Electric Signals & Electric Fish

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Synopsis

Electric sense (i.e. the ability to detect low-voltage electrical impulses from other individuals) is found in most primitive fish orders, a few derived teleost fish, some aquatic amphibians, the platypus and the echidna. Electric signals (i.e. self-generated electrical signals used for communication) are best understood in the weakly electric fish. Weakly electric fish include three freshwater teleost groups that produce dual-purpose electric signals to locate objects and communicate in the dark. Their electric organ discharges (EODs) are distinctive to species, and often to age, sex, and condition. EODs are non-propagating electrostatic fields, detectable only a few body lengths from the signaler. Electroreceptive predators may eavesdrop, and many weakly electric fish have signal adaptations that make their signals cryptic to predators. EODs are triggered by nerve impulses but their waveform shapes are regulated by steroid and peptide hormones. The electric eel is a specialized electric fish that produces a low voltage EOD for electrolocation and communication and also a high voltage discharge to stun prey and defend itself.

Introduction

Electric sense is the ancestral vertebrate condition, retained by most of the primitive fish orders, including the lobe-finned fishes from which tetrapods arose. Electric sense is derived in a few teleost fishes, some fully aquatic amphibians, the platypus, and the echidna. While all animals produce electricity through muscle and nerve action, just a limited assortment of fish have evolved specialized tissues the sole function of which is to generate electric fields in the water outside their bodies. These bioelectric fields serve different functions in different taxa. The stargazers, a group of bottom-dwelling marine perch, produce strong defensive electric pulses that deter sharks and rays, though the stargazers themselves are not electroreceptive. Torpedoes (Torpedinidae), the electric eel (*Electrophorus electricus*), and the electric catfish (*Malapterurus electricus*) generate electric discharges in excess of one hundred volts that immobilize small fish long enough to allow these predators to ingest the meal before it can recover and swim away. Weakly electric fish

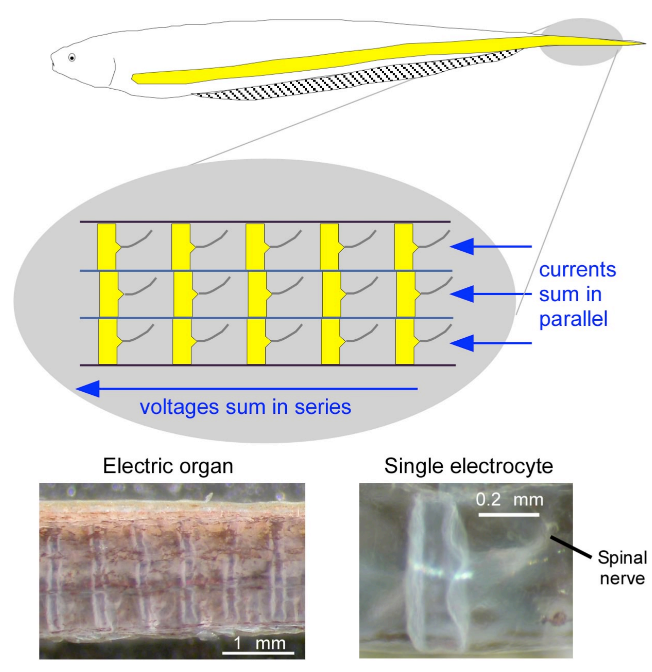

Figure 1. Electrocytes in series (rows) sum their voltages, like batteries in a flashlight. Multiple rows of electrocytes sum their currents. The electric organ and electrocyte shown are from the gymnotiform *Brachyhypopomus pinnicaudatus* (photos courtesy of Michael Markham).

