return to the opposite pole of the source. This is important in freshwater fish with water conductivity far below the conductivity of body fluids (usually below 100 μS/cm for tropical freshwaters vs. 5,000 μS/cm for body fluids, or, in resistivity terms, 10 kOhm × cm vs. 200 Ohm × cm, respectively) [4].

In strongly electric fish, impedance matching to the surrounding water is especially obvious, both on a gross morphological level and also regarding membrane physiology. In freshwater fish, such as the South American strongly electric eel, there are only about 70 columns arranged in parallel, consisting of about 6,000 electrocytes each. Therefore, in this fish, it is the voltage that is maximized (500 V or more). In a marine environment, this would not be possible; here, it is the current that should be maximized. Accordingly, in the strong electric rays, such as the *Torpedo* species, there are many relatively short columns arranged in parallel, yielding a low-voltage strong-current output. The number of columns is 500–1,000, the number of electrocytes per column about 1,000. The discharge amplitude is only 50 V in air, corresponding to a massive power output of greater than 1 kW at the peak of the pulse. For an unknown reason, marine electric fish generate (unusually large) postsynaptic potentials (PSPs) rather than muscle action potentials.

References

1. Moller P (1995) Electric fishes: history and behavior. Chapman & Hall, London
2. Kramer B (1996) Electroreception and communication in fishes. Gustav Fischer Verlag, Stuttgart
3. Kramer B (1990) Electrocommunication in teleost fishes: behavior and experiments. Springer, Berlin Heidelberg New York
4. Bennett MVL (1971) Electric organs. In: Hoar WS, Randall DJ (eds) Fish physiology. Academic Press, London New York, pp 347–491
5. Zakon HH (1988) The electroreceptors: diversity in structure and function. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer, Berlin Heidelberg New York Tokyo, pp 813–850
6. Gosse JP (1984) Mormyriformes. In: Daget J, Gosse JP, Thys van den Audenaerde DFE (eds) Check-list of the freshwater fishes of Africa (CLOFFA). Office Rech Sci Tech Outre-Mer (ORSTOM), Bondy (France)/Mus R Afr Cent (MRAC), Tervuren (Belgium), pp 63–124
7. Albert JS, Campos-da-Paz R (1998) Phylogenetic systematics of Gymnotiformes with diagnoses of 58 clades: a review of available data. In: Malabarba LR, Reis RE, Vari RP, Lucena ZM, Lucena CAS (eds) Phylogeny and classification of neotropical fishes. Edipucrs, Porto Alegre, pp 419–446
8. Kramer B, van der Bank FH, Wink M (2004) The *Hippopotamyrus ansorgii* species complex in the Upper Zambezi River System with a description of a new species, *H.* szaboi (Mormyridae). Zoologica Scripta 33:1–18
9. Zakon HH, Unguez GA (1999) Development and regeneration of the electric organ. J exp Biol 202:1427–1434
10. Westby GWM, Kirschbaum F (1978) Emergence and development of the electric organ discharge in the mormyrid fish, *Pollimyrus isidori*. II. Replacement of the larval by the adult discharge. J Comp Physiol A 127:45–59

Electric Organ

Definition

So far only electric fishes are known to possess electric organs. In most cases myogenic organs generate electric fields. Some fishes, like the electric eel, use strong fields for prey catching or to ward off predators, while others use weak fields for electrolocation and communication.

Specialized organs in electrosensitive fishes – mostly derived from muscle tissue – that give off electrical discharges, both pulse-like and sinusoidal, under the control of the nervous system.

►Electric Senses in Monotremes: Electroreception and Electrolocation in the Platypus and the Echidna
►Electrolocation
►Electroreceptor Organs
►Reafferent Control in Electric Communication
►Temporal Coding in Electroreception

Electric Organ Discharge

Bernd Kramer
University of Regensburg, Institute of Zoology,
Regensburg, Germany

Synonyms

EOD; organ discharge

Definition

Certain fish possess an electric organ that, on brain command, generates a three-dimensional electric dipole field around their bodies. Compared to incidental stray fields as measured close to any organism [1], an electric organ discharge (EOD) is characterized by a stronger amplitude, higher temporal and spatial stability, and a species-specific orientation that is adapted to its function.

