Organisms have adapted to different environments and evolved sense organs that respond selectively to particular forms of energy. Because we lack specialized receptors, we are “blind” to weak forms of electric and nonphotic electromagnetic energy that surround us constantly. The shocking experience with a faulty electric outlet is not mediated through an electric sense but through direct stimulation of the nervous system.

*Elephantfish, Gnathonemus petersii. At right, elephantfish swimming in a tank.*
The underwater environment is packed with electric and electromagnetic events. If we were able to sense this electric environment, a whole new world would reveal itself: weak electric fields emanate from many aquatic organisms, especially from fishes and wounded crustaceans, and to a lesser extent from mollusks, starfish, and sponges. In most cases, we would feel direct current (DC)* voltage gradients that in the ocean range from as low as one hundred millionth of a volt per centimeter to as large as one hundred thousandth of a volt per centimeter. In freshwater, the voltage gradient is about one hundred times greater. We would also detect alternating current (AC)** voltage gradients associated with an organism's movements, breathing, or locomotor behavior. Soon we would discover that many inanimate objects produce DC fields, their interface with water acting as a battery. Lightning discharges and man-made radio waves are sources of electric noise pollution that certainly would not escape our underwater electric ears or eyes. Blaxter has said (see page 28) that sound "has much to recommend it as a form of sensory stimulus." So, too, does electric energy, and nature, not surprisingly, has exploited it.

A number of aquatic organisms have evolved specialized receptors with which they are able to perceive many aspects of the underwater electrical world. Another group of electric signals in an aquatic environment are supplied by species that have evolved the ability to generate their own electric energy which they use in predatory, orientation, and communication behavior.

**Electric Signals in Water**

Let us for a moment contemplate the fate of an electric signal underwater and compare it with other energy forms. The conduction of electric signals in water is almost instantaneous and thus comparable with that of visual ones. Acoustic, mechanical, and chemical stimuli travel considerably slower. Like sound, an electric signal does not persist once it is discontinued; both types of signals, then, differ from chemical stimuli, which can linger for quite some time. Turbid water and darkness do not impede the transmission of electric, acoustic, chemical, and mechanical signals but do restrict visual ones. Dense vegetation, submerged trees, roots, and even small rocks present barriers to visual stimuli, but are not obstacles to electric currents, which can go around them.

As animal behaviorists, we are concerned with the biologically meaningful range within which such a stimulus can affect the sense organs of another organism when the stimulus is no longer clouded by environmental noise, thus serving in social communication and orientation. To assess such a biologically effective range we must look at the amount of emitted or available stimulus energy, the sensitivity of the receptors involved, the spherical spread of the signal, and the attenuating effects of the surrounding medium on the transmission of the stimulus.

We have studied the effective range of electric signals in weak-electric fishes (Table 1), which are characterized by their ability to emit and perceive weak electric discharges. In contrast to the admirable long-distance performance of acoustic sensory stimuli (up to several hundred kilometers), the range of the electric sense in mormyrids* is restricted to a humble 100 centimeters for electrocommunication and a mere 10 centimeters for electrolocation (Figure 1).

The effective ranges of the organism's electric sense in electrolocation and electrocommunication were found to vary with several factors — including species, body shape, and electrical resistance of the fish's skin; physical and electrical properties of the object; and, most important, conductivity of the surrounding water, that is, the degree of its dissolved ionic material. The optimal ranges of 10 and 100 centimeters are associated with low levels of water conductivity that conform well with measurements taken in the fish's natural habitats.** Even over short distances, the organism is supplied with enough electrical information to avoid obstacles, maintain proximity to conspecifics, and compromise with extraneous electric noise.

**Electroreceptive and Electrogenic Fishes**

There are two groups of fish species distinguished here (Table 1): those which have evolved electroreceptors only (electroreceptive fishes) and those which, in addition, have evolved specialized electric organs capable of generating electric discharges (electroreceptive and electrogenic fishes). Species in the first category sense electric fields that are not self-generated, but rather, are produced by other sources in the environment (passive electroreceptive group). Species in the other category also sense electric fields that they actively generate themselves (active electroreceptive group). Both groups have representatives among the

*A family of African freshwater fish (members of the order Mormyriformes), many of which are distinguished by their long, tube-like snouts.

**Less than or equal to 100 micro-Siemens per centimeter compared with distilled water, which is 0 micro-Siemens per centimeter, and New York City tap water, which is 70 micro-Siemens per centimeter.
cartilaginous and bony fishes and can be found in both marine and freshwater environments.

