ELECTROSENSORY ORGANISMS

By detecting weak electric fields from animate or inanimate sources, many aquatic animals acquire information used for orientation, communication and other critical behavior.

Joseph Bastian

Many aquatic animals have the ability to sense very weak electric fields. This electric sense is found in numerous species of marine and freshwater fish and in several amphibian species. Electrosensory abilities have also been reported in "higher" animals including the platypus and a semiaquatic mole.[1–3]

The sensitivity of the electrosensory systems responsible for this ability can be impressively high. Freshwater catfish respond to electric field gradients as low as 1 microvolt per centimeter, and marine sharks and rays are sensitive to gradients of less than 5 nanovolts per centimeter. This high sensitivity enables electrosensitive animals to locate prey using the weak fields due to current leakage from aquatic organisms. The animals with the highest sensitivities, marine sharks and rays, can navigate using the voltage gradients induced by ocean currents flowing in Earth's magnetic field as well as voltage gradients induced by their own movements.[4]

A subset of fish with electrosensory systems also possess electric organs, and these animals generate electric fields. In a few species, such as the Nile catfish and the South American electric eel, the electric organ can produce outputs of hundreds of volts. These fish use their strong discharges defensively to ward off predators as well as offensively to stun prey. Two large groups of so-called weakly electric fish, the South American Gymnotiformes and the African Mormyriformes, produce discharges in the millivolt range. These weak discharges, coupled with electroreceptors that are preferentially sensitive, or "tuned," to the discharges' frequency characteristics, make up an "active" sensory system analogous to the echolocation system used by many species of bat. Active electrosensory systems provide the fish with a communication channel as well as a means of detecting the presence and quality of objects, or "electrolocation targets," in their immediate vicinity.[5,6]

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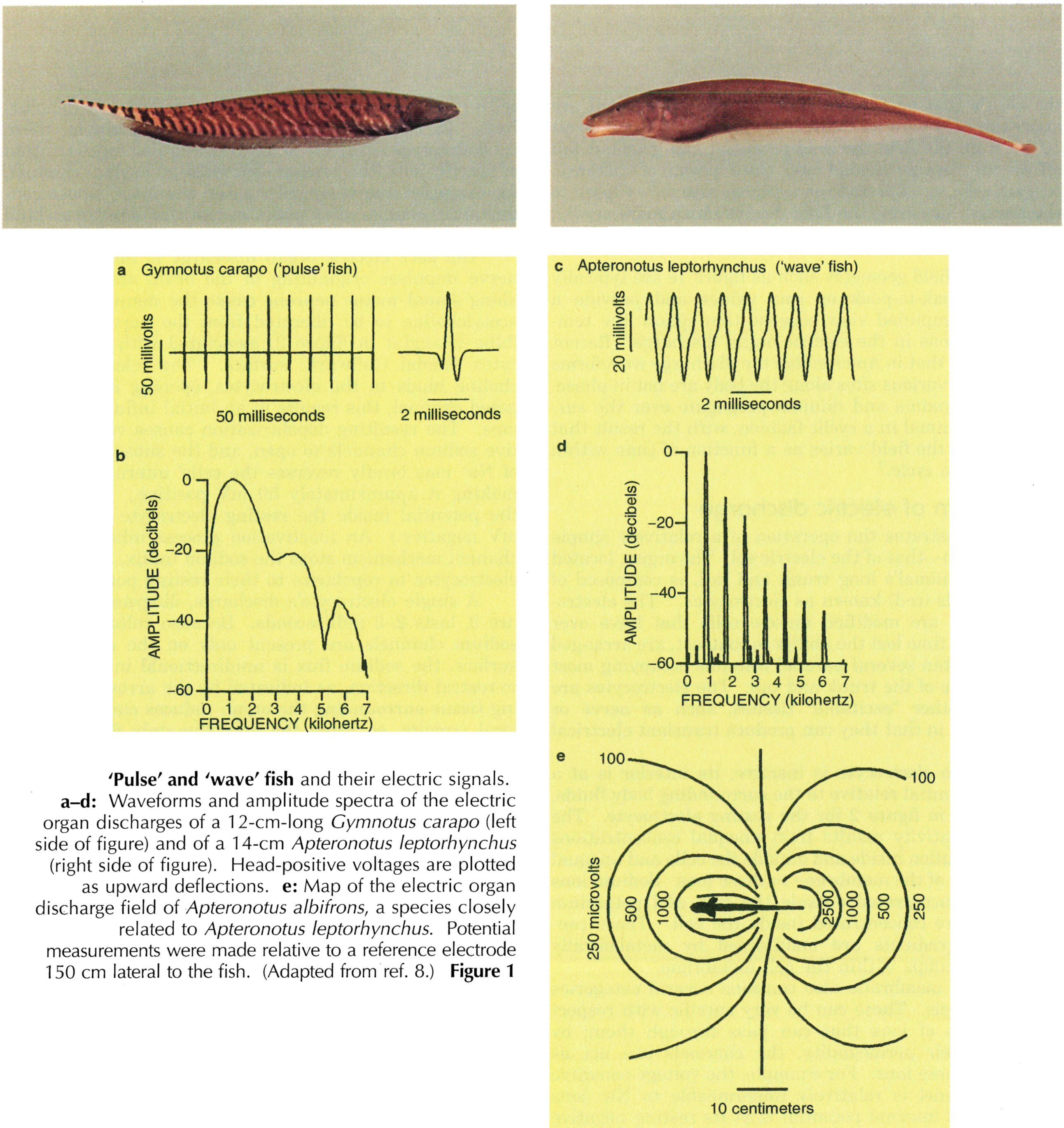
Electric organ discharges and fields