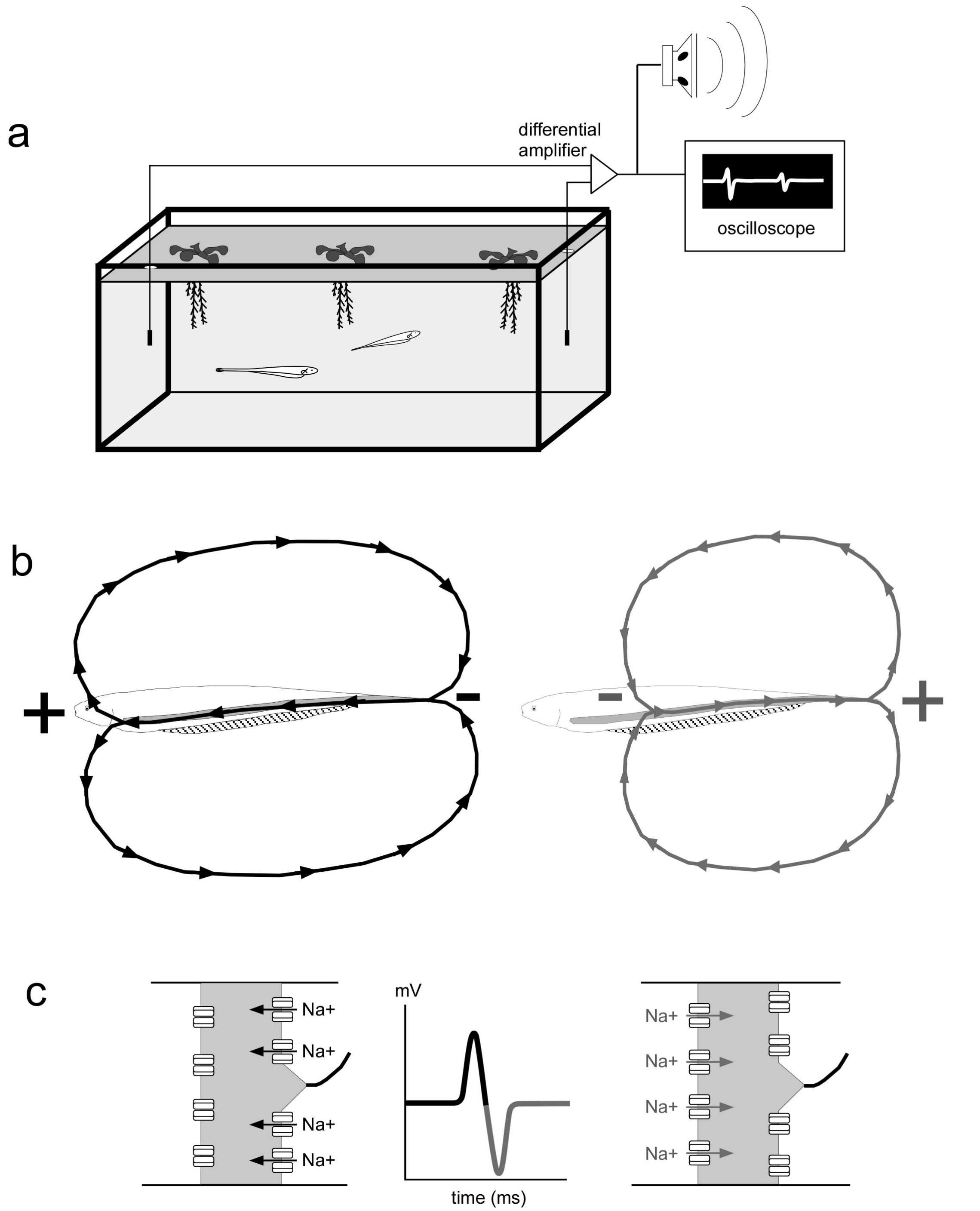

Figure 2a. Signals of electric fish can be recorded by placing two non-corrosive wires in the water and amplifying the voltage differences between them. Electric signals can be visualized on an oscilloscope or heard by playing the amplified signals through an audio speaker. B & C. Gymnotiform pulse fish may produce biphasic EODs by generating two action potentials from each electrocyte. The innervated, posterior face fires an action potential (c - left), causing a headward sodium ion flux. These fluxes sum through the electric organ (b) producing a positive polarization of the head and a negative polarization of the tail. The anterior, non-innervated face of the electrocytes fires an action potential (c – right), causing a tailward flux of sodium ions. The tail becomes positive relative to the head. These two phases sum to produce a biphasic EOD (c – center).

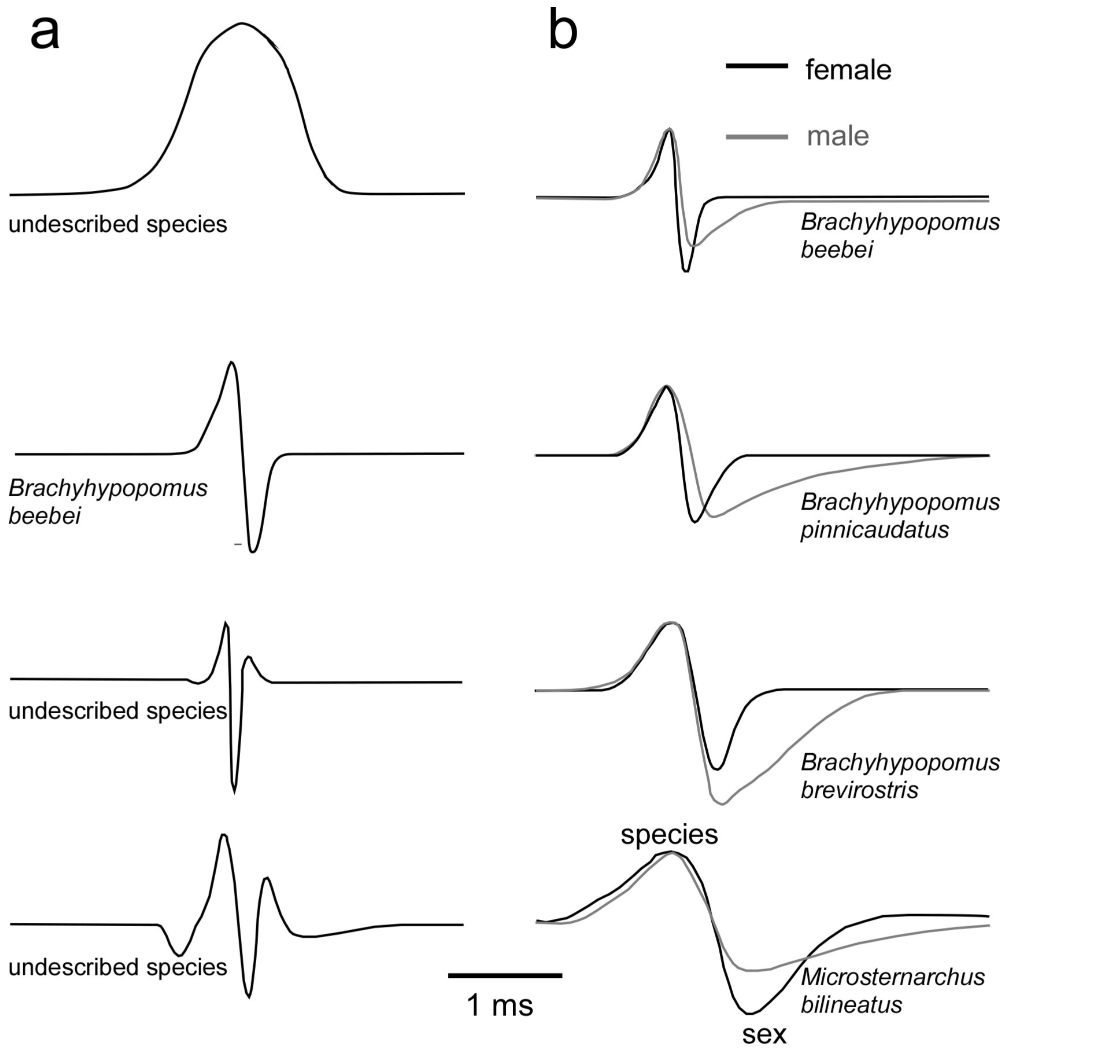

Figure 3. EOD waveforms can vary considerably, even within a single family. Shown here are EODs from the gymnotiform family Hypopomidae. A. EOD of species in this family may have from one to five phases. Many species were undescribed at the time these recordings were made. B. Even simple biphasic EODs may encode multiple properties. Here the first phase duration is distinctive of species, while the second phase duration is distinctive of the sex.

of three orders generate electric fields measuring only a fraction of a volt per centimeter, used for imaging nearby objects in dark and murky waters, and for communication. These weakly electric fish include the Mormyridae and Gymnarchidae of Africa (order Osteoglossiformes), the electric knifefishes of the Neotropics (order Gymnotiformes), and a few sinodontid catfish from Africa (order Siluriformes). Signals produced by weakly electric fish will constitute the main topic of this review.

