Eigenvector

Definition

A vector whose direction is unchanged by an operator. During optokinetic after-nystagmus (OKAN), an eye velocity vector in three-dimensional space whose direction remains fixed along the stimulus velocity as the eye velocity declines toward zero. It has also been termed an "orientation vector."

►Optokinetic After-Nystagmus (OKAN)
►Velocity Storage

Eighth Cranial Nerve

►Auditory Nerve

Eimer's Organ

Definition

In the snout glabrous skin of the mole, the epidermis contains an abundance of Merkel cell-neurite complexes and well-developed intra-epidermal sensory axons almost reaching the surface of the epidermis. In addition, there are many lamellated corpuscles immediately beneath the epidermis. Eimer's organ is the composite unit of sensory nerves of different modality.

►Merkel Cell-Neurite Complex Regeneration

Einstein Summation Convention

Definition

A notational device whereby a monomial of indexed quantities is interpreted as a summation over every index that appears diagonally repeated.

►Mechanics

Elastic Energy

Definition

The energy stored in a stretched spring, related to its extension (x) and spring stiffness (k) by $\frac{1}{2}\,k.x^2$.

►Energy/Energetics

Elastic Energy Savings

►Muscle and Tendon Energy Storage

Elasticity

Definition

A material model whereby the stress tensor at a point is just a function of the (present value of the) deformation gradient at that point.

►Mechanics
►Muscular Stiffness

Elderliness

►Olfaction and Gustation Aging

Electric Communication and Electrolocation

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Synonyms

Electrocommunication

Definition

Electric Communication: Via their electric organ discharges, which are under brain control, certain fish broadcast biologically relevant information into their environment. The information may include species, age, sex, or individual identity, and motivational state.

Electrolocation: The detection of usually weak electric fields of abiotic or biotic origin for orientation or object location, thanks to the electric sense that is present in all classes of lower aquatic vertebrates and monotreme mammals (platypus, echidna). Electrolocation is passive for ambient, extraneous electric fields. It is active when a weakly electric fish locates nearby objects that distort the fish's electric field.

Characteristics

Function

Electrocommunication

Electrocommunication differs greatly between the different taxa of electric fish [reviews 1–3].

Batidoidimorpha (Rays)

Torpedinidae (Electric Rays): The exclusively marine electric rays, such as *Torpedo* or *Narcine* species, discharge their strong electric organs for prey capture or defense (see entry "Electric organ discharge"). As with all strong-electric fish, a communication function of the electric organ discharge cannot be excluded, but evidence for such a hypothesis is lacking.

Rajidae (Skates): The predominantly marine weakly electric skates carry electric organs in their tail filament, the only known function of which is communication. *Raja* skates discharge only rarely, not even when swimming; however, in social encounters, such as when lying on top of each other, discharge sequences were recorded quite often. Depending on the species, electric organ discharges of 70–217 ms pulse duration were recorded in trains of less than 100, at less than 8 Hz. Although a correlation between electric organ discharges and overt behavior has been observed, much remains to be studied in skates.

Mormyriformes

Only Found in African Freshwater Bodies: (i) Gymnarchidae: The only living representative of the Gymnarchidae, *Gymnarchus niloticus*, is a large, piscivorous predator with a constant-frequency wave discharge. Its social behavior in relation with electrocommunication is virtually unexplored. However, it displays a Jamming Avoidance Response (JAR), or frequency shift, to an electric A.C. wave stimulus (if sufficiently close to its electric organ discharge frequency), which resembles the JAR in the South American gymnotiform *Eigenmannia virescens* (with similar discharge). (ii) Mormyridae (snoutfish): All snoutfish (about 200 species) studied to date generate electric organ discharges of the pulse type, waveform and duration of which are species-specific. Fish are active at night, when their electric organ discharge serves in group cohesion, at least in certain species [1].