The signals generated by electric fish are amazingly diverse not only in amplitude but also in their temporal characteristics. Species are characterized as having "pulse" electric organ discharges or "wave" electric organ discharges depending on the frequency and regularity of the discharges. Figure 1 shows the South American weakly electric fish *Gymnotus carapo* and *Apteronotus leptorhynchus*, examples of "pulse" and "wave" fish, respectively, along with their electric organ discharge waveforms and spectra.

The discharges of pulse fish (figure 1a) consist of brief waveforms separated by longer intervals. Each species produces a characteristic pulse shape; the shapes range from simple monophasic waveforms to complex events consisting of several sequential phases, such as the triphasic discharge of *Gymnotus* (inset in figure 1a). The discharges of various species of pulse fish range[5] in width from about 100 microseconds to about 10 milliseconds. Although the pulse waveform for a given species is typically very constant, male and female pulses can differ, providing a cue for sex recognition, as discussed later.

The amplitude spectrum of the electric organ discharge of pulse fish is broad, having energy spread over a wide range of frequencies; however, the dominant frequency components vary among species. These spectral



'Pulse' and 'wave' fish and their electric signals. **a–d:** Waveforms and amplitude spectra of the electric organ discharges of a 12-cm-long *Gymnotus carapo* (left side of figure) and of a 14-cm *Apteronotus leptorhynchus* (right side of figure). Head-positive voltages are plotted as upward deflections. **e:** Map of the electric organ discharge field of *Apteronotus albifrons,* a species closely related to *Apteronotus leptorhynchus.* Potential measurements were made relative to a reference electrode 150 cm lateral to the fish. (Adapted from ref. 8.) **Figure 1**

differences, as well as time-domain differences in the discharges, facilitate recognition by individuals of the same species and minimize confusion resulting from the occupation of a given habitat by many species.[5]

Wave fish produce continuous, quasisinusoidal waveforms of very constant frequency. The discharge frequencies of individuals of a given species are confined to a "species range" (500–900 Hz for *Apteronotus leptorhynchus*), and within a species individuals typically have different frequencies. The amplitude spectra of wave discharges (figure 1d) consist of narrow peaks at the fundamental frequency and at several higher harmonics. When only a few species of wave fish occupy the same habitat, the species' frequency ranges usually overlap only minimally, insuring clear communication and electrolocation channels for each group.[5] However, when larger numbers of species coexist, communication and electrolocation may at times be compromised because the species' electric organ discharge frequencies overlap significantly.[7] Although the discharge frequency of individual wave fish is usually very constant, they do sometimes modulate their frequency, as do pulse fish; both groups engage in electrical signaling behavior during mating and aggressive encounters.

The geometry of the field resulting from the electric organ discharge is roughly dipole-like, as figure 1e shows. The field surrounding the rostral (headward) portion of the animal is expanded in the headward direction, with the result that equipotential lines near the animal are approximately parallel to the body surface. Beyond about 10 cm from the fish, the field potential and gradient fall off as the inverse second and third power of distance, respectively, as expected for a dipole source.[8] Closer to the animal, however, the field decays much more slowly; the potential falls off approximately as the −0.5 power of distance.

Plots of field geometry such as figure 1e are typically based on peak-to-peak or rms values and provide a somewhat simplified view because they ignore the temporal variations in the electric organ discharge. Recent studies show that in *Apteronotus* the discharge waveforms measured at various sites along the body are not in phase. Discharge maxima and minima propagate over the surface of the animal in a cyclic fashion, with the result that the shape of the field varies as a function of time within the discharge cycle.[9]

Mechanism of electric discharge

Figure 2 illustrates the operation of a relatively simple electric organ—that of the electric eel. The organ, located within the animal's long trunk and tail, is composed of flattened cells (red) known as electrocytes. The electrocytes, which are modified muscle cells that have over evolutionary time lost the ability to contract, are arranged in series within several parallel columns occupying most of the volume of the trunk and tail. The electrocytes are similar to other "excitable" tissues, such as nerve or muscle cells, in that they can produce transient electrical events.