Electroreceptors

An electroreceptor is a sense organ that responds selectively to natural electric fields. We use both electrophysiological recordings and behavioral tests to determine whether a particular sense organ functions as an electroreceptor. Most known electroreceptors are related to the lateral-line organs (see page 27) (which are water vibration receptors characteristic of all fishes) and are of two types—ampullary or tuberous organs (Figure 2).

The ampullary receptor consists of a flask-shaped ampulla embedded beneath the surface of the skin. The bottom of the ampulla contains the sensory cells which are in contact with the outside through a jelly-filled canal. In sharks, rays, skates, and marine catfish, in which the ampullary organs are called ampullae of Lorenzini (after the man who first described them in the 17th century), these canals may be as long as one-third of the organism’s body (see Figure 4, p. 58). In contrast, in all electroreceptive freshwater fishes these canals are short, often microscopically so.

Ampullary organs are the more sensitive electroreceptors. Sharks and skates respond to stimuli as low as 0.01 microvolts per centimeter, which would correspond to a voltage gradient set up between the poles of a flashlight cell placed more than 1,500 kilometers apart. Sharks within close range of prey are particularly sensitive to the electric fields around aquatic animals. In some electrogenic mormyrid species, the ampullary
Figure 3. Electric organs have evolved independently in several groups of marine and freshwater fishes. In most cases these organs develop by modification of muscles in various parts of the fish’s body (darkened areas).

Table 1. Electroreceptive and electrogenic fishes.
Types of electroreceptors: (AL), ampullae of Lorenzini; (AR), ampullary receptors; (TR), tuberous receptors; (N), electrosensitivity not investigated.
# ELECTRORECEPTIVE and ELECTROGENIC FISHES
(with electroreceptors and electric organs)

## Strong electric organ discharges (EODs)

<table>
<thead>
<tr>
<th>Type III &quot;volley species&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intermittent, 2 to several hundred discharges</td>
</tr>
</tbody>
</table>

(EODs serve in defensive and predatory behavior)

- **(AL) TORPEDONOIDEI Torpedinidae**
  - *Torpedo marmorata, T. nobiliana* (electric rays)

- **(N) PERCIFORMES Uranoscopidae**
  - *Astroscopus y-graecum* (stargazer)

## Weak electric organ discharges (EODs)

- **(AL) Rajoidae, Rajidae, Raja**
  - (electric skates)
  - (Significance of EODs unknown)

## AFRICAN SPECIES

- **(AR, TR) MORMYRIFORMES**
  - Mormyridae
    - (>200 species)
  - Gymnarchidae
    - *Gymnarchus niloticus*

- **(AR, TR) CYPRINIFORMES**
  - Gymnotidae
  - Rhamphichthyidae

## S. AMERICAN SPECIES

- **(AR, TR) MORMYRIFORMES**
  - Gymnarchidae
    - *Gymnarchus niloticus*

- **(AR, TR) CYPRINIFORMES**
  - Gymnotidae
  - Rhamphichthyidae
  - Apterontidae
    - (S. Amer. knifefishes)

## Type II "pulse species"

- Continuous, less than 1 to about 100 Hz

- (EODs serve in electrolocation and electrocommunication)

- **AFRICAN SPECIES**
  - Mormyridae
    - (>200 species)
  - Gymnarchidae
    - *Gymnarchus niloticus*

- **S. AMERICAN SPECIES**
  - Gymnotidae
  - Rhamphichthyidae
  - Apterontidae
    - (S. Amer. knifefish)

## Type I "wave species"

- Continuous, from about 100 to 1,800 Hz

- **(EODs serve in electrolocation and electrocommunication)**

- **AFRICAN SPECIES**
  - Mormyridae
    - (>200 species)
  - Gymnarchidae
    - *Gymnarchus niloticus*

- **S. AMERICAN SPECIES**
  - Gymnotidae
  - Rhamphichthyidae
  - Apterontidae
    - (S. Amer. knifefish)
discharge, but only under low water-conductivity conditions where electrolocation and electrocommunication performances appear to be most effective.

The tuberous receptor consists of an epidermic capsule containing sensory cells with no direct connection to the exterior. Tuberous organs are up to 10,000 times less sensitive than ampullary receptors and have exclusively evolved in the electrogenic, weak discharge-generating fishes (Figure 2). Here, each electric discharge affects two types of tuberous receptors, the mormyromasts and the knollenorgans. As a class they respond optimally to stimulus frequencies from 60 to 1,800 Hertz (Hz). For a particular species, however, the range of optimal frequency sensitivity is limited and species specific.