Characteristics

Quantitative Description

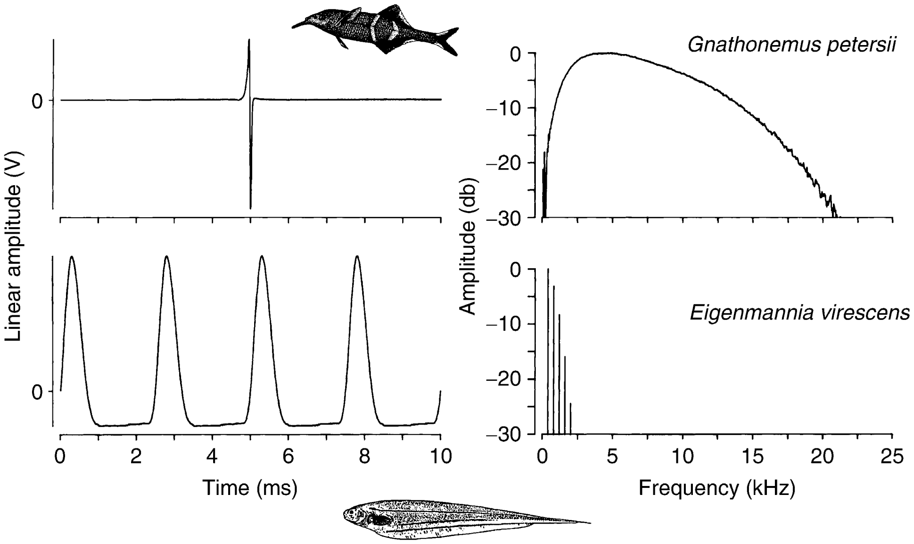
Strongly electric fish all generate monopolar (D.C.) pulses. They are head-positive or head-negative in horizontally attacking fish, and dorsal-negative or dorsal-positive in vertically attacking fish. The time course of an individual EOD pulse is that of a muscle action potential, or of a postsynaptic potential (PSP) in the marine skates, rays, and stargazers (skates possess only weak organs). For the human touching a fish, perceived amplitudes range from mild discomfort associated with the EODs of the weakest strong-electric fish, the marine stargazers (up to 5 V with its dorsal surface in air), to intense pain caused by, for example, the electric catfish's (►*Malapterurus electricus*) or the electric eel's EODs (►*Electrophorus electricus*; several hundred Volts).

There are two phenotypes of weakly electric freshwater fish (Mormyriformes, Gymnotiformes), pulse and wave species (Fig. 1).

Played through a loudspeaker, wave EODs sound tonal and are termed "hummers," whereas pulse species are sometimes termed "buzzers." In wave EODs, pulse duration and the inter-pulse interval are of about the same length, and merge into a constant-frequency wave. Frequencies range from about 50 to about 1,800 Hz. The amplitude spectrum of a wave EOD, such as that of ►*Eigenmannia virescens,* shows a few discrete frequency lines only where all the energy is concentrated. These frequencies are the fundamental frequency (which is the repetition frequency of the discharge "pulse," or of a single signal period), and the higher harmonics which are integer multiples of the fundamental.

Pulse EODs are single-cycle clicks repeated at rates from below 1 to about 65 Hz at rest. Pulse discharges are separated by pauses that are long (and often variable) compared to the duration of an EOD. The amplitude spectrum of a single pulse shows energy over a broad and continuous frequency range with a flat peak region; that is, the signal is broadband. Frequencies of peak amplitude are usually below 10 kHz (but may be as high as 25 kHz). For intraspecific and interspecific waveform or frequency differences see the entry "electric communication and electrolocation."

Wave EODs represent a continuous drain of energy for the sender; there are no strong-electric wave fish. Compared with most wave EODs, pulse EODs are of lower repetition rate and stronger amplitude. Pulse EODs may be detected over a greater distance because of their usually stronger amplitude. This would be an advantage for both communication and active electrolocation. However, wave EODs compensate for being weak by strongly contrasting from background noise by their harmonic structure. There is no or little D.C. component to the EOD of wave fishes (only a few studied), unlike that of many pulse species, making them less prone to detection by certain predators [2,3,4].



