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Introduction

Electric Fishes

This article concerns electrical communication in fish, an unusual modality of communication found only in fishes that are capable of both generating and receiving weak electric signals in water. Electrogenesis in fish arose independently in six groups of marine or freshwater fishes (Table 1). Electric organs are derived from modified muscle or nerve cells. Some of these fish are strongly electric and have been known since antiquity; others are weakly electric and went unnoticed until the 1950s. Communication is most highly developed among weakly electric fishes.

Occurrence of Electroreceptors

For electric communication to occur, an electric fish must have the ability to sense electric signals in water. The electric sense was discovered in only 1961 but has since been found among most primitive orders of fishes, even those that do not possess electric organs. There is good evidence for electroreception in lampreys, sharks, rays, sawfishes, chimeras, lobe-finned fishes, and primitive ray-finned fishes including the bichirs, polypteriformes, sturgeons, and paddlefishes. It may have been present in many extinct groups of fishes. However, this special 'sixth sense' does not occur in most species of modern ray-finned fishes (bowfins, gars, and teleosts) except for two separate phylogenetic lineages or clades of teleosts: the catfishes worldwide plus gymnotiforms of South America and the notopterid plus mormyriform fishes from Africa. Although fish in these taxa emit both weak and strong discharges in social contexts, they also do so in isolation, during prey capture and defense. The signals are irregular and difficult to study. Little is known about the social context and behavioral consequences of signals. Most of the information about electric communication comes from studies of gymnotiform and mormyriform fishes (Figures 2 and 3), in which the communication modality is highly complex and well developed.

Dual Functions

Fishes that communicate electrically also use electroreception for detecting objects in the environment, sensed as distortions in the self-generated fields from their own organs. The dual functions of 'electrolocation' and communication help explain the adaptive significance of weak electric organs, which must have been intermediate stages in the evolution of more-powerful electric organs used for prey capture and defense.

Electric Signal Production and Signal Transmission

Electric Organs

Electric organs (Table 1 and Figure 2) are specialized for generating electric currents outside the animal's body. They are usually located in the fish's tail, which prevents current shunting by the body tissues and maximizes signal range. Electric organs are composed...
Table 1  The six known groups of electric fishes, arranged taxonomically

<table>
<thead>
<tr>
<th>Electric fishes</th>
<th>Picture</th>
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<tbody>
<tr>
<td><em>Rajiformes</em> (electric skates): marine, worldwide <em>Rajidae</em> (weak, pulse</td>
<td><img src="image1" alt="Image" /></td>
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<tr>
<td>discharges, ampullary receptors) (14 genera, 200 species) including <em>Raja</em>,</td>
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<tr>
<td>all with electric organs</td>
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<tr>
<td><em>Torpediniformes</em> (electric rays): marine, worldwide <em>Narcinidae</em> (strong,</td>
<td><img src="image2" alt="Image" /></td>
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<tr>
<td>pulse discharges, ampullary receptors) (9 genera, 24 species) including</td>
<td></td>
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<tr>
<td><em>Narcine</em></td>
<td></td>
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<tr>
<td><em>Torpedinidae</em> (strong, pulse discharges, ampullary receptors) (2 genera,</td>
<td></td>
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<tr>
<td>22 species) <em>Hypnos, Torpedo</em></td>
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<tr>
<td><em>Mormyriformes</em> (African electric fishes): sub-Saharan Africa and Nile River</td>
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<tr>
<td><em>Gymnarchidae</em> (weak, wave discharges, ampullary ND tuberous</td>
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<tr>
<td>electroreceptors) (1 genus, 1 species) <em>Gymnarchus</em></td>
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<tr>
<td><em>Mormyridae</em> (weak, pulse discharges, ampullary and tuberous</td>
<td><img src="image4" alt="Image" /></td>
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<tr>
<td>electroreceptors)</td>
<td></td>
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<tr>
<td><em>Petrocephalinae</em> (1 genus, 30 species) <em>Petrocephalus</em></td>
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<tr>
<td><em>Mormyrinae</em> (16 genera, 177 species) *Boulengeromyrus, Brienomyrus,</td>
<td><img src="image5" alt="Image" /></td>
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<tr>
<td>Campylomormyrus, Gymnomormyrus, Gnathonemus, Heteromormyrus,</td>
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<tr>
<td>Hippopotamyrus, Hyperopisus, Isichthys, Ivinomyrus, Marcusenius,</td>
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<tr>
<td>Mormyrops, Mormyrus, Paramormyrrops, Pollimyrus, Stomatorhinus</td>
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<tr>
<td><em>Gymnotiformes</em> (neotropical electric fishes): South and Central America</td>
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<tr>
<td><em>Apteronotidae</em> (weak, wave discharges, ampullary and tuberous</td>
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<tr>
<td>electroreceptors) (15 genera, 54 species): *Adontosternarchus, Apteronotus,</td>
<td></td>
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<tr>
<td>Compasaraia, Magosternarchus, Megadontognathus, Orthosternarchus,</td>
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<tr>
<td>Parapteronotus, Pariosternarchus, Platyurosternarchus, Porotergus,</td>
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<tr>
<td>Sternarchella, Sternarchogiton, Sternarchorhamphus, Sternarchorhynchus,</td>
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<td>Tembeassu</td>
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<tr>
<td><em>Gymnotidae</em> (strong, weak, pulse discharges, ampullary and tuberous</td>
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<td>electroreceptors) (2 genera, 33 species): <em>Electrophorus, Gymnotus</em></td>
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<tr>
<td><em>Hypopomidae</em> (weak, pulse discharges, ampullary and tuberous</td>
<td><img src="image8" alt="Image" /></td>
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<td>electroreceptors) (7 genera, 16 species): *Brachyhypopomus, Hypopomus,</td>
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<tr>
<td>Hypopygus, Microsternarchus, Steatogenys, Stegostenops</td>
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<tr>
<td><em>Rhamphichthyidae</em> (weak, pulse discharges, ampullary and tuberous</td>
<td><img src="image9" alt="Image" /></td>
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<tr>
<td>electroreceptors) (3 genera, 15 species): *Iracema, Gymnorhamphichthys,</td>
<td></td>
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<tr>
<td>Rhamphichthys*</td>
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<tr>
<td><em>Sternopygidae</em> (weak, wave discharges, ampullary and tuberous</td>
<td><img src="image10" alt="Image" /></td>
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<tr>
<td>electroreceptors) (5 genera, 30 species): *Archolaemus, Distocyclus,</td>
<td></td>
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<tr>
<td>Eigenmannia, Rhabdolicaps, Sternopygus</td>
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Continued
of cells called electrocytes, derived from nerve or muscle. Weak or strong discharges are produced by the synchronized action potentials from hundreds or thousands of cells acting in series and in parallel. The discharge is initiated in the command nucleus in the medulla and transmitted via a medullary relay nucleus to the electromotor nucleus in the spinal cord. Electromotor neurons innervate the individual electrocytes in the electric organ. For Apteronotid fishes, the electric organ is neural in origin and is simply composed of the spinal electromotor neurons which are anatomically specialized. The discharges of individual electrocytes summate when they are arranged in series, and the currents from individual cells summate when they are arranged in parallel. The voltage of the electric eel, *Electrophorus electricus*, can be an astonishing 500–600 V at the peak of the pulse discharge because of the linear summation of thousands of electrocytes in series. Most of the gymnotiforms and mormyromorphs generate only weak discharges of about 10 V – sufficient for short-range communication and active electrolocation but not for prey capture or defense. The discharges of a few notable large mormyrids such as *Mormyrus* and *Mormyrops* can be felt by humans, but most cannot.