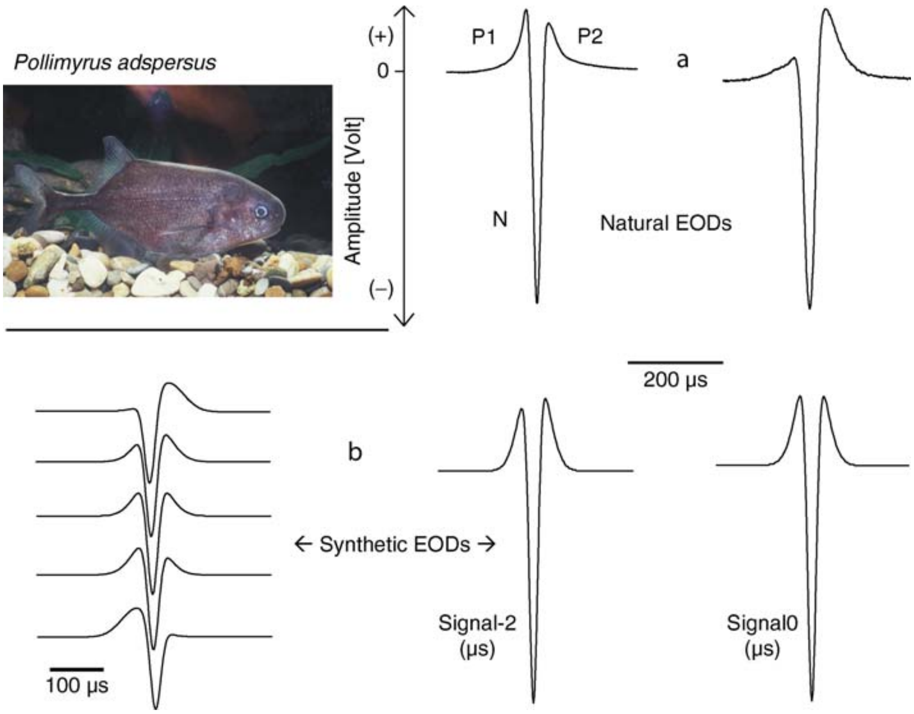
Species and individual signature by electric organ discharge waveform. Electric organ discharge pulse waveforms that differ between syntopic sibling species point to their significance in communication, and aid in systematic research [4]. Despite an electric organ discharge duration far below 1 ms, trained, food-rewarded *Pollimyrus adspersus* discriminated between playback electric-organ discharge waveforms pre-recorded from another species, and even between different conspecific individuals. The intraspecific waveform variability is much greater than the fish's discrimination threshold, suggesting the electric organ discharge waveform is an individual signature (Fig. 1). The discrimination between electric organ discharge waveforms, as present in *P. adspersus*, relies on a purely temporal (and not spectral frequency) analysis, as demonstrated by using synthetic electric organ discharges of different waveforms but identical amplitude spectra [5].

Electric organ discharge waveform and sex. Although the electric organ discharge waveform in individual mormyrids varies within a species-specific range that may be quite wide for certain species, it is highly stable for an individual fish. In the males of certain species, the electric organ discharge waveform broadens with adolescence, or readiness for reproduction. A seasonal sexual dimorphism in electric organ discharge waveform is present in *Marcusenius altisambesi* (Upper Zambezi River), with a tenfold longer electric organ discharge duration in mature males than females; but in many other species, such as *P. adspersus* or *Petrocephalus catostoma* (Upper Zambezi form), only a statistically significant difference between the sexes with wide overlap is found. There is no difference at all between the sexes in still other species (Fig. 2).

The detection of such electric organ discharge waveform variation has been shown to be instrumental for one or more of the following functions: (i) recognition of mate identity during the many hours of a spawning night, with its hundreds of short female visits and retreats; (ii) female choice regarding male quality (that is, intersexual selection); and (iii) intrasexual selection among males competing for resources to gain access to gravid females. Runaway selection for still longer male *M. altisambesi* electric organ discharges is blocked by catfish predators, who detect male electric organ discharges the longer the better, with their low-frequency electroreceptor organs (during the famous "catfish runs" in the Okavango) [6] (Fig. 3). For evolutionary theory, particularly in South American setting, see [3].