Electric Organ Discharge. Figure 1 Pulse and wave discharges. *Left* Oscillograms of EODs (head-positivity is upwards); *right* amplitude spectra with the amplitudes expressed as dB attenuation relative to the strongest spectral component. Same time and frequency axes. Pulse EODs, such as that of the African snoutfish *Gnathonemus petersii*, are short and broad-band; they are repeated at highly variable rates. The wave EOD of the South American knifefish *Eigenmannia virescens* is of constant frequency and harmonically structured.

Higher Level Structures

As two spike-generating membranes arranged in series with each other tend to desynchronize each other's activity, each electrocyte must be innervated separately to receive the central command synchronously [2]. The electric catfish probably has the simplest command system for controlling its electric organ. It consists of only two giant electromotoneurons (>100 μm diameter) in the first spinal segment, one on either side. Both cells are closely coupled electrotonically by presynaptic fibres, and behave functionally as a unit. Each giant cell innervates the millions of electrocytes on its side of the body.

In gymnotiforms, the command system has four levels from peripheral to central: spinal electromotoneurons, medullary relay cells, medullary pacemaker cells, and mesencephalic prepacemaker cells. Pacemaker and relay cells either form two separate, but closely adjacent, midline nuclei (for example, in a ►*Hypopomus* pulse fish species), or are intermingled in a single nucleus, as in an *Eigenmannia* wave species [5].

Depending on the species, there are some 30–200 pacemaker cells activating about 50 large relay cells in gymnotiforms, and they project to hundreds or thousands of spinal electromotoneurons. In all gymnotiforms, except apteronotids, electromotoneurons innervate a number of electrocytes. In apteronotids, the electromotoneurons themselves generate the discharge. The connection of the command system to electroreceptive afferences is by the nucleus electrosensorius rostral from and connecting to the prepacemaker nucleus, which have been shown to modulate the pacemaker firing frequency.

At each level of the gymnotiform command system a single spike occurs for each organ discharge. However, in wave gymnotiforms the electromotor neurons have been observed continuing to firing at a similar frequency after completely cutting their input from relay cells by spinal section. Ringing seems to be an intrinsic property of all parts of the command system in these fish (and has even been observed in electroreceptor organs), and may somehow be necessary for generating the most stable biological rhythm, the wave discharge.

In mormyrids, the electromotoneurons that innervate the electrocytes of the organ form a nucleus in the caudal spinal cord [2,6]. They are driven by the cells of a medullary relay nucleus, a single midline structure, by chemical synapses. Electromotoneurons and relay neurons are coupled together electrically amongst each other. The medullary relay cells fire in "doublets" that evoke a triplet of spikes in the electromotoneurons. The three spikes are propagated out to the electrocyte stalk, where the first spike causes a small PSP, the second spike a greatly facilitated PSP, and the third spike reaches threshold. Thus, each volley of three spikes (about 1 ms apart) evokes only a single discharge. The triplet can be recorded externally.

The pacemaker nucleus is a midline structure of 16–20 relatively small neurons located just ventrally to the medullary relay nucleus. The cells are functionally coupled by gap junctions. In contrast to the cells of the relay nucleus, their dendrites extend far beyond the confines of the nucleus, into the surrounding reticular formation and longitudinally running fibre tracts, where they are presumably contacted by the most diverse sources. It is probably these afferent inputs that mediate the effect of virtually any kind of sensory input on a mormyrid's discharge rate.

Command-associated corollary discharges "inform" afferent brain areas, such as the ELL (electrosensory lateral line lobe), of a reafference to be expected from the fish's own electroreceptor organs that is evoked by the fish's own EOD [7]. The corollary discharges greatly facilitate the task of separating reafferences from exafferences, by blanking "unwanted" sensory input. Reafferences to a fish's own EODs are the adequate response from mormyromast electroreceptor organs (in active electrolocation), and exafferences are the adequate response from the Knollenorgan, to another fish's EODs (in communication). Therefore, mormyromast afferences are facilitated when coincident with a corollary discharge, but blanked when not. For sensory feedback from Knollenorgans, the reversed situation holds: reafferences are blanked, and exafferences are facilitated.