The discharges were unknown until 1951, when Hans Lissmann from Cambridge University, using electronic amplifiers, discovered continuous 300–500 Hz wavelike discharges emanating from the tail of *Gymnarchus niloticus*, a mormyriform (*Figure 2*). Several years later, Lissmann demonstrated that this fish could electrolocate objects in its environment if the objects differed in conductivity from the surrounding water. By the 1960s, MVL Bennett, H Grundfest, C Coates, A Fessard, and others had documented EOD diversity in fishes, and T Szabo and TH Bullock and colleagues had made the first electrophysiological recordings from electroreceptors in weakly electric fish. By the 1970s, P Black-Cleworth, P Moller, B Kramer, W Harder, C Hopkins, M Westby, J Bastian, C Bell, TH Bullock, W Heiligenberg, and others had provided strong evidence for the existence of electric communication in weakly electric fishes. Today, researchers working in Africa and South America and in laboratories continue to search for new species, novel signals, and distinctive patterns and functions for electric communication. Neurobiologists have discovered novel mechanisms for electrogenesis and its control, as well as important general mechanisms of information processing and sensory–motor

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**Table 1** Continued

<table>
<thead>
<tr>
<th>Electric fishes</th>
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<tr>
<td>Siluriformes (catfishes): Africa</td>
<td><img src="https://example.com/table1_image1" alt="Picture" /></td>
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<tr>
<td>Malapteruridae (strong, pulse discharges, ampullary receptors) (two genera, 18 species) <em>Malapterurus, Paradoxoglanis</em></td>
<td><img src="https://example.com/table1_image2" alt="Picture" /></td>
</tr>
<tr>
<td>Mochokidae (weak, pulse discharges, ampullary receptors; one genus known to be weakly electric, at least three species with weak electric discharges) <em>Synodontis</em></td>
<td><img src="https://example.com/table1_image3" alt="Picture" /></td>
</tr>
<tr>
<td>Claridae (weak, pulse discharges, ampullary receptors; one genus known to be weakly electric, at least one species) <em>Clarias</em></td>
<td><img src="https://example.com/table1_image4" alt="Picture" /></td>
</tr>
<tr>
<td>Perciformes (Stargazers): marine</td>
<td><img src="https://example.com/table1_image5" alt="Picture" /></td>
</tr>
<tr>
<td>Uranoscopidae (strong, pulse discharges, electroreception absent; two genera, unknown number of species) <em>Astroscopus</em> (three species), <em>Uranoscopus</em></td>
<td><img src="https://example.com/table1_image6" alt="Picture" /></td>
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</table>

Each of the species in this list is capable of either weak or strong electrogenesis using specialized electric organs (indicated in red). Some of the electrogenic species have weak electric discharges, and others have strong electric discharges, as indicated. Weak, weak electric organ discharge (EOD); strong, strong EOD; wave, wave-discharging species; pulse, pulse-discharging species.
integration. Although unusual, electric fish have become an important model system in neuroethology.

**The Nature of Electric Signals**

There are two components of the electric discharge signals of fish (Figure 4). The first is the stereotyped waveform of the electric organ discharge (EOD), which is fixed for an individual but varies between individuals, genders, and species. The second is the sequence of pulse intervals (SPI), which is generated by the pacemaker or command nucleus in the medulla. Complex neural networks in the midbrain and thalamus modulate activity in the command nucleus, producing the patterns used for communication displays. Both EODs and SPIs are important for this function. EODs are especially important for tonic advertisement of identity, and SPIs are key elements of threats, alarm signals, courtship patterns, and signals of submission. Some patterns and processes that generate them are summarized below.
Signal Transmission: The Geometry of Electric Fields in a Volume Conductor

EODs are transient pulses with durations ranging from 100 μs to 20 ms. They produce nonpropagating electrostatic fields, not propagating electromagnetic waves. This feature contrasts with acoustic communication, in which signals propagate as waves with a finite velocity, generating echoes and reverberations. Electric signals are transmitted instantaneously, with no echoes. Geometric spreading in electogenesis also differs from sound. Acoustic signal intensity decreases according to the inverse square of distance from the source; electric field magnitude decreases according to the inverse cube of distance.

