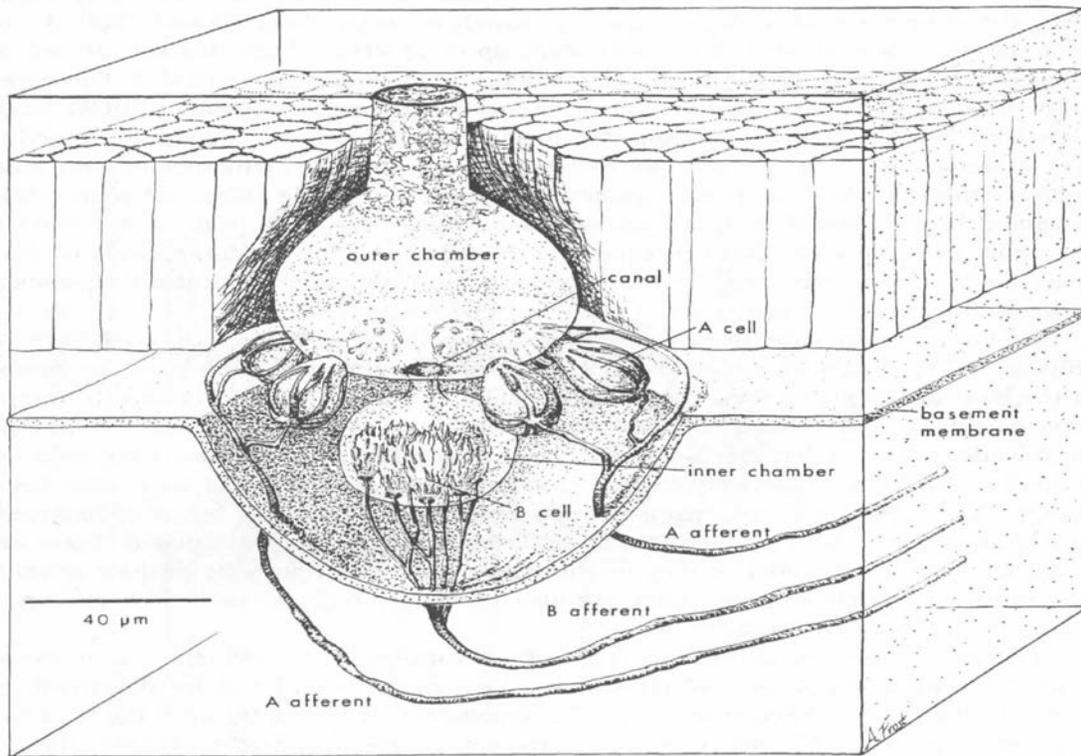
**Figure 2.** Cladogram of electroreception in fishes. Check marks indicate the possession of electroreception, whereas minus indicates absence or loss of electroreception. (From von der Emde, 1998; used without permission).



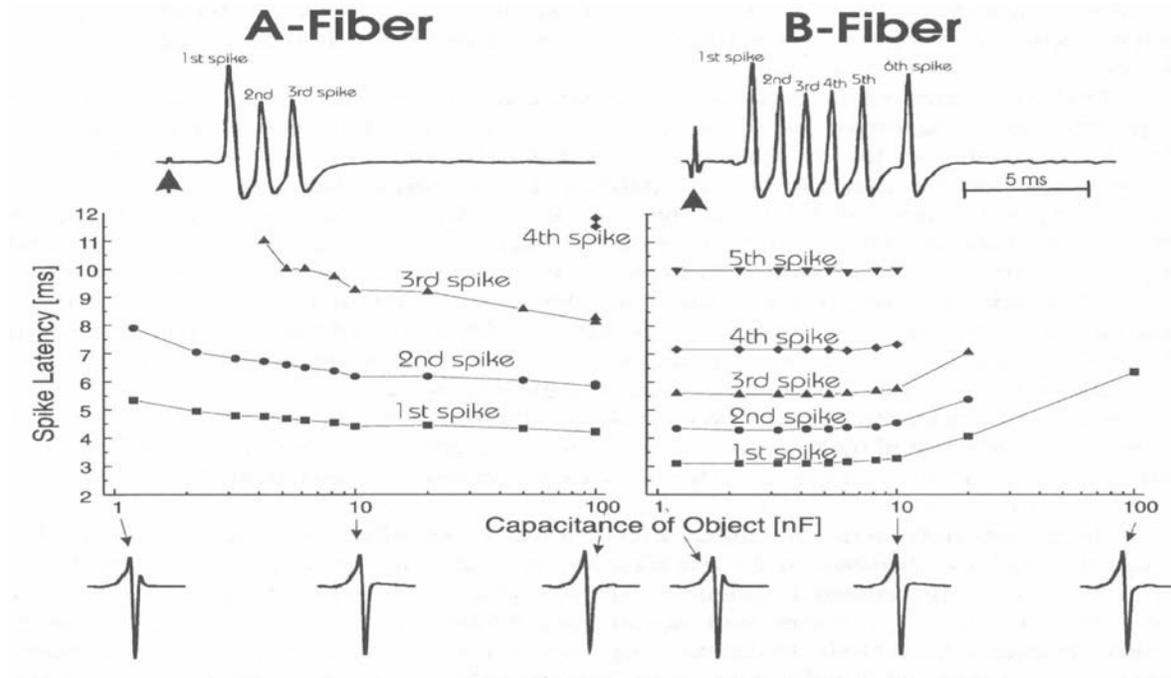
**Figure 3.** A comparison of tuberous organs (left) and ampullary organs (right) common in electroreceptive fishes. (From von der Emde, 1998; used without permission).