Sequence of Inter-Discharge Intervals: The sequence of discharge intervals (SDI) fluctuates with the state

E

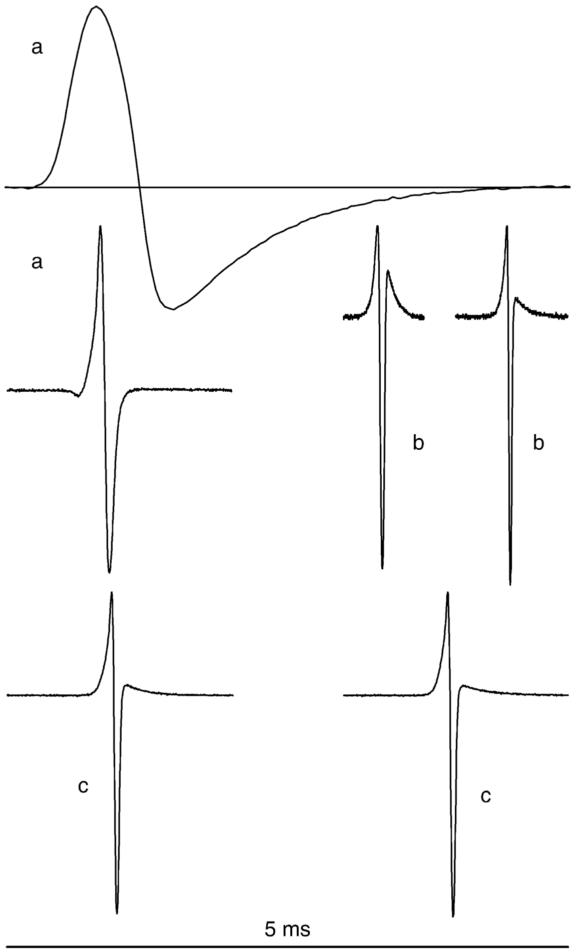


Electric Communication and Electrolocation. Figure 1 (a) Electric organ discharge as an individual signature for two *Pollimyrus adspersus* snoutfish. Note difference in amplitude ratio of *P1* and *P2* phases; *N* head-negative phase. (b) A family of computer-generated stimulus pulses were used to determine the discrimination threshold for an N phase shift. The fish still discriminated the symmetrical Signal0 from Signal-2 with its N phase advanced by 2 µs. Discharges normalized to the same amplitude (peak-to-peak) [5].

of excitation in a mormyrid fish. Therefore, the SDI appears suitable for signaling motivational state, potentially in addition to all the information the electric organ discharge waveform is already transmitting [7]. The signaling of species identity by SDI was demonstrated in *Petrocephalus bovei*, when it showed spontaneous preference for conspecific playback SDIs over those from two other species (*Pollimyrus adspersus* and *Brienomyrus niger*, with electric organ discharge waveform excluded as a factor). Similar results were obtained with *Campylomormyrus rhynchophorus*, which "preferred" conspecific SDIs to those recorded from immature *C. tamandua*; the reverse experiment, however, was inconclusive (difference not statistically significant). The result shows that SDIs may indeed encode species identity, and perhaps sex or age; however, between sibling species, electric organ discharge waveform prevails [2].

Agonistic Signaling: An especially clear correlation of characteristic SDIs with overt behavior has been established for aggression and escape (agonistic behavior) in several species [2]. Overt attack is announced by a transient, short-lived, sharp increase in discharge rate that may be followed by a decrease (SID). The correlation of overt behavior with electric signaling is so strict in *Gnathonemus petersii* and *P. adspersus* that the SID may be considered an integral part of the motor behavior attack, the two components apparently never occurring in isolation. In *G. petersii, P. adspersus*, and *Marcusenius pongolensis*, an attacking fish's SID is often not followed by a decrease, but by a short period of a very high and stable discharge rate (SI-HD). This steady-state, high discharge rate component (HD) may last up to 4 s in *G. petersii*. During this period, *G. petersii* may either display a long sequence of the shortest possible interval for the species (ca. 8 ms), or an interval about twice its duration, or the two intervals may alternate in a sustained double pulse pattern. Any combination of these patterns may occur in a single SI-HD. An aggressive fish's butt or bite of its opponent usually occurs at the end of the SID component, and the ensuing HD component is accompanied by a lateral (often antiparallel) display in close contact with the attacked fish. Compared to the discharge rate at the moment of physical contact, the HD component is usually twice that rate (up to 150 Hz). Multiple SI-HDs are observed in pairs of fish fighting about territorial dominance, with the HD component usually disappearing when one of the two opponents gives up.