Lower Level Components

Electric organs are derived from muscle tissue (nerve terminals in Apteronotidae), although different muscle groups are involved in different taxa. These muscle cells are unusual in that they do not twitch when neurally excited by transmitter substance (acetylcholine); various anomalies have been found in different groups that may explain why in electric organs the electromechanical coupling does not work.

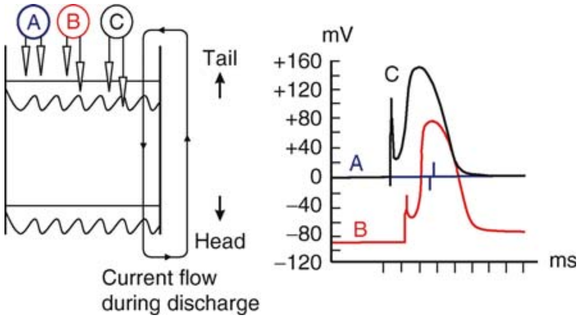
Often these muscle cells, or electrocytes, form short cylinders and are stacked in series, an arrangement that increases the voltage. Several such columns in parallel increase the current, and are enclosed by a tight jacket of connective tissue. There is also connective tissue inside the columns, as well as blood vessels and nerve fibres. In general, the columns are orientated rostro-caudally, as is the potential difference and the direction of internal current flow. In the bottom-dwelling stargazers and the electric rays, the columns are orientated vertically (dorso-ventrally), in accordance with their upwards directed attacks on prey fish [review 4].

In contrast to all other electric fish, the apteronotids (Gymnotiformes) have neurogenic electric organs; their presynaptic nerve fibres have lost their contact with muscle cells and form the organ (larval apteronotids have a temporary organ of myogenic origin; [8]). Apteronotids are outstanding for their very high discharge frequencies, up to 1,800 Hz in certain species. No ordinary nerve or muscle tissue comes close to even half that rate (at least not in sustained activity), and the explanation may reside, in part, in a command pathway with exclusively electrotonic synapses, and the specialized anatomy and physiology of the electric organ.

The ionic mechanisms of electrocyte membranes differ widely among species; these differences are the main source of the wide variation of organ discharge waveforms and frequencies among species [2,5]. The mechanism of the electric eel's discharge was the first to be elucidated (Fig. 2).

The electrocytes are innervated on their posterior face by spinal nerves that contact the cell primarily on short stalks. The anterior faces are uninnervated and have an increased surface area by a large number of papilli. The innervated face responds to depolarization by an overshooting spike of unusual amplitude (150 mV). The uninnervated face of very low resistance is unexcitable (0.2 $\Omega\cdot\text{cm}^2$ as compared with 19 $\Omega\cdot\text{cm}^2$ for the innervated face, and about 3000 $\Omega\cdot\text{cm}^2$ for frog twitch muscle). The two faces of the electrocyte are thus fairly matched in impedance, still more so when the innervated face becomes excited (and its resistance declines). This is clearly an organ adapted to maximum power output, because the circuit for all the Na^+ inward current of a cell is completed by the external environment, and not by local opposing currents [2].

In contrast to freshwater fish, marine strong-electric fish, including the stargazer, generate exceptionally large PSPs (of up to 90 mV amplitude) instead of spikes. Their membranes can only be excited neurochemically, not by depolarisation. The advantage of a PSP- over a spike-generating membrane in the marine environment is unknown.