Figure 3 shows isopotential contours surrounding the gymnotiform Eigenmannia at one phase of its EOD cycle. The potential reverses sign at the midplane between the two poles of the electric organ. The electric field, which is computed as the vector derivative of potential, follows a circular arc from positive to negative pole, declining in magnitude in proportion to the inverse cube of distance from the dipole center.

With movable mutielectrode arrays, EOD fields can now be digitally mapped in both time and space. Eigenmannia produces a very simple electric field which closely approximates an oscillating dipole with one pole located at the midpoint of the body, the other at the tip of the tail (Figure 6). The location of the
poles remains constant throughout the EOD cycle. Other species of gymnotiform fishes are spatially and temporally more complex. *Apterontus leptorhynchus* generates an electric dipole that appears to propagate from the head to tail and then back again during each cycle of the EOD. The electric field vector recorded at a distance rotates once per EOD cycle. The pulse-discharging hypopomid, *Brachyhypopomus*, has a complex multipole EOD with one dipole located in the head and a second in the tail. This pattern is also seen in several species of *Gymnotus* in which the more anterior parts of the organ contain columns of electrocytes with novel innervation that anticipate the firing of electrocytes in the rest of the organ by a fraction of a millisecond. Other pulse-discharging gymnotiforms have ‘accessory’ electric organs in the head in addition to a main electric organ in the tail. Both organs fire together, but slightly out of phase. One remarkable Hypomomid, *Steatogenys elegans*, has two accessory electric organs composed of parallel columns of approximately 100 electrocytes in superficial grooves on the underside of the head. The communicative significance of accessory organs and the spatial patterns that result is unknown.

**Active Space**

The active space of a communication signal is the volume of space within which a signal evokes a response from a receiver. The following factors determine its size: the amplitude of the signal at the source, the rate of signal decrease due to geometric spreading, the amplitude of masking or background noise in the environment, and the sensitivity of the receiver. Empirical measurements of the active space surrounding a 10–20 cm weakly electric gymnotiform or mormyrid reveal an ellipsoidal volume approximately 1 m in diameter. Electric signaling is limited to short range because of the rapid falloff of signal amplitude with distance. For an electric fish to double the distance of communication, it must increase the magnitude of the discharge at the source eightfold. This brings high costs to communication and places limits on how far an electric fish can signal. Many species of electric fish exhibit energy-conserving adaptations for signaling, including the slowed pulse repetition rates, reduced amplitude, and shortened pulse waveforms during the daytime, when the fish are inactive. Males also reduce their seasonally elongated pulse widths during the nonbreeding season, when they are not displaying to attract females, and they turn their discharges off when hiding. Some fish even maximize the external signal energy by matching the impedance of the electric organ to that of the environment, discussed next.

**The Economy of Impedance Matching**

The active space of communication is greatly influenced by water resistivity, as might be expected from the Thévenin equivalence theorem, which states that any electrical source can be modeled as an ideal voltage source in series with a fixed internal resistance. In water, the electric organ is under load, so the external resistance which is in series with the internal resistance experiences a voltage drop proportional to resistance. For a fish in high-resistivity water, the external voltage drop will consequently be higher.
than the internal, so that most of the signal is external, not across the skin. In low-resistivity water, most of the voltage drop will be across the skin, not the environment. A fish adapted to high-resistivity water will experience a serious reduction in active space if it is transferred to water with low resistivity.

Some species of electric fish in the gymnotiform family Hypopomidae appear to be adapted to a narrow range of water resistivity (Figure 7). Those found in relatively low-resistivity (high conductivity) water have short but thick caudal filaments containing the electric organ, with five or more longitudinal columns of electrocytes in parallel. These organs have low internal resistance and are good for generating current, even in low-resistance environments. Fish from high-resistivity (low conductivity) water have extremely elongated caudal filaments containing only three longitudinal columns in parallel. These organs have higher internal resistance but also higher voltage capability, and both are adaptations for generating stronger signals in high-resistivity water. Fish from intermediate resistivity water have intermediate-length caudal filaments containing an intermediate number of columns in parallel. These hypopomids thus appear to have evolved electric organs that are impedance matched to their external environment. Since impedance matching appears to involve rigid restructuring of electric organs, a most interesting consequence may be that these fish might confront invisible barriers when they attempt to disperse into river systems that differ in water resistivity.

Figure 5 Isopotential lines (black) and current lines (color) at the peak of the electric organ discharge (EOD) of an Eigenmannia virescens seen from above and recorded in the midhorizontal plane of the fish. The lower insert shows 1.5 EOD cycles from the head region with a peak voltage amplitude, A, measured relative to an electrode located at infinity. Values of the isopotential lines indicated in the figure are in millivolts. Adapted from Heiligenberg W (1977) Principles of electrolocation and jamming avoidance in electric fish: A neuroethological approach. In: Braitenberg V (ed.) Studies in Brain Function, pp. 1–85. New York: Springer.

Figure 6 The spatial geometry of the electric organ discharge (EOD) potential from the gymnotiform fish, Eigenmannia virescens, as seen from above (above) and from the side (below) as measured using a robotic electrode array. The scalar magnitude of the voltage at one phase of the EOD cycle (shown as inset) is plotted as color contours. The spatial pattern of potential resembles that from an electric dipole. One pole is located at the tip of the tail, the other approximately a third of the body length from the end of the tail. The EOD is a wavelike quasi-sinusoidal discharge. The anterior pole goes positive for approximately 1.5 ms, then negative for the remainder of the EOD. The electric field is computed as the gradient of the potential. Current lines run perpendicular to the isopotential lines shown here. From Assad C, Rasnow B, Stoddard PK, and Bower JM (1998) The electric organ discharges of the gymnotiform fishes: II. Eigenmannia. Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology 183(4): 419–432.