In *G. petersii*, the loser of a fight usually increases its discharge rate during the moment of greatest danger

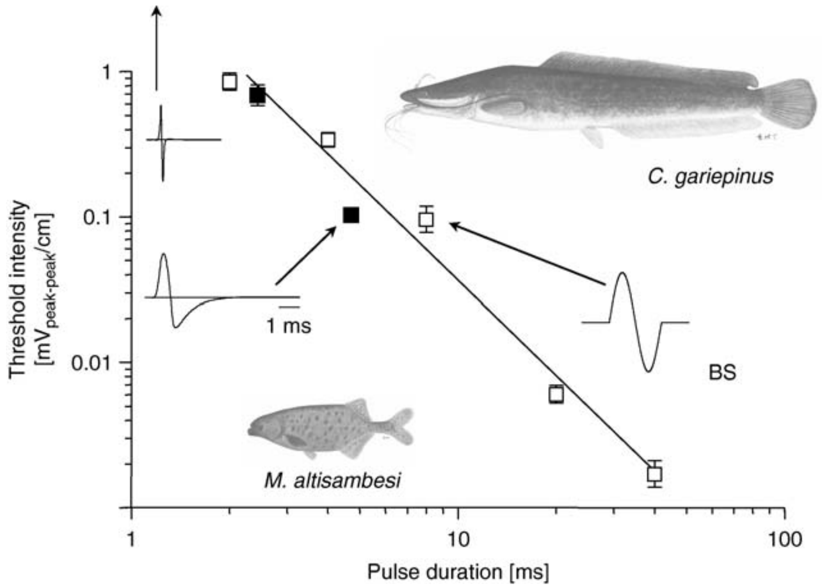


Electric Communication and Electrolocation. Figure 2 Electric organ discharge waveform and sex, in three snoutfish species of southern Africa. All electric organ discharges represented as voltage over time, recorded in the field immediately after capture. Same time bar for all. (a) Sexual dimorphism in *Marcusenius altisambesi* with two distinct waveforms. (b) Sex difference of only a statistical nature in *Petrocephalus catostoma* (Upper Zambezi form) with, in most males, a stronger second positive phase than in females, such as shown here. (c) *Petrocephalus wesselsi* (Sabie River, South Africa) with no difference between the sexes. *P. wesselsi* was recognized as distinct from *P. catostoma* only recently.

of being bitten by a dominant, attacking fish. In contrast to the aggressor, the subordinate fish's discharge rate remains well below the highest possible level. The increases given by a fish when actively escaping are preceded by a short electric organ discharge cessation of up to 1 s, contrasting strongly with the sequence of subsequent, short inter-discharge intervals (IDIs) of constant duration (at up to 55 Hz). As observed repeatedly in certain pairs of fish, these displays deter some aggressors' attacks. Therefore, they are thought to represent threat displays, resulting from a conflict between aggression and escape tendencies.

Playback experiments contrasting "resting" electric organ discharge patterns with "aggression" electric organ discharge patterns (as pre-recorded from fish showing the appropriate behavior), established that the "aggression" pattern was more effective in evoking activity from the resident fish. The "aggression" pattern evoked full-fledged electric and motor behavior of aggression, including butts, bites, and lateral displays with correct orientation towards the dipole model, and with correlated SI-HDs of the highest intensity [2]. This shows that a simple, immobile electrical decoy bearing no physical resemblance with a real fish (except in electric field geometry) is sufficient to evoke the most complex, coordinated social behavior in this animal, as observed in territorial defense and reproduction (*M. pongolensis*). Agonistic signaling is clearly a function of the IDI code of communication in mormyrid fish, and has been confirmed in similar form in other mormyrid species.