Electrogenesis

Electric signals are the products of large arrays of excitable cells, electrocytes, that fire action potentials en masse to produce the Electric Organ Discharge or EOD. Electric organs are made up of many electrocytes arrayed in series, like batteries in a flashlight, summing their

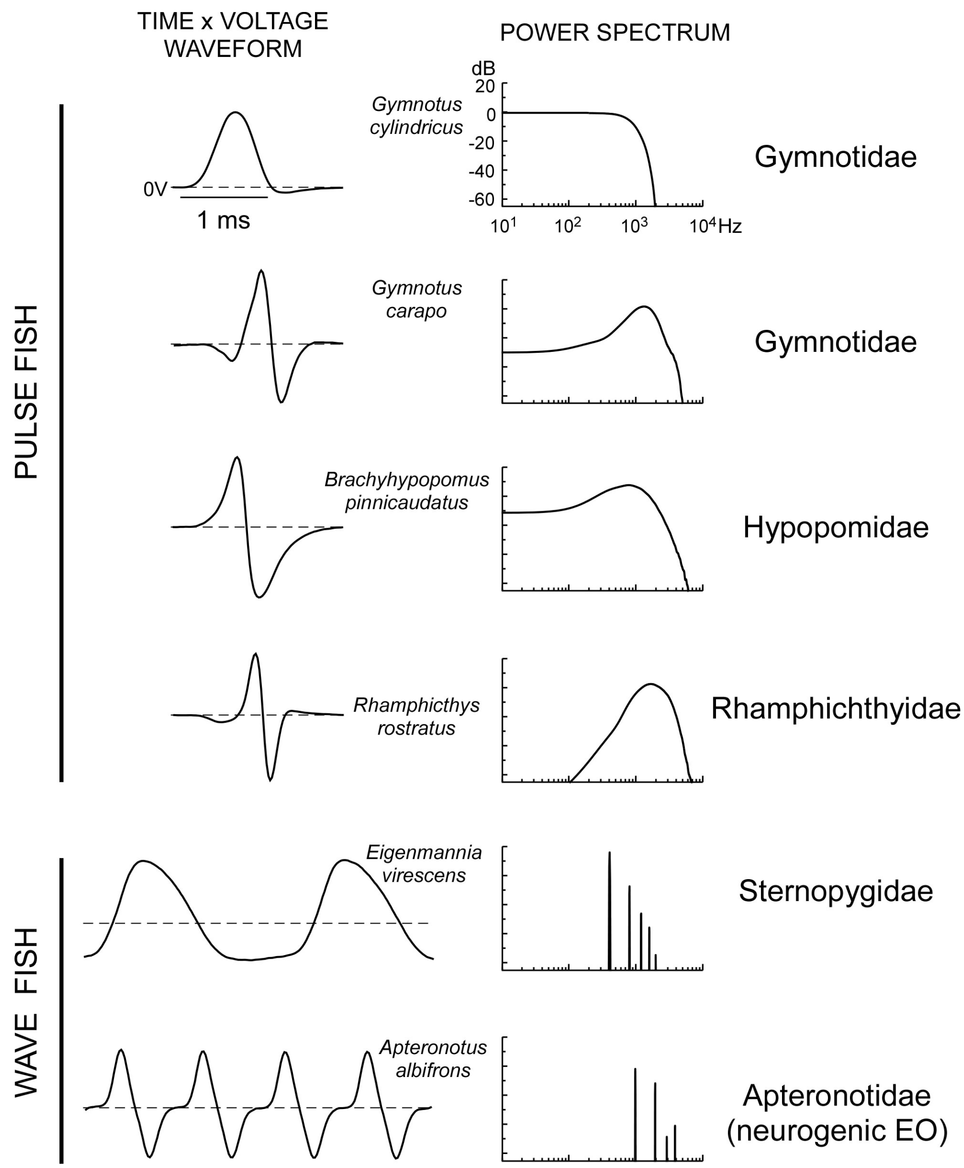

Figure 4. EODs may be delivered either as individual pulses with significant intervals between EODs, or one directly after another with small intervals. Fish with these two temporal patterns are called pulse fish and wave fish respectively. Power spectra of pulse EODs are broad, regardless of discharge rate, whereas those of wave fish are narrow, with discharge rate setting the fundamental frequency. For comparison, white noise would generate a power spectrum with equal energy at all frequencies, and a pure tone would generate a power spectrum with energy at a single frequency. Shown here are typical EODs of the five gymnotiform families. Members of the Apteronotidae produce the highest frequency signals, accomplished with an electric organ (EO) comprised of motor nerve axons instead of muscle-derived electrocytes. Among the weakly electric osteoglossiforms (not shown), the mormyrids are pulse fish and the sole gymnarchid is a wave fish.

individual action potentials to produce a larger voltage. Groups of electrocytes in series can be arranged in parallel arrays to increase current (Fig. 1). Mass flow of sodium ions into the electrocytes polarizes the skin of the fish, setting up electrostatic fields in the water outside the animal. Within the electric organ, net sodium flux in the headward direction polarizes the fish's head positive relative to the tail (Fig. 2). A bare wire in the water near the fish's head can be used to detect this positive potential. Displayed on an oscilloscope, this potential is seen as an upward (positive) voltage pulse. If the net flux within the electric organ is in the tailward direction, the tail becomes positive relative to the head, thus the head becomes negative relative to the tail and the oscilloscope displays a downward (negative) voltage pulse. The net flow of positive ions changes direction with successive action potentials from different membranes. Electric organs of different weakly electric fish species can generate one to five distinct phases in a single EOD (Fig. 3). Depending on species, sex, and reproductive condition, an EOD can last from 0.1 ms to as long as 10 ms.

Some electric fish produce sinusoidal EOD trains consisting of successive EODs with intervals equal to or less than the duration of the EOD pulse itself (Fig. 4). Amplified and played through an audio speaker, the EOD wave train is heard as a tonal sound, the fundamental frequency of which is determined by the discharge rate. Discharge rate, in turn, is generated by pacemaker neurons in the medulla and conveyed to the electrocytes by spinal motoneurons. Pacemaker cells of these so-called "wave fish" are the most temporally stable bio-oscillators known. Other electric fish produce their EODs less frequently, with silent intervals considerably longer than the EOD duration. If the EOD trains of these "pulse fish" are amplified and played through an audio speaker, they are heard as ticks or buzzes, depending on the rate. Most gymnotiforms keep their discharge going all the time, day and night. Mormyrids and the electric eel, the one high-voltage gymnotiform, produce highly irregular discharge trains, often remaining silent for brief periods when they are inactive.

No terrestrial organisms generate electric signals because air is such a poor conductor of electricity. Conversely, the high salinity of marine environments tends to short-circuit in the high conductivity water. In the highly conductive salt-water of marine environments, only large fish can support the large number of cells in parallel needed to produce high-current electric signals necessary to spread over useful distances. In the ion-poor waters of the tropics, smaller fish can generate electric signals because little current is needed to sustain a detectable voltage (this property follows directly from Ohm's Law V=Ir). Thus, the relatively small weakly electric fish have radiated extensively in the tropical fresh water river systems of the New World and Africa.