Encyclopedia of Neuroscience (2009), vol. 3, pp. 813-831
conductivity from that to which their electric organs are most efficiently matched.

**Nonpropagated Signals**

Because electric communication signals are nonpropagating electrostatic fields, signals are unaffected by the echoes and reverberations that corrupt acoustic signals during transit. Electric receivers, therefore, may be able to make use of precisely encoded properties of signals, including zero crossing times, details in waveforms on a submillisecond timescale, signal polarity, and minor inflection points on signals that might be altered in transit if propagated as a wave. Electric fish exhibit remarkable sensory specializations for encoding, preserving, and recoding the temporal features of communication signals, often with a precision on the order of microseconds.

Since there is no delay to an electric communication signal, receivers will not be able to use signal arrival times at different parts of the body surface to localize electric sources. Nevertheless, research has shown that electric fish can align their body axis parallel to the local electric field vector as an alternative strategy for finding signal sources even if the pathway leading there might be curved.

**Noise**

The greatest source of environmental electrical noise in the signal bandwidth of electric fish comes from distant lightning activity, which propagates globally over hundreds or thousands of kilometers as electromagnetic waves. The signature clicks, ‘chirps’, ‘tweeks’, and other disturbances from lightning can be recorded continuously using dipole electrodes immersed in water. Although there is no evidence that electric fish respond to this noise, quantitative measurements suggest that its magnitude in different environments correlates with the sensory threshold of electroreceptors of the inhabitants. In marine environments, where the magnitude of noise from lightning is 0.01 that found in freshwater, electroreceptor thresholds tend to be 100 times more sensitive than those of freshwater fish. Many resting mormyrid seem to take advantage of this noise, blending into it by discharging at irregular intervals when they are alone and standing out with more regular intervals of discharge in the presence of conspecifics.

**Signal Reception**

Electric communication depends on sensitive lateral-line-derived electroreceptors located on the head and trunk of certain fishes. These sense organs direct the flow of current through low-resistance canals and through loosely layered patches of epithelial cells to a sensory epithelium where specialized transducer cells carrying voltage-gated ion channels in their cell membranes convert outside electrical stimulation into internal neural responses. Receptor organs filter the stimulus waveform, impart directionality to signal reception, adjust the sensitivity of the receptor, and
ensure that the sensory epithelium is ideally positioned for maximal sensitivity.

Electrosensory cells make synaptic contacts with afferent nerve fibers which project to the electrosensory lateral-line lobes in the medulla via the acousticolateralis or VIIIth nerves. Ampullary receptors are found in every electroreceptive species; tuberous receptors are unique to gymnotiforms and mormyriiforms. Receptors resembling tuberous organs were once reported from a species of blind catfish, *Pseudocetopsis*, from South America, but this has not been confirmed physiologically. Figure 8 shows the morphology of ampullary and tuberous electroreceptors in mormyrids, *Gymnarchus*, and gymnotids.

**Ampullary Electroreceptors**

Ampullary receptors have a sensory epithelium at the base of a blind, mucus-filled, low-resistance canal leading from the external environment. Receptor cells are sensitive to electric stimuli in the range of 0.05–50 Hz. The receptor cells contact tonically active afferent nerve fibers and modulate their firing rate upward or downward depending on stimulus polarity.

Ampullary receptors typically function in the passive electrolocation of predators and prey. For example, sharks and rays detect fish buried in sand by sensing the weak electric fields of a fraction of 1 μV cm⁻¹. In tanks they dig up buried electrodes playing electric potentials from prey. Male round stingrays

![Figure 8](image-url)

**Figure 8** Anatomy of ampullary and tuberous electroreceptors in the freshwater teleosts: Gymnotiformes, Mormyrids, and *Gymnarchus*. Ampullary receptors have a highly conducting jelly-filled canal leading from the receptor epithelium at the base of the ampoule to the skin surface; tuberous receptors have a loose plug of epithelial cells over the receptor organ. Mormyromasts have two receptor subclasses, RC₁ and RC₂, which are innervated by separate nerves: two nerve axons innervate RC₁ receptors (also called Type A receptors); one axon innervates RC₂ receptors (Type B). Tuberous receptors function in amplitude coding or in time coding. RC, receptor cells; n, nerve axon; b.m., basement membrane. Adapted from Szabo T (1965) Sense organs of the lateral line system in some electric fish of the Gymnotidae, Gymnarchidae, and Mormyridae. *Journal of Morphology* 117: 229–250 and Hopkins CD (1999) Design features for electric communication. *Journal of Experimental Biology* 202(10): 1217–1228.
(Urolophus) use ampullary receptors to find females which produce low-frequency electric signals during ventilation. Electric rays, skates, and catfishes use ampullary receptors to sense conspecific EODs.

In addition to prey sensing, wave gymnotiforms use ampullary organs for sensing brief discharge interruptions (see below). A resting-wave EOD lacks energy in the range of 0.05–50 Hz and will not stimulate ampullary receptors, but during discharge cessations, a residual head-negative offset strongly stimulates them.

**Tuberous Electroreceptors**

Tuberous organs have an interepidermal cavity lined with sensory-receptor cells but lack an open canal to the exterior. Instead, a plug of loose epithelial cells covers the receptor and behaves like a series capacitor to block direct currents. Tuberous organs are sensitive to stimuli in the range of 100–10,000 Hz and are used for communication and for active electrolocation of objects. They are electrically tuned to the most prominent frequencies of the species-typical EOD (Figure 9). Mormyrid fishes have two types of tuberous organs: Knollenorgans, which are used for communication, and mormyromasts, which are used for active electrolocation (Figures 8 and 9). Gymnotiforms also have two physiological types of tuberous organs (Figure 8), but each is used for both communication and electrolocation. One receptor type is specialized for detecting stimulus amplitude; the other is specialized for timing.