When an electrocyte is inactive, its interior is at a negative potential relative to the surrounding body fluids, as indicated in figure 2 for the resting electrocyte. The internal negativity results from unequal concentrations of ions in solution inside and outside the cells and unequal permeability of the membrane to these ions. Sodium ions are more concentrated outside the cell, and potassium ions are more concentrated inside the cell. These concentration gradients are maintained by metabolically driven ion pumps within the cell membrane.

The cell membrane also contains several categories of ion channels. These can be very specific with respect to the types of ions that can pass through them; by changing their permeability, the channels can act as "gates" for these ions. For example, the voltage-sensitive sodium channel is relatively impermeable to Na^+ ions when a cell's internal potential is at its resting negative value—about −90 mV for the eel electrocyte. But the channel conductance increases dramatically when the cell's internal potential becomes less negative or depolarized. In addition to voltage-sensitive channels, there exist channels sensitive to the intracellular concentration of specific ions (the calcium-activated potassium channel, for example) and chemically gated channels, whose conductances change when neurotransmitter substances bind to receptor molecules on the surface of the membrane.

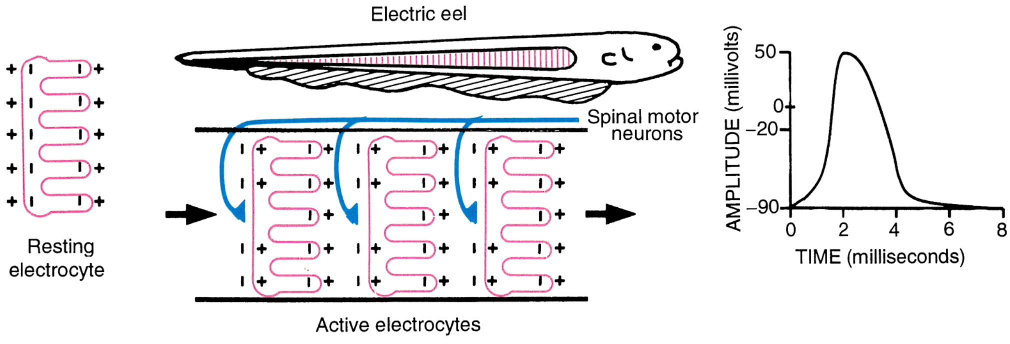
The eel's electric organ discharge is initiated when nerve impulses originating in the brain and conducted along spinal motor neurons cause the neurotransmitter acetylcholine to be liberated from the nerve terminals (blue triangles in figure 2) associated with the electrocytes' caudal (tailward) surface. The released acetylcholine binds to the electrocytes, opening a chemically gated channel; this results in an initial influx of positive ions. The resulting depolarization causes voltage-sensitive sodium channels to open, and the subsequent influx of Na^+ ions briefly reverses the cells' internal potential, making it approximately 50 mV positive. (Recall that the potential inside the resting electrocyte is about 90 mV negative.) An inactivation process inherent in the channel mechanism stops the sodium influx, allowing the electrocytes to repolarize to their resting potential.

A single electrocyte's discharge, diagrammed in figure 2, lasts 2–3 milliseconds. Because voltage-sensitive sodium channels are present only on the cells' caudal surface, the sodium flux is unidirectional in the caudal-to-rostral direction, as indicated by the arrows. Insulating tissue surrounding the organ reduces current flow in local circuits, so when the approximately 6000 serially arranged electrocytes are synchronously activated, a head-positive discharge in excess of 600 volts results.[10] The more complex discharge waveforms seen in many species of South American and African weakly electric fish arise as a result of further specialization of the electrocytes or more complex activation patterns of subdivisions of the electric organ.[10,11]

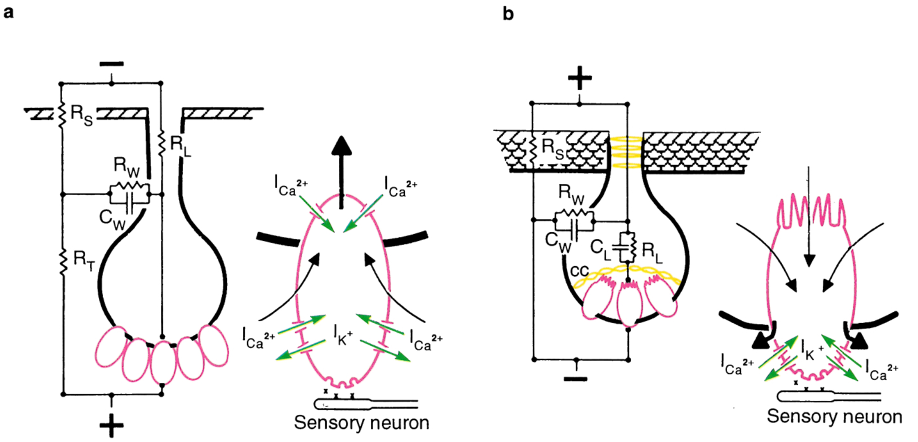
Electroreceptor organs

We now turn from organs that produce electricity to organs that detect it. The initial stage in processing received electrosensory information involves transforming the stimulus, a change in potential across the skin, into changes in the pattern of nerve impulses transmitted to the brain. This is accomplished by electroreceptor cells (related to auditory hair cells) contained in electroreceptor organs within the animal's skin.