Signaling in Courtship and Spawning: The nocturnal reproductive behavior was first observed in captive *P. adspersus* from West Africa. In addition to elaborate electrocommunication and motor behavior, the male produces complex songs at night ("advertisement calls"). A male with a territory and a nest attracts gravid females from a distance. An intensely singing male attacks a visiting female while also displaying attack-correlated SI-HDs. The female quickly escapes, but keeps repeating her short visits at about 2–3 per minute, and the male's aggression and singing slowly wane. Without discharging, the female briefly advances onto the bottom in the male's territory or right inside his hiding place, and rapid antiparallel circling at surprisingly low electric organ discharge rates follows until the female's quick retreat. This provokes courtship attacks and again intense singing from the male. After several repeats, eventually the female allows the male to move into a parallel position from behind, when both fish mechanically link their anal fins. Thus united, the pair performs a full, slow rotation (3–4 s), head-over-tail or tail-over-head both occur, accompanied by a low-rate electric signaling (medium uniform rate). For about 2–5 h on a spawning night, the pair carry on this courtship behavior while the male's singing slowly wanes; he is completely silent during the later stages of courtship and also during spawning. The behavior preliminary to a spawning bout is an abridged version of a courtship bout. On the female's arrival at the spawning site, the male immediately positions himself alongside, stimulating her anal fin region with a quivering motion of his anal fin, followed by oviposition (a few eggs per visit), fertilizing the eggs, and transporting the eggs to the nest. Head-to-tail circling and the elaborate rotation part are omitted. The female marks the end of



Electric Communication and Electrolocation. Figure 3 Electrosensory thresholds of a snoutfish predator, the catfish *Clarias gariepinus* (*ordinate*), as a function of stimulus pulse duration (ms) *(abscissa)*. Food-rewarded catfish detected stimulus pulses the longer the better. □ bipolar, single-cycle sine wave stimulus, ■ electric organ discharge of two male *Marcusenius altisambesi* with electric organ discharges of long duration (compared to females). Note that the thresholds for the two male electric organ discharges agree well with those for bipolar sine wave pulses of similar duration, whereas the brief female discharge was ineffective as a stimulus, and threshold was not reached [6] (Fish pictures from P. H. Skelton).

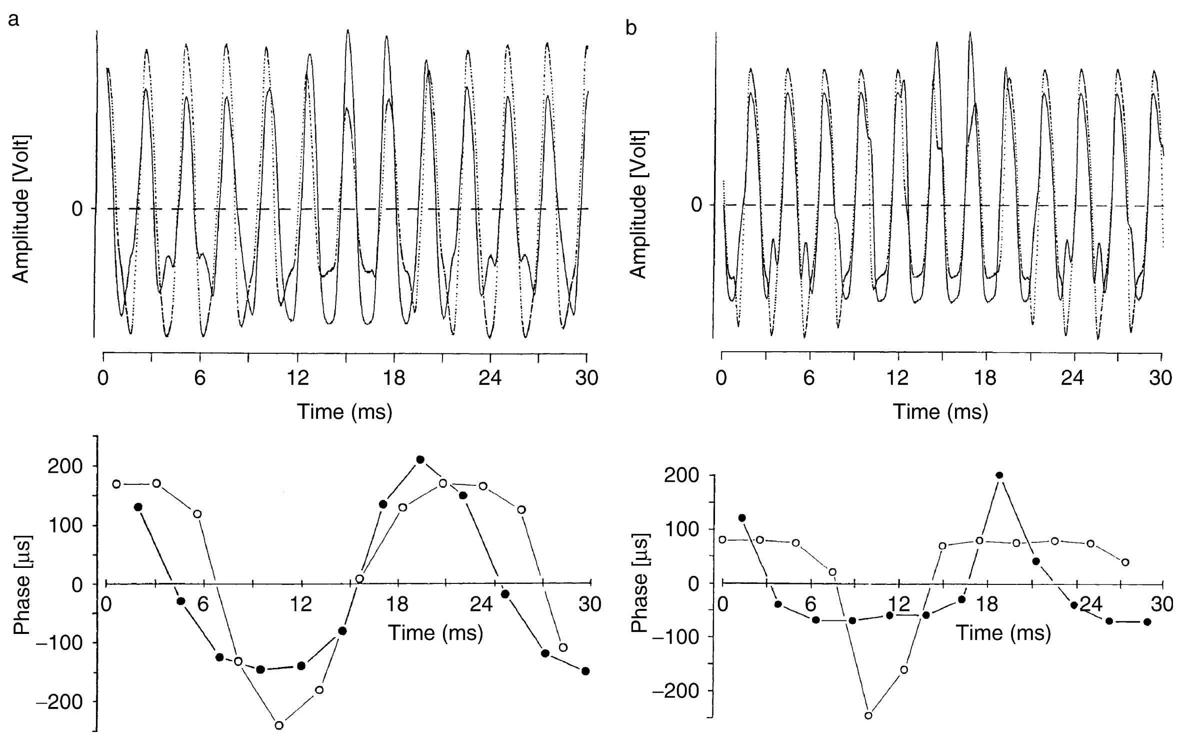
spawning by abruptly switching from a low and constant electric organ discharge rate to a pulse pattern that regularly alternates (at 2/s) between a low and a high electric organ discharge rate (that contrasts with all other patterns). The male's aggression returns immediately and is again accompanied by intense singing [2].