Three lines of evidence suggest that Knollenorgan electroreceptors are used exclusively for communication. First, they have low thresholds, so they are ideally suited for detecting the weak signals from distant fishes; second, the spikes from Knollenorgan afferents are inhibited, or ‘blanked,’ in the hindbrain by neurons carrying a corollary discharge of the EOD command so that a mormyrid never ‘hears’ its own EOD on the Knollenorgan pathway; and third, lesions to the nucleus exteralateralis in the midbrain, which receives all Knollenorgan receptor inputs, blocks responses to all electric communication signals while having no effect on a fish’s ability to electrolocate.

Tuberous receptors are electrically tuned to the peak of the power spectrum of the species-specific EOD waveform both in gymnotiforms and mormyrid fishes (Figure 9).

**Temporal Dimensions of Social Communication Signals**

Electric signals have both tonic features, which are invariant for an individual over a period of days, months, or years, and phasic features, which change from moment to moment, depending on social conditions.

**Tonic Signals in Electric Communication**

An individual’s signature EOD, typically a pulse waveform lasting only 1 ms or more, is one example of a tonic signal. It is typically invariant for days or months and serves to advertise the species, sex, and even individual identity of signalers. The EODs from different species diverge from one another (Figure 10). Pulse duration, number of phases or peaks, order polarity of peaks, and characteristic inflection points all contribute to a signaler’s signature waveform.

EOD waveforms have communicative significance. Males will court electrodes playing female EODs while ignoring the same electrodes playing male EODs or heterospecific female EODs. They will ignore female EODs played backwards, as well as phase-shifted EODs (Figure 11), suggesting that the precise form of the EOD is important, not the spectrum of the signal. In some genera, such as Brienomyrus, Campylomormyrus, Marcusenius, and Mormyrops,
EOD waveforms are highly divergent within close relatives (congeners) living in sympatry. In some species of *Mormyrops* and *Brienomyrus* from Central Africa, EODs may even be polymorphic, exhibiting more than one stable EOD type within a population.

Of course the EOD waveform is also used for active electrolocation of objects, so its properties may be adapted to navigation as well as to advertisement and identification. Consider, for example, that many mormyrid fish sense the electrical capacitance of objects, and the duration of the EOD waveform duration sets the range of capacitances over which they are sensitive. By adopting an EOD waveform with a short rather than a long duration, a fish may be better at detecting low-capacitance objects. Consider also that most mormyriforms and gymnarchiforms produce pulse discharges in which positive and negative phases of the EOD are balanced so that there is very little signal energy below 10 Hz. This appears to be an important adaptation for avoiding exposure to predatory catfishes, which have ampullary electroreceptors sensitive to low-frequency or DC components of signals. For electrolocation, which must function continuously, electric fish must avoid signals with DC components, but for communication displays which are infrequent, DC may be used. In several species of Hypopomidae (pulse-discharging gymnarchiforms), juvenile and female EODs are balanced and have little energy at low-frequency while breeding males have seasonal EODs with stronger DC components. Males of the gymnotid *Brachyhypopomus pinnicaudatus* modulate their EOD waveform over 24 h so that DC components of the discharge are present only at night, when the fish are active, and only during the breeding season. A similar pattern is seen in mormyrids. In *Marcusenius macrolepidotus* from South Africa, males have a stronger DC component to their discharge than females do, and catfish predators

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**Figure 10** Pulse-discharging species of electric fishes in the families Mormyridae, Gymnotidae, and Hypopomidae all produce electric discharges which have a low duty cycle and variable intervals. Wave-discharging species in the families Apterontotidae, Sternopygidae, and Gymarchidae produce quasi-sinusoidal discharges with high duty cycle and extremely regular interpulse intervals. The waveform of the discharge is shown to the left in each case, and the amplitude spectrum of the discharge is shown to the right. From Heiligenberg W (1977) Principles of electrolocation and jamming avoidance in electric fish: A neuroethological approach. In: Braintenberg V (ed.) Studies in Brain Function, pp. 1–85. New York: Springer.
and pattern of innervation of electrocytes within the electric organ; and to the diversity of accessory electric organs in the fish. Much of this diversity is understood at a gross anatomical level but has yet to be fully explored at the molecular level. This is an area of active research that will undoubtedly reveal interesting patterns of evolution, especially within species flocks which show a large diversity of EOD waveforms.

Figure 12 shows variation in anatomy of electrocytes of selected species of mormyriforms arranged on a cladogram which is derived from analysis of mitochondrial and nuclear DNA sequences. Superposition of the pattern of electrocyte morphology on the phylogenetic tree gives insight into the evolution of the electric organs. Complex EOD waveforms emerge in the family Mormyridae very early with the evolution of penetrating stalked electrocytes. Reversions to nonpenetrating electrocytes with simpler EOD waveforms occur frequently. There are also cases in which electrocyte innervation is reversed anterior for posterior and others in which stalks are doubly penetrating electrocytes. All this diversity illustrates how signal diversity parallels species diversity in this remarkable radiation (Figure 12).

A second component to tonic diversity arises from the firing pattern of the pacemaker or command nucleus in the medulla. Wave discharges differ from pulse discharges in both the duty cycle of the discharge waveform and the variance in interpulse intervals. Wave discharges have a high duty cycle and low interval variance; pulse discharges have a low duty cycle and a high interval variance. Figure 10 shows wave versus pulse discharges of Gymnotiforms and Mormyrids.

Wave or pulse discharges vary by taxonomic lineage. For example, all the gymnotiform species in the families Apterontidae and Sternopygidae have wave discharges (Figure 10), whereas all others have pulse discharges. Gymnarchus niloticus has a wave discharge, but all other mormyriforms have pulse discharges (Figures 10 and 13). Wave discharges are a derived character in gymnotiform signal evolution; only the Apterontidae and Sternopygidae produce waves. It is unknown whether the common ancestor of Gymnarchidae (wave) and Mormyridae (pulse) was pulse or wave.