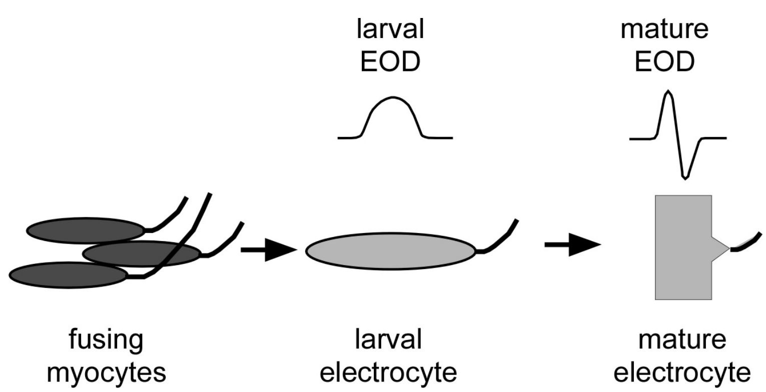

Figure 5. During larval development, muscle cells (myocytes - left) fuse to become electrocytes (center). In the process they stop expressing contractile proteins and become specialized for electrogenesis. In some species, electrocytes change morphology (right), deriving two active faces, which enables them to fire separate and opposing action potentials, making more complex waveforms possible

Embryology & development

Electrocytes are derived embryonically from muscle cells, myocytes. As the electric organ develops, myocytes fuse and stop expressing the contractile proteins and sarcomeres that characterize skeletal muscle. Instead, they transform to produce a neuron-like physiology, packing their membranes with the voltage-gated ion channels and ion transporters needed for larger-scale ion flux (Fig. 5). These cells are large enough to view with the naked eye, and can be seen by shining a light through the fish's tail (Fig. 1). Electrocytes can be nearly one millimeter across. In one gymnotiform family, the Apteronotidae, larval fish develop myogenic electric organs, which they replace over the course of few weeks with electric organs derived from the axons of spinal motoneurons. These neurogenic electric organs can sustain the higher discharge rates (500-2000 Hz) that typify this family's EOD. Ghost knifefish (*Apteronotus* spp.), common in the tropical fish pet trade, are the best-known members of this large family.

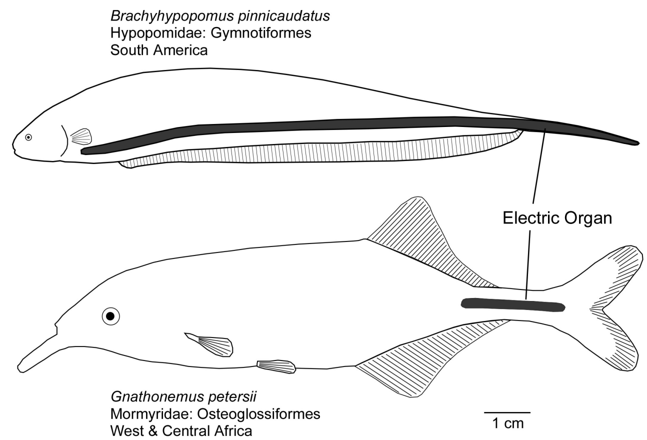

Figure 6. Gymnotiform and mormyrid electric fishes, the two largest groups of weakly electric fish, have different morphologies. In gymnotiforms, the electric organ runs the length of the body, whereas in mormyrids, electric organ is confined to the caudal peduncle

Electric organs are bilateral structures. In gymnotiforms the main organs run from just behind the gill to the tip of the pointed tail (Fig. 6). In mormyrids, electrocytes are restricted to the caudal peduncle, the tissue between the trunk and the caudal fin.

Electroreception, Passive and Active

Electricity is detected by electroreceptors, specialized sensory cells embedded in the skin, typified by jelly-filled pores open to the surrounding water. Structurally and embryonically, electroreceptors resemble the sensory hair cells of the lateral line system, minus the mechanoreceptive hairs. Lampreys and the Condrostei (sharks, rays, sawfish, paddlefish, sturgeons) have electroreceptors, as do the sarcopterygian lobe-finned fishes, the coelacanths and lungfishes. Thus our ancestors certainly possessed electroreceptors before they crawled from the sea. Electroreceptors were lost in the modern teleost lineage of bony fishes, probably because their large eyes enabled color vision, a more useful sense during daylight hours. Electroreception re-evolved independently in select groups of nocturnal teleost fish (Fig. 7). One such group was a lineage of Osteoglossiformes that includes two families of weakly electric fish, Mormyridae and Gymnarchidae, plus the Notopteridae of which some members are electroreceptive but not electrogenic. The second electroreceptive teleost lineage includes the sister orders Siluriformes (catfish) and the Gymnotiformes (electric knifefish). The "ampullary" electroreceptors, whether primitive or derived, detect the extremely weak electric fields produced by muscle action and ventilation of small invertebrates, and thus are used for passive electrolocation of prey. Such electroreception is said to be "passive" because it does not depend on the receiver to generate a signal. Passive electroreception is extremely sensitive. The ampullary system may detect electric