Electroreceptor organs are commonly divided into two categories based on their anatomy and their sensitivity to electric signals.[12] Low-frequency electrorecep-



Mechanism by which the electric eel, *Electrophorus electricus*, generates an electric organ discharge. The plot shows the discharge waveform produced by a single electrocyte. **Figure 2**



Electroreceptor organs. Equivalent circuits and illustrations of receptor cell currents are shown for the ampullae of Lorenzini, low-frequency marine receptors (**a**), and the tuberous, or high-frequency, receptors of weakly electric freshwater fish (**b**). Small x's near the sensory neurons represent neurotransmitter released by the receptor cells; "cc" stands for the covering cells. Other terms are described in the text. (Adapted from ref. 15.) **Figure 3**

tors include the ampullae of Lorenzini of marine sharks and rays and the ampullary receptors of freshwater fish. These are most sensitive to frequencies below 50 Hz, and the minimum voltage gradient, or threshold stimulus, capable of generating responses can be as low as 50 microvolts per centimeter in freshwater species and 1 μV/cm in marine organisms. The South American and African weakly electric fish possess high-frequency receptors, or tuberous receptors, in addition to low-frequency receptors. These are less sensitive to voltage gradients, having thresholds ranging from tens to hundreds of microvolts per centimeter, and are "tuned" to the major frequency components of the electric organ discharges of the respective species.[13,14]

Figure 3a summarizes the operation of a marine ampullary receptor. Hundreds of individual receptor cells (red) are grouped together at the base of an epidermal pit, which communicates to the surface of the skin via a canal roughly 1 mm in diameter and up to 20 cm in length. The canal is filled with a jelly-like substance having a resistivity approximating that of seawater, while the tissue lining the canal has a higher resistance. Because the resistance along the canal (the luminal resistance R_L) is much lower than the resistance R_W across the wall, the canal forms a very effective cable connecting the interior of the organ to the external environment. The wall capacitance C_W, attributable to the cell membranes lining the canal, provides a low-impedance pathway shunting high-frequency signals away from the receptor cells. This contributes to the organ's low-frequency tuning; however, mechanisms intrinsic to the receptor cells themselves also determine their frequency selectivity.[15]

The receptor cells lie embedded in the tissues below the ampullary floor, with only the small "apical" portion of their membrane protruding into the lumen, or interior, of the canal. The larger, "basal" portion of the cells resides below the ampullary lining and communicates with the electrosensory neurons. The apical membrane is coupled to the exterior of the animal via the low-resistance canal, and the basal region is in direct contact with the animal's internal tissues. Therefore the receptor cells effectively measure any voltages that develop across the skin resistance (R_S) and across the resistance R_T of the internal tissues.

When the outside of the animal becomes negative relative to its interior, current flows through the receptor cells and into the lumen of the ampullae, as illustrated for the enlarged receptor cell by the black arrows. Current entering through the large-surface-area (and therefore low-resistance) basal portion of the receptor causes an insignificant voltage drop compared with that which develops across the higher-resistance apical membrane. Hence the inside of the receptor cell becomes less negative or depolarized. This initial depolarization opens a voltage-sensitive channel, allowing calcium ions to enter the cell. The calcium current $I_{Ca^{2+}}$ further depolarizes the cell and increases the rate at which the receptor cell releases neurotransmitter, increasing the frequency with which nerve impulses are sent to the brain. The depolarizing effect of the Ca^{2+} influx is counterbalanced by an outward flow of potassium ions I_{K^+}, which repolarizes the cell after a short delay. The potassium channel is probably activated by the increased intracellular Ca^{2+} ion concentration (a calcium-activated potassium channel).[16]

The opposite stimulus polarity, outside positive, increases the receptors' internal negativity, with the result that transmitter release and nerve impulse frequency are reduced.