The average frequency of a pulse or wave discharge is another important tonic signal. It is controlled in the pacemaker in the medulla. Discharge frequency varies between species and sometimes between sexes. The first documented case of a sex difference in electric signaling was the firing rate of the gymnotiform wave species, Sternoptygus macrurus. Adult males discharge in the range of 50–90 Hz, and females discharge in the range of 100–150 Hz (Figure 14(a)). This tonic feature has communicative significance, as shown by playing pure sine waves to male Sternoptygus.

Figure 11 shows a gender difference in the electric organ discharge (EOD) waveform, the pulse duration for the male (m) being nearly double that for the female (f). During the breeding season, which starts with the seasonal rains, males court passing females by producing bursts of EODs at high frequency, making stereotyped displays called ‘rasps.’ (b) In experiments, males produce rasps in response to digitized EOD waveforms of females, as shown in the histograms of responses in (c). If the female EOD is phase-shifted by 45°, 60°, or 90° or if the EOD is reversed (played backwards in time), the male shows reduced responsiveness, but if the female EOD is phase shifted by 180°, responses are as strong as for the normal female EOD. This is not surprising given that a 180° phase shift is equivalent to inversion of polarity of the waveform, which would happen if the a real female were to turn around in space. These experiments strongly suggest that males attend to the temporal properties of EOD waveforms, not the amplitude spectral characteristics, which are all identical. In addition to courting digitized female EODs, males will also court a highly simplified square wave as long as the duration of the square wave is 0.5 ms, a close approximation to the duration of the head-positive phase of the female EOD (not shown). This can be explained by showing that female EODs and 0.5 ms square waves evoke from Knollenorgan electroreceptors the same neural code based on spike timing. (c) Reprinted from Hopkins CD and Bass AH (1981) Temporal coding of species recognition signals in an electric fish. Science 212: 85–87, with permission from AAAS.
Figure 12  A hypothesis for the evolution of electrogenesis among mormyroid fishes of Africa based on a phylogenetic tree of Gymnarchus and 31 species of mormyrids. The tree, which is derived from mitochondrial and nuclear DNA sequence data, is largely consistent with classifications based on osteology and other morphological characters. Taxa sampled are shown as outlines to the right. The structure of electrocytes in the electric organs is shown to the left, color coded. Type S electrocytes are ‘stalkless.’ They are found in adult Gymnarchus niloticus and in larval stages of all known mormyrids. The innervated faces of these electrocytes are nonspecialized, lacking the ‘stalk’ system which characterizes electrocytes in adult organs of mormyrids. Type S electrocytes are innervated on the posterior face (post.), which fires an action potential that produces a head-positive monophasic electric organ discharge (EOD). The anterior face (ant.) is electrically unexcitable. Gymnarchus has a wave type EOD in which the monophasic potentials are superimposed on a head-negative DC potential. All the fishes in the family Mormyridae have electrocytes with ‘stalks.’ The electrocytes are located in an adult electric organ in the caudal peduncle. All the species in the genus Petrocephalus, toward the base of the tree, have stalked electrocytes in which the stalks are ‘nonpenetrating’ and are innervated on the posterior side (type NPp). Many of the Mormyridae have electrocytes with type Pa ‘penetrating’ stalks in which an elaborate stalk system, innervated on the anterior side, penetrates through the electrocyte to fuse with the posterior face. Action potentials are generated in the stalk, in the posterior face, and in the anterior face. The EOD is typically triphasic. Penetrating stalked electrocytes appear first in the genus Myomurus at the base of the phylogenetic tree. Penetrating stalked electrocytes appear throughout the family tree, although there are multiple paedomorphic reversals to nonpenetrating stalked electrocytes. Two additional morphologies are known: doubly penetrating with nonpenetrating stalked electrocytes (DPNP) and penetrating stalks with posterior innervation (Pp). These occur in isolated lineages. Tracing the evolution of electrocyte diversity gives insight into the origin of signal complexity in this group of fishes. In this reconstruction, arrows point to the hypothesized origin of a novel electrocyte morphology. Representative EOD waveforms accompany each type of electrocyte. Alternating color bars to the left of a clade indicate that the ancestral type of penetrating stalk electrocyte is equivocal. From Sullivan JP, Lavoué S, and Hopkins CD (2000) Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. Journal of Experimental Biology 203(4): 665–683.
at night during their breeding season in small creeks in Guyana. The males responded with electrical courtship songs (Figure 14(b)) whenever the stimulus frequencies were in the females’ range of 130–150 Hz (see Figure 14(c)). The males did not sing to electrodes playing sine waves in the male range or to signals in the ranges of two other sympatric wave species, *Eigenmannia* and *Apteronotus* (Figure 14(c)).
Figure 14  Sex differences in the discharge frequency of *Sternopygus macrurus* observed under field conditions in Guyana. (a) A plot of discharge frequency versus standard length for males (squares), females (triangles), and juveniles (circles) shows that sex differences emerge in individuals longer than 300 mm. The inset shows the fish's outline and a sample of the electric organ discharge waveform. From Hopkins CD (1974) Electric communication in the reproductive behavior of *Sternopygus macrurus* (Gymnotoidei). *Zeitschrift für Tierpsychologie* 35: 518–535. (b) Sound spectrogram of a male *Sternopygus* producing electrical courtship song in presence of a female. The male’s discharge is a wave discharge in the 50–70 Hz frequency range. During courtship, males produce ‘rises’ in discharge frequency and ‘interruptions’ in the discharge song. (c) When presented with an electrical sine wave stimulus, delivered via electrodes placed in the water near the fish, the male *Sternopygus* gives courtship rises and interruptions if the frequency of the sine wave is in the 130–141 Hz range of a female *Sternopygus*. The male does not court sine wave frequencies in the 55–72 Hz range typical of other males, nor in the 450–550 Hz range typical of *Eigenmannia*, nor in the 900–1010 Hz range typical of *Apteronotus*, two other species that are sympatric to *Sternopygus*. (C) Reprinted from Hopkins CD (1972) Sex differences in electric signaling in an electric fish. *Science* 176: 1035–1037, with permission from AAAS.
Phasic Signals