Siluriformes (Catfish)

Worldwide Occurring Freshwater Fish (Only a Few Marine): The African strong-electric catfish, *Malapterurus electricus*, stuns its prey and deters predators with its powerful discharges, and intraspecific electrocommunication is unknown in this fish (see the entry Electric Organ Discharge). Reports about weak electric potentials recorded from other African catfish (Mochokidae, squeakers, and the sharptooth catfish, *Clarias gariepinus*), suggestive of electric organs and electrocommunication, await confirmation or extension.

Gymnotiformes (Electric Knifefishes)

Only Found in South American Freshwater Bodies: The electric knifefish comprise perhaps 150 species, all of which seem to be nocturnal. All species known so far are weakly electric, except the electric eel, which is both strong and weakly electric (see entry Electric Organ Discharge). (i) *Pulse type knifefish:* Compared to the more erratically-discharging Mormyridae, pulse type knifefish generate electric organ discharges at either fairly constant (e.g. *Gymnotus carapo*, 35–55 Hz at rest) or even highly constant pulse rates (e.g. *Steatogenys elegans*, ~60 Hz). The former will respond to most kinds of disturbances by electric organ discharge rate changes, and give SIDs during agonistic behavior and attack on prey. Social messages and/or changes of excitation are thus encoded as pulse rate modulations, similar to (if less varied and less specific than) mormyrids. Some species feature sex differences in electric organ discharge waveform [3]. The latter species will change their electric organ discharge rates exclusively to specific electrical stimuli, as occurring in social context. Effective pulse stimuli are of nearly (or exactly) the same rate, especially at specific phase relationships relative to the receiver's discharge cycle. (ii) *Wave type knifefish:* Wave knifefish are probably the most stable biological signal sources. The Sternopygidae (at least 24 species) discharge at about 15–800 Hz, the Apteronotidae (at least 45 species) at about 500–1,800 Hz; a circadian rhythm does not seem to be present (unlike some pulse knifefish). Wave knifefish may signal to conspecifics by electric organ discharge waveform, by frequency modulations, by brief pauses that, especially when repeated, form a social signal, and by phase-locking to another fish's electric organ discharge cycle of identical frequency. As in pulse knifefish, much of the social behavior has yet to be explored. In *Eigenmannia virescens*, age and sex are encoded in electric organ discharge waveform; the fish even detect a difference in waveform in artificial wave stimuli when spectral amplitude cues are lacking, a feat the human ear cannot repeat for acoustic signals [8]. A wave fish such as *E. virescens* (individual A), detects another wave fish's electric organ discharges (individual B) of slightly different frequency, when B's electric organ discharges rhythmically modulate A's own electric organ discharges in amplitude and phase, that is, when B's electric organ discharges beat against A's electric organ discharges. Fish A analyses such a beat pattern for (i) the frequency difference, including its sign, (ii) the intensity of the spectral component, or harmonic, closest to its own electric organ discharge fundamental, and (iii) waveform of B. If (i) is small in absolute terms, fish A may give a Jamming Avoidance Response, or frequency change, usually increasing the difference from B, in order to improve the resolution or speed of its signal analysis. The strength of JAR increases with (ii), and strongly depends on motivation (age, sex, habituation, hunger, etc.). A trained, food-rewarded fish A is incapable of discriminating between two different stimulus waveforms of its own frequency, B and B', when an electronic frequency clamp is used that is designed to "frustrate" A's attempts of a JAR, by dynamically maintaining frequency identity of the stimulus with A's electric organ discharge. No sooner is the frequency clamp disabled than A (now successfully) performs a JAR and discriminates again. Stimulation experiments with a frequency clamp that, in addition to frequency identity of B with A, also controlled for a dynamically constant phase relationship of the B stimulus to the electric organ discharge cycle of A, showed that beat analysis is a purely temporal sensory mechanism, suggesting the involvement of only one kind of tuberous electroreceptor organs, the T units (Fig. 4).