The tuberous, or high-frequency, receptors (figure 3b) are restricted to the South American and African freshwater fish that generate electric organ discharges. There are two subtypes of these receptors. One is specialized to encode precisely the timing of the electric organ discharges, while the second encodes discharge amplitude. Several features of tuberous receptors relate to the freshwater habitat and to the receptors' frequency tuning; as a result, they contrast with the characteristics of marine ampullary receptors. The canals linking the receptors to the exterior are much shorter in freshwater animals. The skin of freshwater fish is of very high resistance compared with that of the internal tissues, and therefore the principal voltage drop occurs across the skin. Unlike in marine sharks and rays, the voltage drop across the relatively low-resistance internal tissue contributes little compared with that developed across the skin, so there is no advantage to placing the cells deep within the body. The lumen of the tuberous receptor canal is filled with a loose collection of epidermal cells (yellow in figure 3b), and a sheet of covering cells further protects the receptor cells from the dilute freshwater environment.[12]

The position of the receptor cells within the organ also differs from that in marine fish. The cells lie predominantly within the lumen of the organ, with only small basal portions of their membrane penetrating the floor. This arrangement results in reversed polarity sensitivity for freshwater electroreceptors compared with that of the marine ampullary receptors. Outside-positive stimuli depolarize these cells, because the predominant voltage drop occurs across the smaller, high-resistance basal region of the cell, as illustrated by black arrows for the enlarged tuberous receptor.

The tuberous electroreceptors act as bandpass filters tuned to the spectral characteristics of the fish's electric organ discharge. This tuning is due partly to the passive electrical properties of the organ itself and partly to the characteristics of the receptor cells' ion channels. The walls of tuberous organs are constructed in a manner that reduces wall capacitance C_W, minimizing the shunting of high frequencies to the surrounding tissues. The series capacitance of the covering cells' membrane, plus that of the large, convoluted apical surface of the receptors, summarized as C_L, acts as a blocking capacitor and contributes to the receptors' low-frequency insensitivity.[10] Outside-positive stimuli initially depolarize tuberous receptor cells and, as in marine ampullary receptors, probably activate an inward calcium current $I_{Ca^{2+}}$. The influx of Ca^{2+} ions further depolarizes the cells and increases the rate at which neurotransmitter is liberated. An outward potassium ion current I_{K^+}, which is probably calcium activated, follows the depolarization.[15]

Brief stimuli cause these receptors to resonate, or "ring." The resonant frequency of these receptors, recorded as damped oscillations outside the receptor pore, typically matches the frequency to which the receptors are tuned. This electrical resonance underlies the cell's tuning and is thought to be due to cyclic activation of the inward calcium and outward potassium currents. Electrical resonance similar to that first observed for electroreceptors[10] was later found in hair cells in auditory systems and probably contributes to auditory frequency selectivity in some cases.[17] (See the article by A. J. Hudspeth and Vladislav S. Markin on page 22.)

Electric communication

The unique characteristics of electric organ discharge waveforms (such as the pulse duration and number and the sequence of phases in pulse fish or the discharge frequency and harmonic content in wave fish) contain sufficient information to enable individuals to recognize one another as members of the same species. Additionally, in many species, discharge characteristics differ between males and females, facilitating sex recognition.

A South American wave fish, *Sternopygus*, was the first example found in which the electric organ discharges of males and females differ. Carl Hopkins of Cornell University, studying these fish in their natural habitat, found that mature males have electric organ discharge frequencies of about 60 Hz, while mature females have frequencies of about 120 Hz. During the breeding season, males produce stereotyped changes in their discharges when females swim by: transient frequency increases termed "rises" and brief pauses, or "interruptions." Hopkins used an electronic signal generator to mimic fish signals and showed that the males readily produced these electrical courtship displays in response to sinusoidal signals as long as the signal frequency was typical of females. Signals mimicking the discharges of males or of other species failed to elicit courtship responses. These studies demonstrated that the fish use their ability to generate and receive electrical signals as a communication channel.[5]

Pulse fish also can identify members of the opposite sex on the basis of their electric organ discharges. In this case, however, time-domain rather than frequency-domain cues seem most important. The discharges of male and female pulse fish often differ in waveform duration, and males will respond with courtship displays to tape recordings of the discharges of females and to mimics as simple as square pulses, as long as the waveform duration is similar to that of a female's electric organ discharge pulse.[18]

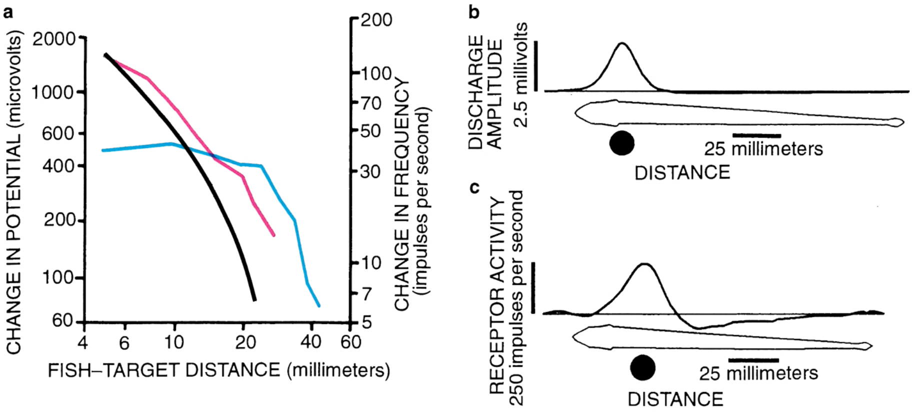
The temporal cues resolved by the fish can be amazingly subtle; one species of African fish discriminates between pulses differing in duration by only 200 microseconds. This acuity relies on electroreceptors specialized to detect the precise timing of electrical events and requires that the signals themselves be minimally distorted by the aquatic environment. Unlike acoustic signals, which can be significantly degraded as they are transmitted through the environment, electric signals, owing to their nonpropagated nature, can maintain their temporal fine structure over the range of distances within which they are detectable.[18] The repetition rate of pulse fish discharges is also variable, and such fish use stereotyped sequences of pulse-rate modulations of the electric organ discharge in communication as well.[5,19]