Phasic signals vary rapidly in response to changes in the social environment, typically over a period of seconds or minutes. Phasic signals are produced by modulating the firing rate of the command or pacemaker nucleus in the medulla or by interrupting or silencing the discharge in the pacemaker or in the descending neural pathway from the command nucleus. Pulse and wave fish both produce two types of phasic signals: frequency modulations and discharge interruptions. Frequency modulations are either upward or downward shifts in the pacemaker frequency, lasting seconds to minutes, and consist of small shifts in frequency (long rises, low-frequency modulations, warbles, and jamming avoidance responses) or large shifts in rate (sudden increases in frequency, followed by decrease, ‘chirps,’ ‘rasps,’ ‘scallops,’ ‘accelerations,’ and a variety of other types of pulse bursts). Discharge interruptions are either short cessations in the discharge, lasting less than 0.5 s, or long-lasting periods of silence. All these phasic signals contrast with the constant rate of the tonic discharge.

Figure 14(b), showing the courtship singing of a male *Sternopygus macrurus*, illustrates both types of signals. There are short interruptions in the 50–90 Hz wave discharge, lasting less than 0.5 s, and there are brief modulations in the fundamental frequency upward by as much as 50 Hz above base rate. Interruptions and frequency modulations make the complex patterns of song, which may continue for hours at night during the breeding season.

There are striking parallels in the phasic displays of *Gymnarchus* and *Eigenmannia*, which independently evolved wave discharges in the range of 300–500 Hz on separate continents (Figure 15). Both produce short interruptions during attacks, approaches, head butts, and other aggressive acts. These acts are most common from dominant fish. They are rare from subordinates.

They both also produce subtle frequency modulations as displays of submission. Subordinate *Eigenmannia* produce long rises, which are elevations in frequency in the range of 5–10 Hz, when being attacked (Figure 15), and subordinate *Gymnarchus* produce similar displays if attacked, but the frequency decreases by 5–10 Hz rather than increasing (Figure 15). Subordinate *Gymnarchus* turn their discharges off altogether for many minutes or hours when attacked. The similarity in both form and function of these displays is striking, considering their independent evolution in Africa and South America.

Pulse fish also produce phasic displays, as illustrated in Figures 11 and 16, and these can be evoked by playback of the appropriate stimulus. Figure 11

Figure 15  Sound spectrograms comparing the communication displays of *Eigenmannia virescens* from South America with those of *Gymnarchus niloticus* from Africa. Both species have wave discharges in the same range (300–500 Hz), and both produce discharge interruptions as aggressive threat displays (solid arrows) and frequency modulations (dashed arrows) as signals of submission. The sound spectrograms on the left are on an expanded timescale and broad bandwidth so that the rapid temporal features of the displays may be seen. The spectrograms on the right have a compressed timescale and narrow bandwidth to better visualize the small but slow changes in frequency over time. There are two fish in each interaction; the lower-frequency fish is labeled F1, the higher, F2. Fundamental and higher harmonics are clearly evident for fish 1 on left. Adapted from Hopkins CD (1977) Electric communication. In: Seboek TA (ed.) *How Animals Communicate*, pp. 263–289. Bloomington: Indiana University Press.
shows the ‘rasp’ display from a pulse-discharging mormyrid. The displays are strong, sudden bursts of pulses, up to 100 s⁻¹, lasting 200–400 ms. Males make these high-frequency bursts when courting females.

Some phasic displays in mormyrids consist of ‘regularization’ of the irregular tonic discharges. Female Pollimyrus adspersus regularize their discharge at low rates when entering a male’s territory for spawning. This signal appears to indicate that the female is ready to spawn, and in response, males allow the females to enter their territory without attacking them.

**Jamming Avoidance Responses (JAR)**

Several species of electric fish which electrolocate objects in their environment have evolved behavioral

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**Figure 16** Two types of temporal displays, ‘interruptions’ and ‘frequency modulations,’ produced by pulse-discharging gymnotiforms in the family Hypopomidae (above) and Mormyridae (below) as illustrated by waveforms and pulse rate plots. The gymnotiform Brachyhypopomus brevirostris produces discharge interruptions by turning its discharge off for brief or extended periods. Shown here are two types: one (a) in which the discharge is turned off suddenly without a decrease in pacemaker frequency, and the other (b) preceded by a frequency drop. Similar patterns are seen for mormyrids in the genus Brienomyrus (c) and (d). In (c), pulse intervals are plotted as a function of time; in (d), pulse rate is plotted against time. During agonistic behavior, a fish may turn its discharge off for short periods (less than 1–2s) as an aggressive threat. During courtship, males may turn their discharges off for several seconds, in alternation with rasp displays. Cessations contrast with the regular resting discharge intervals of 250–500 ms. Both groups of pulse fish also modulate the frequency of their discharge. (e), (f) Brachyhypopomus also produces frequency drops, frequency rises, and ‘chirps’ or ‘decrement bursts.’ Chirps are male courtship signals. Brienomyrus brachyistius (g)–(i) produces accelerations, scallops, and rasps as communication displays, with the rasp display used for male courtship calling. (a, b, e, f) From Kawasaki M and Heiligenberg W (1988) Distinct mechanisms of modulation in a neuronal oscillator generate different social signals in the electric fish Hypopomus. Journal of Comparative Physiology A 165: 731–741. (g, h, i) From Carlson BA and Hopkins CE (2004) Central control of electric signaling behavior in the mormyrid Brienomyrus brachyistius: Segregation of behavior-specific inputs and the role of modifiable recurrent inhibition. Journal of Experimental Biology 207: 1073–1084.
strategies for avoidance of the jamming effects of EODs from other fish. These complex reflex-like responses were studied extensively by WH Heiligenberg and others, especially in the wave species *Eigenmannia*, which uses its 500 Hz discharge for electrolocation of objects. *Eigenmannia* is jammed when a second individual’s EOD is in the range of 4–10 Hz above or below its discharge frequency, and it is unable to sense objects. It shifts its frequency upward or downward by as much as 10–20 Hz to prevent frequency overlap with the external stimulus. Electrolocation performance is then restored, and the jamming effects avoided by this behavior. Later, on removal of the stimulus, the jammed fish relaxes its EOD back to its original resting frequency. In some species, which move in shoals and are routinely jammed by other fish, prolonged jamming avoidance may produce a long-term elevation in frequency that persists for many hours or days.