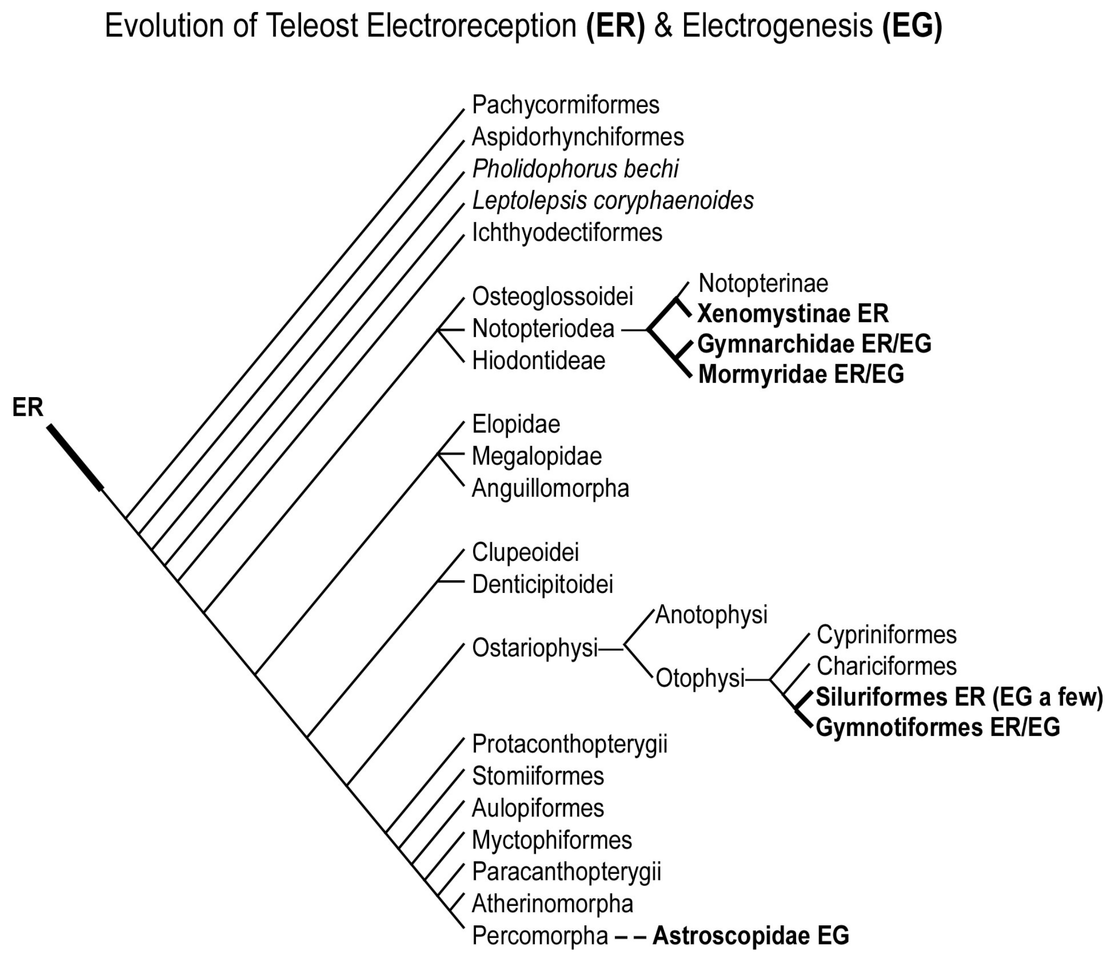

Figure 7. Electroreception was lost in the modern bony fish lineage Teleostei, then re-emerged in two separate lineages. Electrogenesis evolved independently in the Gymnarchidae/Mormyridae lineage, the Gymnotiformes (electric knifefishes), and at least twice within the Siluriformes (catfish). Electrogenesis emerged in the stargazers (Astroscopidae), which are not electroreceptive.

fields as weak as 100 microvolts/cm in freshwater species, or just a few microvolts/cm in marine species (Fig. 8). Ampullary electroreceptors detect electric fields in the spectral range of 1-100 Hz. Ampullary electroreceptors of marine species have best frequencies in the low end of this range, catfish in the middle, and weakly electric fish at the high end.

Mormyrids and gymnotiforms evolved new types of "tuberous" electroreceptors specifically adapted to detect EODs. In contrast to ampullary electroreceptors, the tuberous receptors are tuned to the higher frequencies of the species-typical EOD. Mormyrids have two varieties of tuberous electroreceptors, the mormyromasts, used for active electroreception of nearby objects, and the Knollenorgans, used for detection of conspecific signals in communication contexts. Gymnotiforms have only a single morphological class of tuberous electroreceptor, used for both active electrolocation and communication. Some of the gymnotiform tuberous receptors are specialized for encoding temporal features of the EOD, others for encoding EOD amplitude. In general tuberous electroreceptors have higher sensory thresholds than ampullary electroreceptors, however, they can encode exquisitely small changes in the self-generated electric field, enabling active electrolocation.

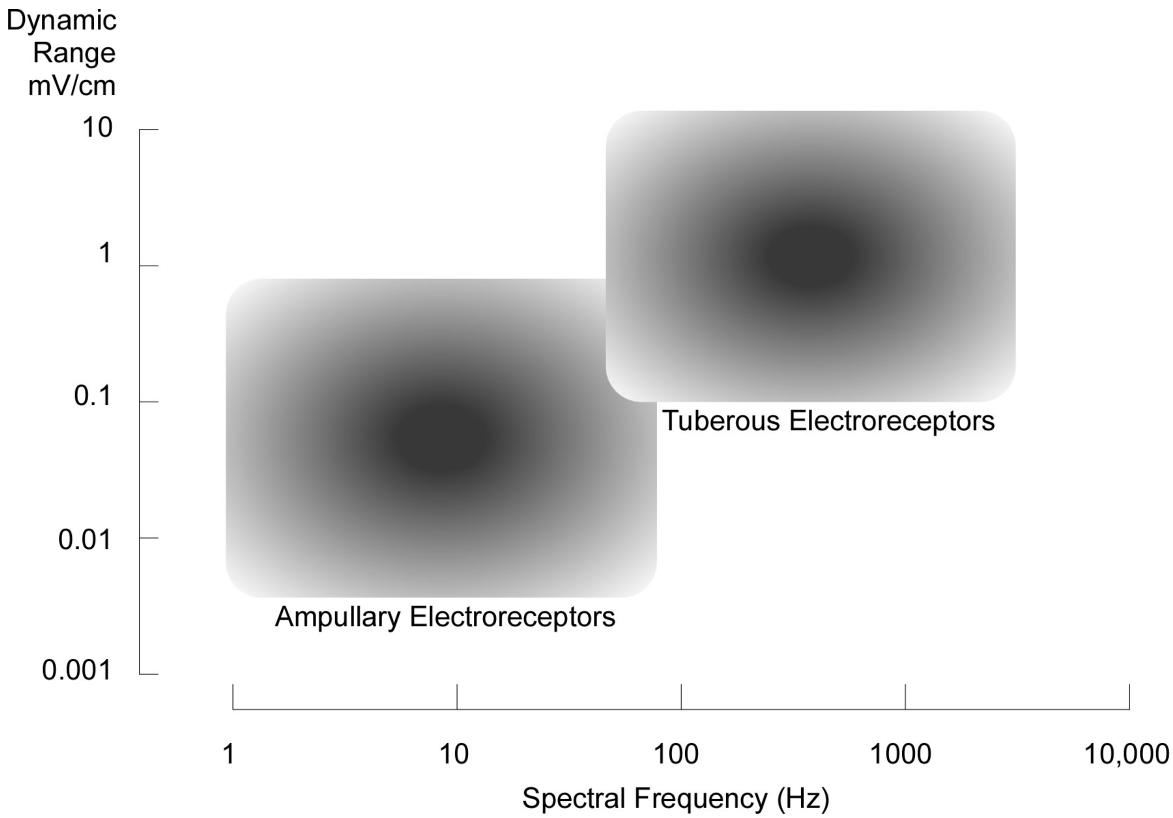

Figure 8. Approximate dynamic sensitivity ranges of the ampullary and tuberous electroreceptors. As a general rule, ampullary electroreceptors encode lower frequencies and are more sensitive than tuberous receptors.