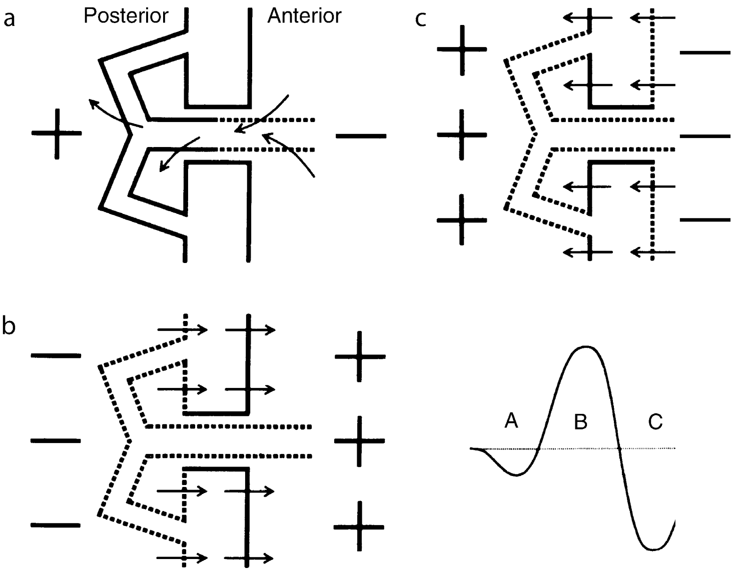
Electric Organ Discharge. Figure 2 The mechanism of the electric eel's discharge. (A) A pair of recording electrodes external to the innervated face of an electrocyte records no response to a brief stimulus (*blue*; note a small, diphasic stimulus artifact). (B) One electrode is advanced into the cell. The inside negative resting potential of about 90 mV and an overshooting action potential of about 140 mV are recorded (*red*). (C) When the exploring electrode is advanced to outside the uninnervated face, the resting potential disappears, but the spike is essentially unchanged [after Keynes & Martins-Ferreira 1953, modified B. Markowski].

Most weakly electric freshwater fishes tend to have little or no D.C. associated with their discharges, which allows them to have a more effectively dual electrosensory system: one for low-frequency voltages of primarily external origin, and another for monitoring the higher-frequency organ discharges. The wave fish ►*Gymnarchus niloticus* (perhaps also *Eigenmannia* species) achieves an organ discharge free from D.C. by modification of one electrocyte face (the uninnervated one) to pass current only capacitatively. This face has a large capacitance and a high resistance and is unexcitable [2]. Essentially, diphasic pulse fish, such as some *Hypopomus* species, *Gymnotus carapo*, and most mormyrids, have the opposed faces of their electrocytes act in sequence to achieve a similar effect. The uninnervated face is electrically excited to generate a spike that is slightly delayed compared to the spike of the innervated face. The net result is a diphasic potential, because the currents flow in opposite directions (with some cancellation in the shorter discharges).

In contrast to mormyrids, many gymnotiforms (excepting the sternopygids) have more than one organ, which are either anatomically distinct (as in the eel, and certain hypopomids and apteronotids that carry rostral accessory organs), or functionally heterogeneous (as in *G. carapo* where the dorsal portion of the organ is fired ½ ms early; in addition with reversed polarity because of its reversed pattern of innervation). This complexity is reflected in additional phases or inflexions to the basically diphasic discharge waveform, and additional deviations from the geometry of a dipole source at close range, making them species- or even individually specific signatures.

Mormyrids have more or less elaborate stalks of the innervated face of the electrocytes. The simplest (probably primitive) stage is that of ►*Mormyrus rume*, with multiple innervations on fine and numerous stalks. In species with shorter discharges, the number of innervation sites is reduced to the final limit of one, suggesting that more precise synchronization can be achieved with fewer innervation sites. Synchronization is especially important in these bi- or triphasic discharges, because slight out-of-phase firing would lead to cancellation. The stalks may, in certain species, penetrate the electrocyte and find their nerve on the "wrong", usually the anterior, side of the cell, and this shows up in the overall organ discharge by an initial, weak head-negative potential in addition to the diphasic "main" discharge (Fig. 3).

In a few species, the stalks penetrate the cell twice so they contact their nerve on the "correct" side of the cell



Electric Organ Discharge. Figure 3 Schematic explanation of a diphasic electric organ discharge (EOD) of a mormyrid, which in certain species is preceded by a smaller prepotential (*A* in EOD diagram, *lower right*). *Arrows* show direction of current flow; active membranes are indicated by *dotted outlines* in order to show which stage in the excitation sequence (a, b, c) corresponds to which phase in the EOD waveform. A head-negative prepotential (*A*) is present when electrocyte stalks (formed by the posterior face) penetrate the electrocyte to contact the motor nerve from the "wrong" anterior face (such as here). The stalk potential invades the caudal face of the electrocyte, giving rise to the head-positive main phase of an EOD (*B*). The associated current flow through the electrocyte (b) triggers an action potential of the opposite, uninnervated cell face (c), giving rise to the head-negative main phase of an EOD (*C*). Evolving a bipolar EOD reduces the D.C. component detectable to catfish predators. The cost of a bipolar EOD is a loss of amplitude, especially in the many species that terminate the *B* phase early by fast triggering of C [2].