Passive electrolocation

The ability to locate objects in the environment using information acquired with the electrosensory system is termed electrolocation. Electrolocation is considered passive when the animal relies on electrical signals emanating from extrinsic sources. It is active when the information arises from the interaction of a target with an individual's electric organ discharge field or when the information results from the animal's own movements.

A shark's ability to discover fish buried in the sand by orienting to the potentials produced by the prey's gills is an example of passive electrolocation. Elegant experiments by A. J. Kalmijn of the Scripps Institution of Oceanography demonstrated that sharks will preferentially attack electrodes producing very weak electric fields even when sources of food odor are present.[4] The threshold voltage gradient capable of eliciting this feeding behavior is on the order of 5 nV/cm. This astounding sensitivity is one to two orders of magnitude lower than the measurable threshold sensitivity of individual electroreceptor neurons. Presumably, central nervous system processing that integrates inputs from populations of receptors enables the fish to resolve such weak signals.

The electrical sensitivity of sharks and rays is sufficient to allow these animals to respond to voltage gradients induced by the flow of ocean currents through Earth's magnetic field. Induced fields range from less than 5 to at least 500 nV/cm. It is likely that these electric fields provide important orientational cues or electrical landmarks that aid electroreceptive animals as they navigate. Kalmijn showed that free-swimming stingrays, in a locale where the strength and direction of the environmental electric fields were known, changed course in a predictable manner when the field direction was altered with an imposed field.[4] It is also possible



Effect of distance on active electrolocation. **a:** Changes in potential across the skin of *Apteronotus leptorhynchus* due to a 12-mm-diameter cylindrical metal object (black curve), and corresponding changes in electroreceptor and cerebellar nerve impulse frequencies (red and blue curves, respectively), as a function of lateral fish–target distance. **b,c:** Spatial profiles of changes in electric organ discharge amplitude and electroreceptor activity due to the presence of the 12-mm metal target (black circles). **Figure 4**

that sharks and rays respond to the voltage gradients induced as *they* swim through Earth's magnetic field—a type of active electrolocation—and use this information as the basis of a compass sense. Kalmijn trained stingrays to choose an enclosure based on its position relative to Earth's magnetic field—for example, to enter an enclosure in the magnetic east of a holding tank and to avoid enclosures in the west. Reversing the horizontal component of the magnetic field with Helmholtz coils reversed the animals' preferences, providing evidence that the animals can sense and orient to Earth-strength magnetic fields.[4]

Active electrolocation

Weakly electric fish also locate and identify objects by analyzing the distortions of their electric organ discharge fields caused by those electrolocation targets. For an object to be detectable, its impedance must differ from that of the water; the fish can discriminate both resistive and capacitive characteristics.[20] The stimulus encoded by the electroreceptors during active electrolocation consists of amplitude and, in some cases, phase modulations of the electric organ discharge waveform. The range and resolution of active electrolocation are determined both by the characteristics of the distortion in the electric organ discharge due to the target and by the amplitude sensitivity and AM frequency response characteristics of the electroreceptors.

The distance between the fish and the target is the principal determinant of the distortion amplitude; as the black curve in figure 4a shows, voltage changes measured across the animal's skin decay rapidly as a function of fish–target distance. Larger objects will, of course, cause larger amplitude distortions. However, distortion gains resulting from increased object size are small relative to losses due to increased target distance: The diameter of cylindrical objects must be increased roughly fivefold to compensate for the amplitude reduction resulting from doubling the fish–target distance.[21,22] The spatial extent of a given object's effect, or "electrical image," is large relative to the actual target size, as shown by measurements of voltage changes across the skin (figure 4b). Because there is no focusing mechanism associated with the electric sense, changes in receptor activity (figure 4c) closely parallel the spatial distribution of voltage changes, and "fuzzy images" are conveyed to the brain.

Motion of the fish relative to electrolocation targets imparts a temporal component to the electric organ discharge distortions, and the spectral characteristics of these amplitude modulations also influence an electrical target's detectability. Electroreceptors and many higher electrosensory neurons are most sensitive to relatively high AM frequencies, between 32 and 64 Hz, so shifting the frequency components of a given electric organ discharge distortion toward this range improves detectability. Thus the animals can enhance an object's detection simply by altering the speed at which they move past it.