During active electrolocation, objects in the water within half a body length of an electric fish distort the self-generated electric field in ways that can be detected by arrays of cutaneous tuberous electroreceptors (Fig. 9). Objects more resistive than the surrounding water produce an electric shadow on the skin, whereas objects more conductive than the surrounding water produce electric hotspots on the skin. Objects with capacitive properties (most living things) phase shift the EOD, distorting the waveform. Some electroreceptors respond to these phase shifts. Electric fish can identify the shape, distance, size, and material of a nearby object. They can even tell a small, proximate object from a large, distant object. By this means, electric fish can see in darkness of night or in "whitewater" rivers opaque with suspended minerals. Electric fish cannot resolve distant objects with active electrolocation, but they can "see" through submerged mud, sand, or root tangles. With similar sensory abilities, we would readily view the contents of each other's pockets, we would know whether our friends' teeth have dental fillings, and whether those fillings were made of acrylic or silver amalgam.

Electric communication – signal production

If one animal is signaling for its own purposes, active electrolocation for instance, another fish can listen in. If that fish is a predator, the signaler has an immediate problem. Indeed, hostile eavesdropping from electroreceptive catfish is believed to have led to the origin of more complex, high frequency signals that escape detection by catfish equipped with ampullary electroreceptors. But gymnotiforms and mormyrids with high-frequency sensitive tuberous

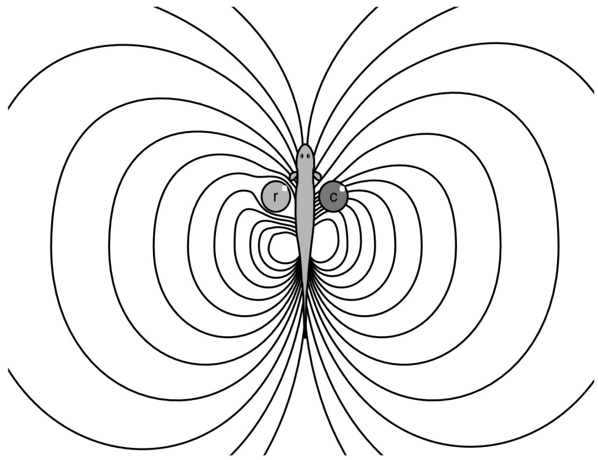

Figure 9. Electric fish are exquisitely sensitive to distortion of their self-generated electric fields. Objects more resistive than the surrounding water ('r' object on left) produce a "shadow" in the electric field detected on the skin, measurable as a reduction in field intensity and a phase shift in the waveform. Objects more conductive than the surrounding water ('c' object on right) produce an electric "hot spot" on the skin, measurable as a localized increase in electric field intensity. The brains of these fish process these localized electric field distortions to determine location, distance, size, shape, and material of nearby objects.

electroreceptors can readily detect EODs of other fish, opening the channel for electric communication.

Electric fish use their signals to communicate the standard conversational topics that interest most animals: identity, sex, aggression, and real estate. That said, most of what we know of electric communication derives from signal usage, rather than response to EODs. First, each taxon has characteristic EOD waveforms. Visually indistinguishable mormyrid species may be readily discriminated by striking differences in EOD waveform. In many but not all taxa, males and females have different waveforms. The most common sex difference is for males to discharge at lower discharge rates or to produce EOD waveforms with lower frequency spectra (Fig. 3), though this pattern is reversed in some species. In some taxa, males even alter their EODs to shift energy into the spectral band of the ampullary electroreceptor system, readily detectable by predators. Such signals may prove a male's quality to prospective mates, as long as he can survive. In those taxa where signal intensities of sexually mature individuals have been measured without disturbing them, males appear to have stronger intensities than females, another signature of a sexually selected communication signal.

Electric fish alter their temporal discharge patterns in the presence of conspecifics (Fig. 10). Some taxa generate characteristic variations in tempos or rhythms that serve as electric songs for courtship or intrasexual challenge. Changes in rate and tempo can be subtle, but played through an audio speaker some of these compound signals are obvious to the human ear, often being described as chirps, accelerations, rasps, or silences. Absent such changes in discharge rate, it