Electric Organs

The ability to generate and emit electric discharges has evolved independently in a small number of marine and freshwater fishes (Table 1). The electric discharge is produced by an organ consisting of several columns of flattened cells, the electroplates or electroytes, whose embryonic origin has involved the modification of certain muscle groups: the eye muscles in the stargazer, branchial muscles in the torpedinid rays, pectoral muscles in the electric catfish, and axial and tail muscles in the Neotropical gymnotoid knifefishes and the African mormyriforms (Figure 3). (The exception is the South American gymnotoid Apteronotidae, whose electric organ is derived from nerves.) Like muscle fibers, the electroytes are innervated by motoneurons that depolarize simultaneously, thereby generating an electric organ discharge (EOD) whose waveforms are species-specific characteristics.

It has been customary to distinguish between strong and weak EOD-emitting fishes (Table 1). The EODs from electric eels, marine torpedoes, and African electric catfish are so powerful that they can stun and even kill passing prey fish. Baby catfish of 2 centimeters can produce up to 10 volts, sufficient to prey on tadpoles; large electric catfish and electric eels can generate several hundred volts; and torpedoes can produce up to 50 amperes. The electric organ discharges in all strong-electric fishes thus function as defensive and predatory weapons. There is some evidence that the EODs also serve in locating prey (in the electric catfish) and as signals in social communication (in the electric eel and catfish).

Strong-electric fishes do not continuously emit EODs but intermittently generate volleys consisting of from two to several hundred individual discharges. In field observations, the nocturnal electric catfish was seen to produce significantly more and longer-lasting volleys during the night than during the day. The volley-type repetition rate illustrated in Figure 4 is characterized by an initial period of short interdischarge intervals (approximately 2 milliseconds) which gradually increase in duration (up to more than 100 milliseconds).

Weak electric organ discharges that are generated by the freshwater gymnotoids and mormyriforms are too small to aid in offensive or defensive behavior. It was H. Lissmann of Cambridge University who in 1958 proposed that the weak EODs aid the fish in object location and social interaction.

The Electric Sense in Weak-Electric Fishes

Ryan (see page 55) discusses the electric sense as it pertains to sharks, skates, and rays. I will focus on the electric sense in weak-electric fishes and illustrate its role in electrolocation and electrocommunication.

Two major groups of unrelated freshwater fishes are both electroreceptive and electrogenic. The South American knifefishes are characterized by an elongate body and anal fin; the electric organ runs almost the entire length of the body. In the African mormyriforms, one species, Gymnarchus niloticus, possesses an elongate body with a long dorsal fin. The mormyrids are diverse in body shape, reflecting their adaptation to a great variety of habitats. The electric organ is always located in the tail (Figure 3).

Each time a fish emits an EOD, an electric field propagates from the fish. To map the electric fields we have to take snapshots. At the height of each discharge we determine the positions around the fish where the electrical potential between a measuring electrode and a distant reference electrode remains constant. Figure 5 illustrates such lines of potential (isopotential lines). The physicist will tell us that in a large volume of water the fish's electric field resembles that of a dipole field when measured at distances that are long compared to the length of the fish. Within close range, owing to the animal's body shape, the field differs considerably from an ideal dipole field.
emission and reception of the signal could hardly be exploited by the fish in locating objects, as is the case with organisms producing sound signals with about 20,000 times slower conduction time (see page 27). Object location in weak-electric fishes works differently.

**Electrolocation**

Any object whose conductivity is different from the surrounding water, such as a metal or plastic rod, or another fish, will distort the fish's self-generated electric field. For example, objects with conductivities lower than that of the water lower the density of the electric field lines in an area of the fish's skin that is nearest to the object. On the other hand, objects with higher conductivities increase the density of electric field lines. Electrophysiologists have studied these changes in current density and found that the presence of, say, a plastic object results in a decrease of the receptor's "firing rate" — the process of sending coded neural messages to the brain — whereas the presence of a metal object results in an increased receptor response.

The tuberous electrorceptors involved in electrolocation are scattered throughout the fish's body surface. The presence of an object will therefore affect some receptors more than others. From the mosaic of local receptor responses, the fish may obtain information about the object's position and its electric nature. We could say that such an object casts its electric image on part of the fish's body wall.