Electric Communication and Electrolocation. Figure 4 Stimulus waveform detection by left-right comparison of beats (for the left and right body sides) in a wave gymnotiform, as mediated by its polarity-sensitive T electroreceptor units. (a) female *Eigenmannia virescens'* electric organ discharge (400 Hz) is superimposed by that of a close-by female in A, male in (b) (of both 30% amplitude and 450 Hz). *Top panels* additive superposition of signals (shown as *lines*) for one body side facing, say, the near pole of the stimulus source, subtractive ones facing the other pole (by curved field lines), *dotted* (representing the adequate stimuli for local T electroreceptor organs of the receiving fish's right and left body sides, respectively). One full beat cycle (20 ms) is shown centered. *Bottom panels* time disparities between the zero-crossings of the two curves (of *top panels*) as a function of time. Whether positive- (●) or negative-going (o) zero-crossings are chosen is irrelevant, as the time disparities between both represent the waveforms of the superimposing electric organ discharges in the same way and at greatly reduced speed (similar to using a stroboscope). The only difference is a 180° phase shift relative to the beat cycle. At such a high beat frequency as chosen here for illustration (50 Hz), the waveform reconstruction is rather crude; a more realistic beat frequency of 10 Hz (that is, a beat cycle of 100 ms) yields a fivefold better resolution [8].

The fish's threshold was lowest when the phase-locked stimulus evoked strong phase changes in a fish's electric organ discharge (measured as zero-crossings time shifts, detected by T units) but little amplitude change, and highest when amplitude change was strong (that is, optimal for the more "sloppy" amplitude-coding P units) but phase change minimal. Furthermore, with a free-running, not phase-locked, stimulus the JAR may already be evoked at stimulus detection threshold (that is determined by the sensitive T units), when the relatively insensitive P units are not responding.