(usually the posterior one, just like in species with non-penetrating stalks). Some species have a combination of penetrating with non-penetrating stalks [2,3,9].

In some species such as *Pollimyrus adspersus* and *P. isidori*, the relatively long-lasting head-positive potential generated by the posterior face is split into two by an overriding, strong and brief spike of opposite polarity generated by the anterior face. Microsecond-timing of the second potential relative to the first is critical for the overall waveform within a relatively wide intraspecific variability (see "electric communication and electrolocation").

Structural Regulation

Impedance matching is clearly seen in marine and freshwater strongly electric fish, with both adapted to most efficient shocking in their respective environments. The marine species have flattened organs with many columns in parallel (500–1,000 columns, each with about 1,000 cells in series in ►*Torpedo* rays; 150–200 in the stargazer). Their organs generate a low-voltage strong-current output as is adequate for their conductive medium; for marine rays, 50 V measured in air, but >1 kW at the peak of a 5-ms pulse. In contrast, electric organs of freshwater species (teleosts) are often long, generating a high-voltage, low-current field (>500 V), as indeed they must in a medium of high resistivity. The eel has about 6,000 electrocytes in series, and dorsoventrally about 35 (bilaterally) in parallel [2,3,9].

Higher Level Processes

For the ionic mechanisms of firing rate in a pacemaker nucleus, see [5]. In wave gymnotiforms, androgen hormones affected the discharge frequency [5].

Lower Level Processes

There are clear effects of androgen hormones on EOD waveform when administered to mormyrids, especially females that usually respond by increasing their pulse duration [3,9,10].

Process Regulation

A sudden, strong decrease of water conductivity may cause complete or partial loss of a mormyrid's head-negative EOD main phase (that is electrically evoked). The waveform is restored after a period of about two days, supposedly by the synthesis of additional ion channels [4,5].

Function

Electric communication and Electrolocation: see the special entry on these topics.

Prey capture and defence. Strong-electric fish discharge for prey capture, defence, or related functions. Volleys of monopolar pulses lead to more effective shocking, irrespective of polarity. There is little or no evidence for an intraspecific communication or active electrolocation function in these fish; however, the negative evidence is compelling only in the non-electroreceptive stargazers.

Torpedo marmorata (electric ray). A ray is an ambush predator with a flattened, disc-shaped body with short tail that is usually buried under sand, with only its eyes and spiracles visible. A ray will start its predatory attack, accompanied by its deadly discharge volley, whenever a fish comes sufficiently close to the front rim of its body. Within half a second, the ray lifts itself up on its pectoral fins, jumping up and forward, landing on top of its prey in a successful attack. By rocking movements involving its tail, the ray tries to seize the head of its prey with its mouth and to swallow it; this takes from 7–24 s.

The electric organ is fired 80 ms after the onset of a ray's jumping attack. The duration of the discharge volley varies between 0.1 s (when the prey escaped) to 24 s, corresponding to 20–340 EODs. The discharge rate is high and stable up to the moment of landing (140–290 Hz); afterwards, when the ray tries to seize the prey with its mouth, the pulse rate is low and unstable (<10 Hz after 3 s of discharging).

The effect of a ray's electric discharge is quite devastating. Fish were partially immobilised, slowly turned black on one or both body sides, or had a broken spinal cord. Fish that closely managed to escape died one or a few days after. This is astonishing since the current density, as measured in seawater, was not particularly high (30 mA/cm^2, at 15 V). Stimuli that effectively evoked an attack were touch and water current or pressure waves from objects passing by, at a distance not greater than ½ the diameter of a ray's disc.

Malapterurus electricus (electric catfish).This species of electric catfish is a large, strong-electric predator of up to 1.2 m (there are several new members of the genus in African freshwaters). Its head-negative EOD of 1.3 ms duration at 28°C is evoked by mechanical and gustatory stimuli. In an attack on prey, a feeding volley may be up to 562 EODs at 300 Hz; still longer volleys of still higher frequency were observed when defending itself against a superior predator (such as a conspecific or a *Clarias* catfish of bigger size). A surgically denervated catfish unable to discharge had a drastically lowered success rate in prey capture.