To enhance an electric image, fishes have developed several peripheral focusing strategies, analogous perhaps to the accommodation response of a lens to nearby objects. Gymnotoids, while exploring a novel object, often bend their tail (containing the electric organ) around it. Many of the South American knifefishes have tail filaments several times longer than the body. These filaments considerably extend the range of electrolocation in the tail region. By swimming backward into prospective shelters, holes, and crevices, the fish maximizes the electric image the surroundings cast on the body wall. Mormyrids, which with some notable exceptions do not have long tails and whose electric organ is restricted to the tail, improve on the electric image of a nearby object by probing it. At well-defined distances, in the presence of novel stationary objects, the fish displays tail bending — lateral and/or tangential motor probing acts. When the fish moves rapidly backward and forward along the object, a maximum number of electrorceptors are optimally affected and thus the electric image is improved. When we try to see and locate a difficult visual target our heads move in a similar way.

In addition to having a motor response, the fish has an electric focusing strategy. While probing an object it accelerates its variable and low EOD repetition rate to a stable and higher level (Figure 6). An increased EOD rate means more receptor responses and thus more information sent to the brain per EOD and time unit. Immediate distortions of the self-generated field aid the fish in close-range, local orientation. Several mormyrid

![Figure 5. The electric field generated with each electric organ discharge propagates in all three dimensions and can be visualized as a bubble around the fish expanding almost at the speed of light. Isopotential lines (drawn in one plane only) show the extension of such an electric field. Values are given in microvolts per centimeter. (From Boudinot, in Szabo, 1977, courtesy of Springer-Verlag)](image)

![Figure 6. Electric organ discharges from a mormyrid fish, Marcusenius cyprinoides, during resting, object probing, and swimming. The duration of the consecutively plotted intervals between discharges indicates how the variable resting activity became regular during probing with a stable interval of 28-30 milliseconds. (Courtesy of M. J. Toerring)](image)
species are seasonal migrants and others show daily migratory patterns from large rivers into small creeks and vice versa. One may speculate that because the fish learns and later remembers the electric images cast upon its body during migration, the active electric sense may play a supporting role in long-range orientation.

**Electrocommunication**

What do we expect a communication system to accomplish? Basically, two broad classes of information must be transmitted: identity information (species, sex, developmental stage or age class, and individuality); and motivational information (reproductive readiness, threat, and submission).

The same EODs that weak-electric fishes use in electrolocation can stimulate members of their species and other species at much greater distances; they can thus serve as signals in social communication. In fact, the specific temporal patterning of EOD activity during social encounters in fishes has led researchers to suggest that it is analogous to bird song, with a similar variety of functions, such as mate seeking, territorial defense, and other social and orientation roles.

Weak-electric fishes have evolved different strategies for "electrically" transmitting identity and motivational information. Among mormyiform and gymnotoid fishes we distinguish two types of electric discharge rhythmicity (Table 1). Type I "wave species" emit nearly sinusoidal EODs at extremely stable repetition rates ranging from 100 to 1,800 Hz. These stable frequency bands are species specific. Type II "pulse species" have considerably lower EOD repetition rates ranging from less than 1 Hz to 140 Hz. In many gymnotoid pulse species the EOD rate remains stable. In mormyrids, on the other hand, the repetition rate is quite variable most of the time. In contrast to the wave species, pulse species show a wide interspecific overlap in the species-typical ranges of EOD repetition rates.

**Identity Information**

Wave species broadcast within species-specific frequency bands. In mormyrid pulse species, identity information is coded with the characteristic waveform of the individual discharge. Figure 7 shows species-specific differences related to the duration as well as amplitude and polarity of the different phases of the single EOD. To test the hypothesis that individual EODs (in pulse species) and stable frequency bands (in wave species) are important cues in species recognition, we played recordings of species-specific and modified, computer-generated signals to the fish. Under these conditions, the receiver fish's electroreceptors responded optimally and the fish was optimally attracted to the source of those signals which exactly simulated the species-specific waveform and/or rhythmicity.

To signal maleness or femaleness some species have developed characteristic differences in their EOD frequency bands or waveforms. Male gymnotoid *Sternopygus macrurus* broadcast within a 50-90 Hz range and females within 100-150 Hz. Figure 8 illustrates the striking sexual difference in the waveforms of a mormyrid pulse species. Sexual differences in electric signaling serve in mate attraction and courtship behavior.

Characteristic differences related to age class were found in juveniles of *S. macrurus*, which emit an EOD frequency of around 80 Hz, an intermediate

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*Examples include gymnotoids such as *Sternopygus macrurus*, 50-150 Hz; *Eigenmannia virescens*, 240-625 Hz; and *Apteronotus albifrons*, 750-1,250 Hz; and mormyiforms such as *Gymnarchus niloticus*, 200-450 Hz.*
between their parents' frequencies. Correspondingly, juveniles of some pulse species generate intermediate waveforms (Figure 8). Larval mormyrids emit an EOD that is first generated by a larval electric organ eight days after hatching. After about six weeks, when the definitive tail organ becomes functional, the larval discharge is gradually replaced by the differently shaped adult EOD. It may be that larval EODs serve in signaling identity to the parent fishes and maintaining group cohesion among the larvae.