Because the two parameters that most strongly influence the detectability of an electrolocation target—fish–target distance and velocity—are under the animal's control, it can use exploratory behavior patterns to optimize the perception of a target. Additionally, although the amplitude of the electric organ's output is normally constant, the geometry of the electric field changes as the animal changes posture. By bending its trunk and tail into an arc, an animal can increase the field strength on the side of the body toward which the tail is displaced. As a fish explores a novel electrical target, it continuously sweeps its tail to and fro, effectively "painting" the target with fluctuating field intensities. Simulations indicate that these active alterations in field geometry not only enhance the magnitude of electrical images but also increase contrast, facilitating the separation of images when multiple targets are present.[22]

The range of active electrolocation is limited by the rapid decay in the amplitude of the electrical image as the target distance increases, as shown in figure 4a for a 12-mm-diameter cylindrical metal object. A nonlinear relationship exists between changes in voltage across the skin and receptor responses, with the result that the latter decay somewhat more slowly (red curve). When the object is further than about 30 mm lateral to the fish, however, changes in a single electroreceptor's activity are not discernible from spontaneous fluctuations (noise). Electrosensory neurons in higher brain regions show about a 30% improvement in range, responding to targets at least 40 mm away. The ability of cells at higher levels within the brain to respond to such weak stimuli presumably results from noise reduction strategies based on averaging information collected from large populations of electroreceptors. Behavioral experiments confirm the physiological results that indicate that active electrolocation is a very short-range system.[6,21,22]

Electrical noise and jamming avoidance

Unwanted signals, or noise, can seriously degrade the operation of any sensory system, and electrosensory organisms must deal with interference from both animate and inanimate sources. The major nonbiological source of interference is lightning. Because the electromagnetic waves resulting from lightning flashes propagate very effectively over long distances, electrosensory organisms can be faced with a nearly continuous barrage of electrical events.[18] Other potential nonbiological noise sources include magnetic storms and electrical events associated with seismic activity.[13] The strange behavior of catfish documented to occur prior to earthquakes is thought to be due to their perception of changes in the electrical environment. Man-made sources also probably interfere with electrosensory systems, but the effects of these have yet to be studied.

Weakly electric fish are themselves the major biological source of interfering signals for other electric fish, and several species have developed specific behaviors—jamming-avoidance responses—for preserving their ability to electrolocate in the face of the deleterious effects of their neighbors' discharges. When two fish approach to within about 1 meter, each senses their summed discharges, which in the case of wave fish result in a beat waveform like that shown in figure 5a. If the difference in the animals' discharge frequencies, or beat frequency, is less than about 15 Hz, electrolocation ability deteriorates, because the amplitude modulations of the beats are similar to those resulting from electrolocation targets.[6,22]

The jamming-avoidance response of the South American weakly electric fish *Eigenmannia* is now perhaps the most thoroughly understood vertebrate behavior. Walter Heiligenberg of the Scripps Institution of Oceanography and his colleagues have unraveled the algorithms used by the brain to produce this behavior and have described the neuronal hardware implementing these computations.

Upon sensing a beat pattern such as that diagrammed in figure 5a, each *Eigenmannia* alters its discharge frequency. The animal discharging at the higher frequency increases its frequency, while the lower-frequency animal reduces its discharge frequency. This maneuver increases the beat frequency to higher values that can be distinguished from the lower-frequency amplitude modulations due to most electrolocation targets, and electrolocation performance improves.

The animals determine the optimum direction in which to shift their respective frequencies virtually immediately and without error.[23] The decision to increase or decrease the electric organ discharge frequency is based on each individual's analysis of the amplitude and phase modulations of the beat pattern that it perceives. The time course of the amplitude modulation sensed by either fish, illustrated in figure 5b, is independent of whether the interfering discharge frequency is higher or lower than the individual's own. That is, the AM portion of the beat cannot provide the information needed to decide whether to shift the electric organ discharge frequency upward or downward.