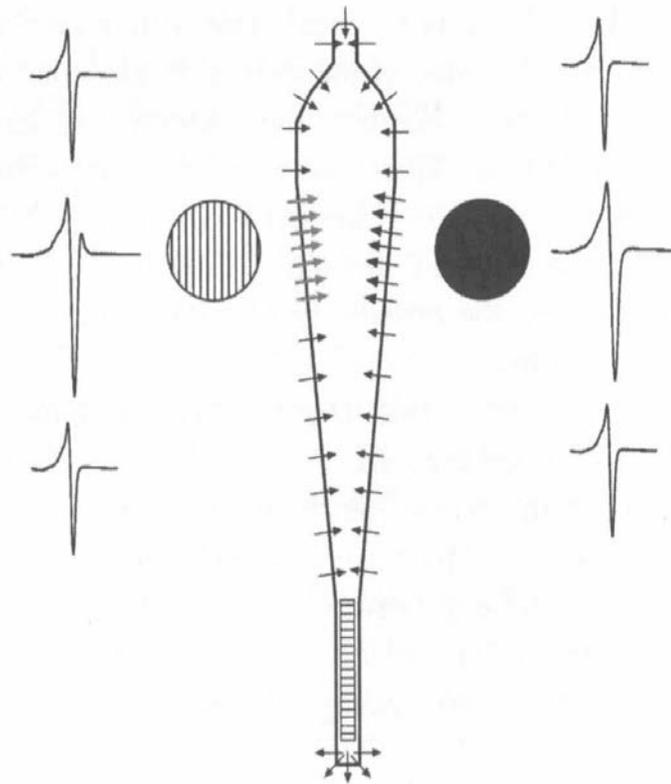
**Figure 4.** A trace of the amplitude of an electrical impulse after it had been initiated and interacted with a capacitive object or a resistive object. P-phase is the positive phase, and N-phase the negative phase of the amplitude. (From von der Emde, 1998; used without permission).



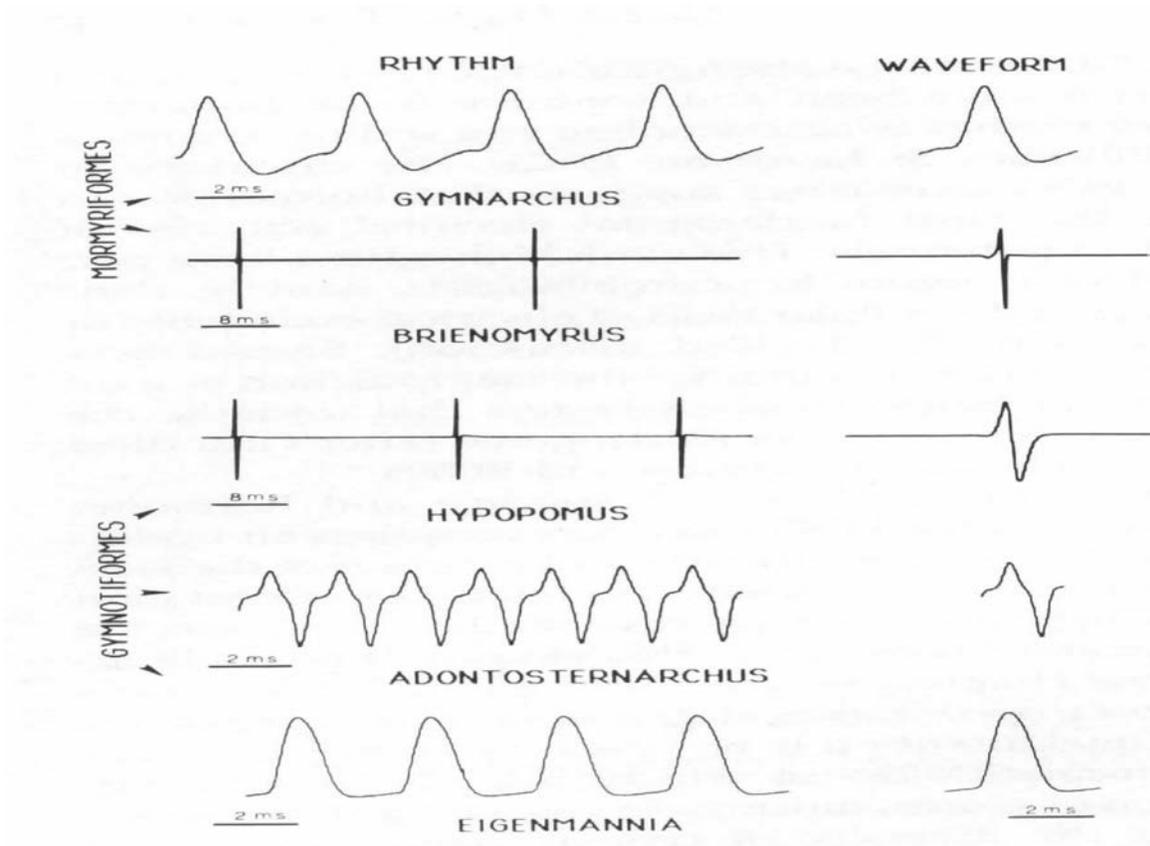
**Figure 5.** A mormyromast (tuberous organ) from an African mormyrid. (From von der Emde, 1998; used without permission).