We noted earlier that the EOD repetition rate in mormyrid pulse species is quite variable with regard to the average interval maintained between successive discharges. If we look at the distribution of these intervals over a longer period of time (let us say, 10 to 20 minutes), we discover characteristic modal distributions, which in some mormyrid species are individual-specific "fingerprints" (Figure 9). We do not yet know whether such fingerprints are actually being used in individual recognition among members of a given species.

Motivational Information

The modifiability of EOD rhythmicity (that is, the temporal sequence of EODs) and the fish's immediate EOD-responsiveness to a variety of stimuli, including electric, magnetic, optic, mechanical, thermal, and chemical, have made EOD rhythmicity changes prime candidates for transmitting motivational information. In both mormyrids and gymnotoids we find characteristic relationships between overt behavior and EOD activity. The behavioral situation and the social status of a pair of interacting individuals affect whether the pulse fishes rapidly increase their baseline frequency, decrease their activity, or cease discharging altogether for various lengths of time. In addition, the variable interval between discharges may temporarily become extremely stable at a given frequency level or alternate between two intervals of fixed duration. In the gymnotoid wave species, different types of sharp EOD rate increases and discharge cessations (breaks) were observed during social encounters and were related to threat, attack, submission, and courtship behavior.

Comparable with procedures testing the transmission of identity information, play-back experiments have convincingly demonstrated that motivational information is transmitted via
particular EOD activity patterns. For example, when an electric dipole mimicking the fish's electric organ is concealed in a plastic model fish, it is attacked less often when it broadcasts resting activity than when it emits an "attack pattern." Similarly, male *S. macrurus* respond to playback of female EOD patterns with typical frequency increases and EOD cessations, but do not respond to male EOD patterns.

During social encounters, two fishes could potentially jam each other's signals. The outcome of such jamming should be similar to the result of two people talking to each other at the same time: the information exchange is close to zero. When the fishes, under laboratory conditions, were subjected to coincident discharges or identical frequencies (emitted by an electric dipole in a model fish) they failed to locate nearby objects. If we want to understand our neighbor's comments we stop talking and listen before responding. Under natural conditions, pulse species avoid jamming — one fish places its own discharge at a fixed delay following the other's discharge in a kind of waiting or echo response. Wave species shift their own frequency away from an identical or similar stimulus frequency in a jamming avoidance response.

**Evolutionary Considerations**

Striking similarities and differences in the structure and functioning of electric organs and electroreceptors, as well as in electric signaling and overt behavior, have evolved independently in two unrelated groups of fishes, the South American gymnotoids and the African mormyriforms. We assume today that the presence of a passive electrosensory system, which depends on external electric energy, preceded the evolution of an active electric sense, in which the animal produces its own signal energy. The distribution of ampullary organs in most elasmobranchs and catfish as well as in the weak-electric fishes suggests the possibility of prior evolution of electrolocation and electrocommunication, in concert with other sensory modalities to aid the fishes in seeking mates, food, and shelter, establishing territories, forming and dispersing social groups, and moving about in their habitats.

Independently, the African mormyrids evolved electroreceptive and electrogenic structures. Here, the evolution of a noise-resistant communication system has taken quite a different path. Mormyrids evolved a tremendous species-typical diversity in EOD waveforms. The co-evolution of precisely tuned tuberculous electroreceptors aids mormyrids in recognizing conspecific, mate-specific, or age class-specific signals in a noisy environment.

Last but not least, the complex communication and orientation systems in weak-electric fishes have certainly not evolved along one single sensory modality, the electric one. Without their electric sense, these fishes are by no means left in the "dark." They have a functional lateral line, respond to chemical stimuli, react to changes in light intensity and temperature, can hear, and have dim-light vision (as was demonstrated for the mormyrid *Gnathonemus petersii*). Thus the fishes' electric organ discharges, serving their dual function of electrolocation and electrocommunication, act in concert with other sensory modalities to aid the fishes in seeking mates, food, and shelter, establishing territories, forming and dispersing social groups, and moving about in their habitats.

Peter Moller is an Associate Professor in the Department of Psychology, Hunter College, City University of New York, and a Research Associate at the American Museum of Natural History, New York.

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**Selected Readings**


*Acknowledgment*

The moral of the story is that the habits of the preceding year presaged the habits of the following year.