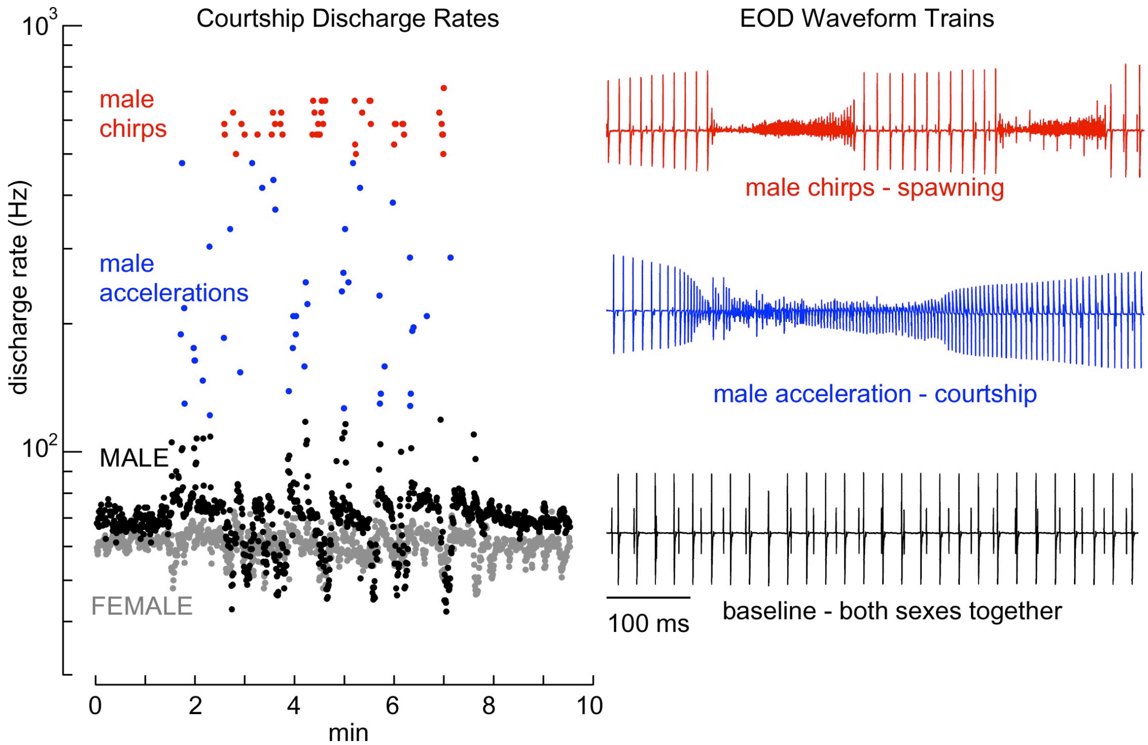

Figure 10. Electric fish can produce complex, compound signals by increasing the rate of discharge until individual EODs diminish in size. These signals are given during social encounters. Shown here are two types of complex signals given by the gymnotiform *Brachyhypopomus pinnicaudatus* during courtship and spawning. During the courtship phase, males run their snouts into the females and accelerate their discharges ("acceleration signals"). If the female proves interested, the males leads her to his chosen ovoposition site and lowers his basal discharge rate (lowest frequency dots) while giving high frequency "chirps". The female deposits eggs, the male fertilizes them, and the cycle begins again. Shown here are six such courtship-spawning cycles between a captive breeding pair in an aquarium.

can be hard to know whether an electric fish is attempting to communicate, since they also discharge to electrically image their surroundings.

These compound signals are most commonly given by sexually mature males and appear most frequently during social encounters (Fig 10). The structure of the compound signals varies with the sex of the fish being encountered – some signals are typical of same-sex aggressive encounters while others are given during courtship and spawning. Brief silences are used to punctuate communication sequences, contrasting sharply with rapid-fire EOD trains. But silences can have just the opposite function as well. Weakly electric fish of the genus *Gymnotus* are a preferred food of electroreceptive predators, including the electric eel (*Electrophorus electricus*). Upon detecting EODs of electric eels, or even crude mimics in the lab, *Gymnotus* may go silent for minutes at a time, an apparent strategy to avoid being detected and eaten. Individual females that are not ready to spawn, but find themselves confined to an aquarium with a persistently amorous male of their own species, will silence their EOD entirely for a few minutes, rendering themselves difficult for their suitor to locate. Viewed under infrared light, which fish cannot see, this scene is amusing to watch – the male visibly startles when he suddenly loses track of the female he has pursued relentlessly up to that point.

Electric communication – signal detection & identification

Mormyrids use their sensitive Knollenorgan electroreceptors to analyze EODs of other individuals. The Knollenorgans encode the time and polarity of the rises and falls of an EOD. Distinctive phase durations and intervals thus characterize the mormyrid EODs. Gymnotiforms have a special problem in that few can turn off their own signal.. Imagine the problem of trying to listen to other individuals while talking non-stop. Their solution appears to be distortion analysis – gymnotiforms take advantage of their exquisitely sensitive distortion analysis circuitry to analyze each other's EOD waveforms as distortions of their own EOD waveforms. In fact, they should be nearly deaf to EODs of other individuals unless they themselves are signaling. One exception to this principle would be ampullary detection of the small number of fish that include low-frequency energy in their EODs. At the time of writing (late 2008), studies have just begun to emerge showing that, as one would expect, mormyrids actually do recognize species and sex by the EOD waveform. The same has yet to be shown rigorously for many gymnotiforms, though in one study, *Gymnotus carapo* discriminated individual conspecifics by their waveforms.

Electric communication – risky signals

Risky behavior is a widely adopted mate-attraction strategy among sexually selected species. Male electric fish of a few species produce EODs with energy in the spectral sensitivity ranges of both the tuberous and ampullary electroreceptors. These dual-spectrum signals are presumed to attract females. Lab studies have shown that these signals definitely attract the unwanted notice of predatory catfish and electric eels for which weakly electric fish constitute a significant fraction of their diet in the wild. In the majority of weakly electric fish taxa, the EOD has little or no energy in the range of the ampullary spectrum. Males of many such species nonetheless can briefly modify their signals to produce energy in the spectral range of ampullary electroreceptors. Extreme or prolonged depolarization of neurons in the EOD control center overdrives the electrocytes in the electric organ so the resulting EODs are distorted in ways that temporarily shift the spectrum.

Hormonal regulation

Sex differences in EOD waveforms are under the regulation of steroid hormones. Over the course of days or weeks, androgens alter the discharge rate of pacemaker neurons, producing male-typical discharge rates. Estrogens exert the opposite effect, causing rate differentiation in the female-typical direction. In the wave fish, change in discharge rate is matched by a commensurate change in pulse duration to maintain an even duty cycle, the ratio of signal to silence.

Many electroreceptors are most sensitive to particular parts of the frequency spectrum. These tuning properties of the electroreceptors are also under regulation of steroid hormones, so the receptors stay in tune with the electric signal to maintain sensory acuity. Interestingly, an increase in circulating androgen levels during the breeding season changes the tuning of ampullary electroreceptors in male stingrays to make their passive electrosensory system less sensitive to prey and more receptive to the bioelectricity produced by passing female conspecifics.

In some taxa androgens alter the morphology of the electric organ, increasing both the size of the tail and the size of individual electrocytes. Within the electrocytes, androgens alter gene expression and RNA splicing of ion channel subunits to change the discharge waveform characteristics at the level of a single cell.

In about half the gymnotiform taxa, pituitary melanocortins, a family of peptide hormones, remodel the electrocytes in minutes to boost signal power as much as 300%, or to exaggerate masculine traits in the EOD waveforms. Melanocortin actions augment EOD waveforms during the night hours, and particularly during social encounters when the signal is used to communicate. At other times, these fish diminish their EOD waveforms, reducing energy expenditure and predation risk. These characters change on a circadian rhythm – fish kept under constant light and fed on a random schedule will continue to augment and diminish the EOD on a nearly 24 hour rhythm for days or weeks.