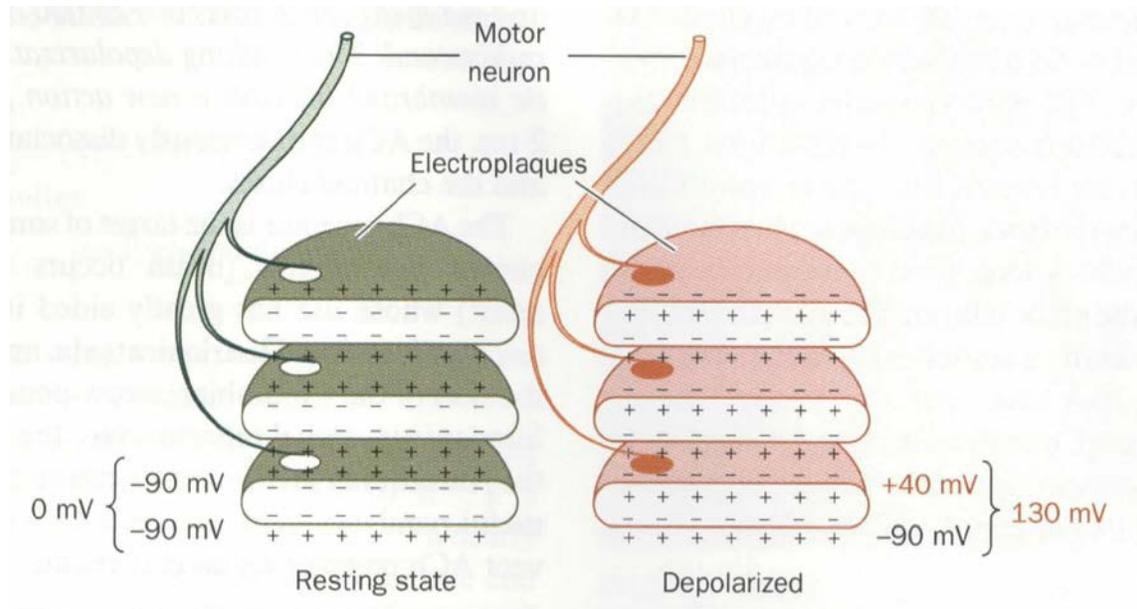
**Figure 6.** Traces of spikes of afferent nerve activity from mormyromast A cells (left) and B cells (Right). (Top) Plot of how the cells respond to their respective stimuli: A cells to a resistive object, B cells to a capacitive object. (Middle) Graph displaying number of spikes and spike latencies of A and B cells relative to the capacitance of the object the electrical impulse interacted with. (Bottom) Plots of the overall capacitance of the objects of interest, which correspond with the graphs above (From von der Emde, 1998; used without permission).



**Figure 7.** Generalized diagram of a gymnotid fish and how it responds to capacitive and resistive objects in its environment, imprinting an image on the fish. The capacitive object (left) distorts the amplitude of the electrical impulse as it returns to the fish (note gray arrows indicating altered amplitude), whereas the resistive object (right) does not (note darker arrows indicating unaltered amplitude). Graphs around the fish show the amplitude of the electrical signal as it returns to the fish (From von der Emde, 1998; used without permission).



**Figure 8.** Traces of electrical impulses generated from waveform and pulse type electric fishes. (Top) Some mormyrid fishes of Africa, (Bottom) some gymnotiform fishes of South America (From Bullock, 1986; used without permission).



**Figure 9.** Diagram of electroplaques in series and their membrane potentials in the resting state (left), and in the depolarized state (right). Note that electroplaques in series will have potentials that are additive, so the total electrical potential of the depolarized cells would be 390 mV (From Voet & Voet, 1995; used without permission).