Species with different tonic discharges have differing avoidance strategies. Wave fish avoid overlapping discharge frequency by moving upward or downward in frequency; pulse fish avoid temporal overlap of EODs by delaying or advancing their pulse times with transient increases in pacemaker firing rate or by making rapid, short-latency echo responses to jamming pulses.

Jamming avoidance responses resemble some of the phasic signals used in social communication, and they are generated by the same neural circuits in the brain. The ‘long rises’ of *Eigenmannia* and the frequency decreases in *Gymnarchus* are both used by subordinate fishes as signals of submission, and the transient rate increases seen in jamming avoidance responses among the pulse gymnotiforms also resemble the burst discharges and rate increases seen in agonistic behavior. The close resemblance of the jamming avoidance responses to social communication displays may not be accidental but may be yet another example of ritualized behavior – adopting physiological reflexes as displays for communication. This may help explain the remarkable convergence in signal form and function in unrelated groups of electric fish.

**Brain Mechanisms of Signal Generation**

Gymnotiform and mormyriform fishes generate patterns of discharges using a hierarchy of control nuclei in the midbrain, the midbrain, and the thalamus. There are many parallels between the electromotor control areas in the brains of these two groups of fishes. Each time the electric organ fires, it is triggered by the firing of neurons in the pacemaker or command nucleus in a ventral medulla. In gymnotiform fishes, this ventral nucleus is called a pacemaker nucleus since it is spontaneously active and generates a regular repetitive discharge frequency. In mormyrids, the equivalent nucleus is called a command nucleus because these cells make the decision to fire each EOD pulse after integrating synaptic inputs from a variety of higher centers in the brain, but they do not show pacemaker-like regularity. In both groups, the pacemaker or command nucleus is located on the ventral midline and is composed of cells which are electrotonically coupled, ensuring synchrony of firing. Command or pacemaker neurons project to cells in a nearby relay nucleus containing very large neurons that project down the spinal cord to the electromotor nucleus near the electric organ.

The primary inputs to the command and pacemaker nuclei come from a column of cells located in the dorsal thalamus. For gymnotiforms, the central posterior nucleus projects to the pacemaker and causes smooth rises in EOD firing frequency. In mormyrids, the dorsal posterior nucleus produces smooth discharge accelerations or bursts. These two thalamic nuclei are heterogeneous along their lengths such that the firing of cells in the rostral regions produces smooth accelerations in discharge rate while the firing of cells in the caudal regions produces sharp transient bursts of pulses.

A secondary input comes from smaller groups of cells in the midbrain. In gymnotiforms, the sublemniscal prepacemaker nucleus (sPPn) causes frequency decreases or discharge interruptions; in mormyrids, the ventral part of the ventral posterior nucleus within the torus semicircularis projects to the command nucleus, but its effects are unknown.

Both these nuclei receive inputs from sensory and motor nuclei which get inputs from a variety of sensory modalities, including electric, auditory, lateral line, and visual pathways. These inputs are important means by which other sensory systems affect the discharge of the electric organ. In gymnotiforms, the nucleus *electrosonorius* sends inputs to both the sPPn and to the PPn and the central posterior nucleus; in mormyrids the *tectum mesencephali* sends fibers to the dorsal part of the ventral posterior nucleus in the torus and to the dorsal posterior nucleus in the thalamus.

Physiological work spanning four decades has resulted in good understanding of the electromotor control system of electric fishes. Building on earlier work by Bennett, Szabo, Fessard, and others, which described command and relay nuclei and electromotor nuclei in spinal cord, more recent work by M Kawasaki, C Keller, WF Heiligenberg, G Zupanc, BA Carlson, K Grant, G von der Emde and others has uncovered many of the higher electromotor control centers in the brain that generate many of the social communication signals discussed here.
Electric communication is a fascinating example of a novel modality of communication that has undergone independent adaptive radiations in two separate lineages of fishes. Both groups exploit electroreception to the fullest, using tuberous electroreceptors for active electrolocation and reception of communication signals. Both have diverse electric organs and diverse signal types. Together, their systems of electric communication provide insight into the evolution of signals; strategies for coping with noise, predation, and jamming; and energetic costs of signaling while maintaining signal diversity. Work on electric fish has led to the development of several model systems for the comparative study of nervous systems and behavior.

See also: Electrocommunication; Electrolocation; Gap Junctions and Electrical Synapses; Signal Transmission in Natural Environments.

Further Reading


Relevant Websites

http://nelson.beckman.uiuc.edu – Bibliographies of electric fish.


http://www.nbb.cornell.edu – Field studies on weakly electric fish.


http://tolweb.org – Tree of Life web project, Gymnotiformes.

http://tolweb.org – Tree of Life web project, Osteoglossiformes.