Ecophysiology of electric signals

Each EOD gives the signaler a brief image of its surroundings, just as you would get by closing your eyes tightly and taking fast, blinking peeks. Successive EODs allow the fish to build up a more detailed image. In the rapidly changing environment of a turbulent stream or river, higher discharge rates allow the fish to track moving objects in the turbulent currents. Gymnotiform species that inhabit the fastest waters of riffles, rapids, and waterfalls may discharge as fast as 1000-2000 EODs per second. In contrast, species that dwell in ponds or sluggish rivers where life is slower may produce only 2-20 EODs per second. Wave fish select a fundamental frequency and stick to it for hours, days, or even months at a time. To change their discharge frequency by more than a few percent, they must also change the tuning of their electroreceptors to maintain the signal-sensory frequency match without losing sensory acuity during active electrolocation. These changes are possible, but require slow and careful hormonal coordination. Pulse fish, on the other hand, have broadly tuned electroreceptors and readily adjust their discharge rates without incurring a sensory mismatch. Most pulse fish, gymnotiforms and mormyrids alike, discharge at low rates during the day when they are less active, and greatly increase their discharge rates at night, when they need to track moving objects.

Even during the day, electric fish continue to discharge. In the field one frequently sees water snakes, herons, and tail-biting fish species hunting in the same habitats where electric fish hide during daylight hours. An ongoing discharge pattern maintains an early warning system. At the slightest disturbance in the water, even a puff of wind rustling the emergent vegetation in which they hide, the fish increases its discharge rate, thereby increasing the temporal and spatial acuity of its active-electrolocation sense.

Physical factors also affect electric fish ecology. For example, dissolved oxygen limits which electric fish can live where. Wavefish with the highest discharge rates are specialists of well-oxygenated moving waters. Most wavefish cannot survive long in low-oxygen conditions. One exception is *Gymnarchus niloticus*, the sole wave discharging species in Africa. *Gymnarchus* is an obligate air breather, and is emancipated from dissolved oxygen restrictions. Another wavefish that survives low oxygen water is *Eigenmannia virescens*, a Gymnotiform wave species with enlarged gills. Beyond those specialists, pulse fish can better withstand the daily anoxia that typifies floating meadows, and the episodic anoxic conditions that follow flushing of organic material into rivers during flood conditions. Some have speculated that pulse fish are specialists of low oxygen waters, limiting their exposure to predatory fish.

Energetics

Producing a single EOD has no energetic cost because opening ion channels allows sodium and potassium cations to flow down their electrical and chemical gradients. The energetic cost of electric signaling comes from pumping these cations back to the side of the cell membrane where they started. Electrocytes thus use ATP to restore the ionic gradients typical of a polarized cell. For most weakly electric fish, EOD production appears to consume about 2-4% of their energy budgets. But males of some species greatly boost signal power around the time of courtship, so that electric signals may consume as much as 25% of their energy consumption.

Biophysical advantages and limitations of communicating with electric fields

Electric signals have very different physical properties than light or acoustic signals. EODs are not electromagnetic waves like light, radio, or X-rays, but rather are electrostatic fields, such as you would get if you placed a battery in the water: current flows out one end and in the other. Unlike electromagnetic waves, electrostatic fields do not propagate. Electric fish approximate electric dipoles, at least at a distance. The electric field intensity, measured in volts per unit distance (mV/cm), attenuates at the reciprocal of the cube of distance from the dipole center. This sharp attenuation curve contrasts with sound waves, which attenuate through spherical spread at the reciprocal of the square of distance. Thus electric fields are useful for communication only within a few body lengths of the signaler. Active electrolocation is limited by coherence of the image distortion, and thus is useful at no more than half a body length.

Unlike sound, electric fields are not subject to harmonic distortion or reverberation. In the tropical rainy seasons, lightening constitutes the major source of background noise. If a thunderstorm is raging within 100 km, the water is filled with electrostatic noise. Electric fish can overcome the background noise through regular repetition of the EOD (wavefish have mastered this science) or by boosting signal power, the strategy employed by mormyrid pulse fish with irregular EOD rates. An interesting hypothesis is that fish can produce irregular discharge rates to hide their signals in the background noise. Perhaps mormyrids use irregular discharge rates to make themselves less conspicuous to electrosensory catfish. Likewise the electric eel may discharge irregularly to elude detection as it moves in on gymnotiform prey.

Special case of the electric eel

The electric eel (*Electrophorus electricus*) is unique among electric fish as the sole species capable of producing either a low-voltage or a high-voltage discharge. A mature electric eel can protect itself or stun fish prey by delivering a one second burst of EODs peaking at 600 volts with a current of 2 amps. The eel's low-voltage EOD, used for active electrolocation and communication, is a mere 10 volts/cm, still 10-100 times stronger than a typical gymnotiform EOD. Electric eels reach sexual maturity at a length of 1 m, and large individuals have been reported in the upper Amazon approaching 3 m.

When the eel detects its small fish prey it forms its body into the shape of the letter C with the prey situated in the gap. The high voltage discharge immobilizes smaller fish, which immediately go belly-up. The eel reverts to its low voltage EOD as it locates the immobile prey and sucks them down.

Electric eels deliver a high voltage shock at the slightest provocation, a memorable experience for any adventurous zoologist seeking to experience one of the true marvels of the natural world. It seems unlikely that any large predator, such as a caiman or anaconda, would persist in attempts to eat an electric eel. Even a baby electric eel 10 cm long can deliver a painful shock. Like *Gymnarchus niloticus* of Africa (also a big fish) *Electrophorus electricus* is an obligate air breather. As such it lurks near the bottom of shallow, sluggish waters during the day, rising to take a breath every few minutes. Local fishermen and unwary biologists have stepped on resting eels with unpleasant consequences that range from sharp pain to heart fibrillation and drowning.

Other interests in electric signals

Electric fish are excellent animals in which to explore the integration of behavior, neural circuits, neurochemistry, and ion channels. Studies of electrosensory systems have revealed the neural mechanisms that underlie temporal hyperacuity, image processing, background cancelation, parallel processing, and network switching. Studies of electric organs have improved our understanding of ion channels, ion pumps, and evolutionary adaptation of these molecules.

Suggested Reading:

Bullock TH and Heiligenberg W (eds.) (1986) *Electroreception,* New York: Wiley.

Bullock TE, Hopkins CD, Popper AN, Fay FR (eds.) (2005) *Electroreception,* Ithaca, New York: Cornell University Press.

Heiligenberg W (1991) *Neural Nets in Electric Fish* Cambridge, Massachusetts: MIT Press.

Ladich F, Collin SP, Moller P, Kapoor BG (eds.) (2006) *Communication in Fishes*. *V*ol. *2*, Enfield, New Hampshire; Science Publisher, Inc.
Moller P (1995) *Electric fishes history and behavior*. London: Chapman & Hall.
Stoddard PK (2002) Electric signals: predation, sex, and environmental constraints. *Advances in the Study of Behaviour* 31: 201-242, New York: Academic Press.
Stoddard PK and Markham MR (2008) Signal cloaking in electric fish. *Bioscience* 58: 415–442.