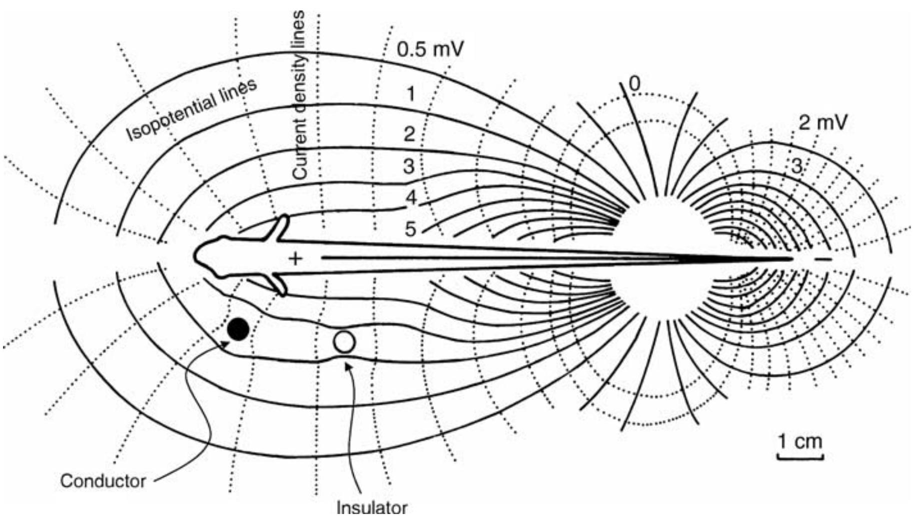
Electrolocation

Passive Electrolocation

Ampullary electroreceptor organs detect weak electric fields of extraneous origin in the passive mode. This is true for both the common, primitive (or original) receptor organ type and its secondarily evolved replica that is found in certain teleosts, such as catfish ("small pit organs") and weakly electric fish. Geochemical and electromagnetic fields of sufficient strength to stimulate these receptor organs are found in natural waters; this is also true for the bioelectric fields that emanate from live organism, including prey. The spectral frequency content of these fields is usually low (or even D.C.), corresponding to the properties of ampullary receptor organs (both kinds). Famous examples are sharks that detect the electric fields generated by their prey, such as flatfish buried under sand, using their ampullary electroreceptor organs, the ampullae of Lorenzini. The observed threshold sensitivities and attack distances were 5 nV/cm and 40 cm in marine sharks, and 5 μV/cm at 5 cm distance in freshwater teleosts [9]. Electric fields may also be used for orientation. In the ocean, electric fields are generated by the flow of water through the vertical component of the earth's magnetic field, while in freshwater bodies fields of electrochemical, rather than electromagnetic origin prevail. These environmental fields are potential orientational cues, as indicated by the behavior of trained animals. In the sea, motional-electric fields of up to 500 nV/cm have been measured; they may inform elasmobranch fish about their drift with the water, or provide them with orientational cues during their movements in familiar territory. Captive freshwater fish (catfish and weakly electric fish) have been successfully trained to orient at field strengths of 1 μV/cm.

Active Electrolocation

Active object detection is an evolutionary feat only present in the Mormyriformes and Gymnotiformes. It is based on a complex sensorimotor system comprising: (i) the generation of a test signal that is broadcast into the environment, the electric organ discharge; (ii) tuberous electroreceptor organs that are co-adapted



Electric Communication and Electrolocation. Figure 5 Active electrolocation in a weakly electric fish. Horizontal section through the electric field generated by a fish's organ (indicated by *central line* in the fish's body and tail). The dipole field is shown as *lines of equal current density*, or lines of force (*dotted*), which are normal to the *isopotential lines* (solid, with *mV* figures). Note that an insulator (*white circle)* and a conductor (*black circle*) distort the fish's field in opposite ways. The fish "feels" the presence of an object as an increase or a decrease of current intensity that is stimulating its electroreceptor organs next to the object. (The current is, of course, generated by the electric organ discharge.) A conductor pushes away the isopotential lines, increasing their density (or voltage gradient) next to the skin. This causes an increase of current flowing across the skin that is detected by tuberous electroreceptor organs. An insulator does the opposite; it decreases the isopotential line density and therefore current intensity (modified from H. Scheich).

to the spectral properties of the electric organ discharge (usually of much higher frequencies than present in ambient electric fields); and (iii) huge brains with specialized areas and somatotopic maps for complex computations on the sensory feedback (reafference) received from autostimulation. In its function and complexity, this system is comparable to the echolocation, or SONAR, system of many bats; however, the reach of this active electric system is severely limited by physical constraints.

A weakly electric fish detects the presence of an object when it distorts the geometry of the electric dipole field the fish generates with each electric organ discharge (Fig. 5).

Nonconducting objects, such as stones, force the electric current to pass around, whereas conducting objects (such as live organisms) attract the electric current. Therefore, a local decrease of resistivity (relative to the tropical freshwater of high resistivity) causes the current passing through the fish's skin next to the object to increase (for conductors), whereas a local increase in resistivity causes a decrease (for nonconducting objects). The tuberous receptor organs embedded in the skin faithfully reflect these changes in the strength of reafference from autostimulation. Receptor organ position on the fish's body and receptor response pattern are mapped to the brain. In mormyrids, active electrolocation is mediated by tuberous receptor organs termed mormyromasts rather than Knollenorgan, in gymnotiforms, it is probably both types of tuberous electroreceptor organs that are involved (B and M units for pulse fish, T and P units for wave fish). In addition to the resistive impedance properties of an object, an electric fish may also detect its capacitive impedance (if present). As long as they are alive, all organisms have considerable capacitive properties that filter the discharge in phase, waveform and spectral properties, making it thus detectable for the fish [10].

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E

Electric Field

Definition

A space-filling force field around every electric charge or group of charges.

►Electric Fish

Electric Fish

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Synonyms

Electrogenic fish

Definition

Some fishes possess electric organs who's only known function is the generation of electricity outside their bodies. Strong organs are for defense and stunning prey, weak organs for active electrolocation and electrocommunication in nocturnal species.

Characteristics

For more detailed reviews, see [1–3]. Any living tissue generates an electric field in its environment. The field is associated with the regulation of the tissue's ionic balance. These fields are D.C. or of low frequency, and, in animals, usually modulated by superimposed field potentials arising from normal nerve and muscle