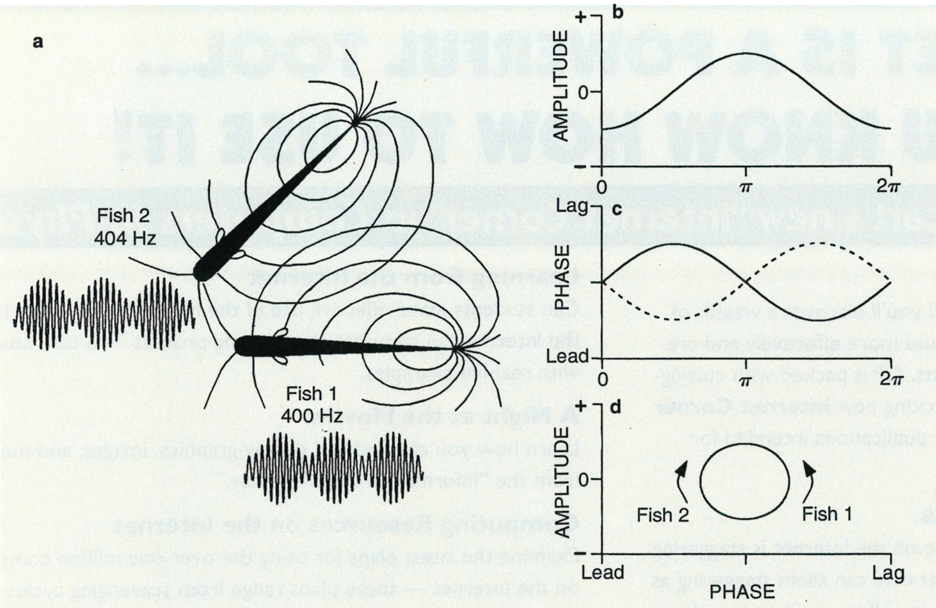
The phase of the beat waveform, however, measured relative to the animal's "uncontaminated" electric organ discharge, does contain information about whether the interfering signal is of higher or lower frequency. If the interfering signal is of higher frequency, as perceived by fish 1 in figure 5, the phase of individual cycles within the beat will lag behind the uncontaminated electric organ discharge as the beat amplitude rises and will lead it as the amplitude falls, as the solid line in figure 5c shows when compared to the curve in figure 5b. If the interfering electric organ discharge is of lower frequency, as perceived by fish 2, then the reverse sequence of phase lead and lag occurs (dashed line). However, a fish cannot unambiguously interpret phase without referring to beat amplitude as well. It isn't possible to determine whether the interfering signal is higher or lower in frequency without knowing where in the beat cycle the phase lead or lag occurs. The animal can obtain unambiguous information by simultaneously evaluating amplitude and phase. One can conveniently represent the modulation of amplitude and phase by a circular graph, or Lissajous figure, as shown in figure 5d. The point representing the instantaneous values of amplitude and phase will rotate counterclockwise when a weaker interfering electric organ discharge has a higher frequency and clockwise if a weaker interfering signal is of a lower frequency.[24]

The amplitude of the interfering electric organ discharge is encoded by amplitude-sensitive electroreceptors. Other electroreceptors encode the electric organ discharge timing with high precision, and cells higher within the nervous system determine phase by computing the timing differences between the electric organ discharge waveforms sensed at different sites on the body. The phase information is then integrated with amplitude modulation data.

Within the highest centers of the processing hierarchy are found neurons that are active only when an interfering electric organ discharge is of higher frequency. Other cells within the same structure are active only when the interfering signal is of lower frequency. These neurons make up a population of specific feature detectors that provide input to the brain centers that ultimately control the animal's electric organ discharge frequency. The neural circuitry controlling the jamming-avoidance response can be thought of as reading the direction of rotation of plots such as the one in figure 5d.[24]

The fish are very sensitive to amplitude and phase modulations: They can resolve changes in electric organ discharge amplitude of less than 0.05% and can resolve phase changes on the basis of timing differences of less than 400 nanoseconds. Heiligenberg has recently summarized the studies of the jamming-avoidance response of *Eigenmannia*, providing the most complete description to date of how a vertebrate brain integrates complex sensory inputs to produce a specific behavior.[24]

The electric sense is perhaps the most recently discovered sensory modality. Since its initial description, less than 35 years ago, enormous progress has been made in defining the biological and physical properties of the relevant signals, of the detectors and of the brain mechanisms involved in integrating electrosensory information. The intense interest in organisms possessing this sense is partly motivated by the desire to understand creatures who view their world so differently than we view ours. More importantly, despite tremendous differences in the nature of the stimuli that organisms exploit, the brain



Interference between the discharges of wave-type weakly electric fish. **a:** Superimposed electric organ discharge fields and the beat pattern perceived by two fish in close proximity. **b:** The time course of the modulation in electric organ discharge amplitude sensed by either fish, plotted over one beat cycle. **c:** The time courses of the phase changes perceived by the lower-frequency fish (solid line) and higher-frequency fish (dashed line) as a function of time within the beat cycle. **d:** Beat amplitude as a function of beat phase. Fish 1 will perceive a counterclockwise rotation of the amplitude–phase relationship; fish 2, a clockwise rotation. **Figure 5**

mechanisms involved in processing that information are amazingly similar. An understanding of the simpler nervous systems of animals like the weakly electric fish provides important clues as to how more complex organisms process information.

Additionally, species such as weakly electric fish are in a sense overspecialized, relying heavily on just one sensory modality. Such animals are particularly useful as model systems, because it is often easier to identify in such animals the critical stimulus features that must be evaluated, and the information that must be extracted, for a given behavior's initiation and control. Studies of "specialists" such as electric fish will continue to provide insight fundamental to understanding the more complex nervous systems of higher animals.

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