Electrophorus electricus (electric eel). The electric eel is the only South American knifefish having both a weak and a strong discharge. There is evidence that the eel may prey largely on other gymnotiforms; unlike the electric catfish, the eel possesses, in addition, the high-frequency electroreceptor organs required for detecting many species' EODs. When roaming around its territory at night, it discharges its weak Sachs' organ at a very low rate (around 1/s or even below). The weak discharge may aid the fish in detecting obstacles etc. by active electrolocation, and warn other eels at a distance. Upon mechanical disturbance of any kind, including surface water waves when sufficiently close, or else a fellow gymnotiform's EOD, the eel strikes at the object with its wide and strong mouth. Concomitantly with an overt attack, the eel turns on its strong discharge (generated by the main organ, assisted by two weaker organs) at a very high rate (500 Hz or more) [2,3,4].

Pathology

Very rarely, certain mormyrid specimens showed EOD waveforms that appeared totally deviant compared with all other specimens ever seen before or thereafter (e.g., *Brienomyrus niger*). An ontogenetic anomaly, or an imperfect regeneration after a predator's attack, are possible reasons for this malfunction. Electroreceptive predators of weakly electric fish are common in both South America (e.g., the electric eel and certain apteronotids) and Africa (several species of non-electrogenic catfish, such as *Clarias gariepinus;* the mormyriform *Gymnarchus niloticus;* the electric catfish). Especially in certain gymnotiforms, specimens sampled from their habitat quite commonly had regenerated or malformed tails.

Immediately after transfer into water of very low conductivity (such as 10 μS/cm, as found in certain tropical forest streams), very rarely certain mormyrid specimens tended to display EOD triplets, rather than one single strong discharge, per command (e.g., *G. petersii*). A propensity for EOD triplets has also been observed in one *Marcusenius macrolepidotus* individual even without conductivity stress.

References

1. Peters RC, van Wessel T, van den Wollenberg BJW, Bretschneider F, Olijslagers AE (2002) The bioelectric field of the catfish *Ictalurus nebulosus*. J Physiol Paris 96:397–404
2. Bennett MVL (1971) Electric organs. In: Hoar WS, Randall DJ (eds) Fish physiology, vol 5. Academic, London, pp 347–491
3. Bass AH (1986) Electric organs revisited: evolution of a vertebrate communication and orientation organ. In: Bullock TH, Heiligenberg W (eds) Electroreception. Wiley, New York, pp 13–70
4. Kramer B (1996) Electroreception and communication in fishes. Gustav Fischer Verlag, Stuttgart

5. Stoddard PK, Zakon HH, Markham M, McAnelly L (2006) Regulation and modulation of electric waveforms in gymnotiform electric fish. J Comp Physiol A 192:613–624
6. Meek J, Nieuwenhuys R (1998) (The brains of) holosteans and teleosts. In: Nieuwenhuys R, ten Donkelaar HJ, Nicholson C (eds) The central nervous system of vertebrates. Springer, Berlin Heidelberg New York, pp 759–937
7. Bell CC, Han VZ, Sugawara Y, Grant K (1999) Synaptic plasticity in the mormyrid electrosensory lobe. J Exp Biol 202:1339–1347
8. Kirschbaum F (1995) Reproduction and development in mormyriform and gymnotiform fishes. In: Moller P (ed) Electric fishes: history and behavior. Chapman & Hall Fish and Fisheries Series, vol. 17. Chapman & Hall, London, pp 267–301
9. Hopkins CD (1999) Design features for electric communication. J Exp Biol 202:1217–1228
10. Landsman RE (1995) Sources of plasticity in behavior and its physiology: sex, hormones, environment and the captivity model. In: Moller P (ed) Electric fishes: history and behavior. Chapman & Hall, London, pp 303–343

Electric Orientation

►Magnetic and Electric Senses

Electric Senses in Monotremes: Electroreception and Electrolocation in the Platypus and the Echidna

GERALD LANGNER[1], HENNING SCHEICH[2]
[1]Neuroakustik, Fachbereich Biologie, TU Darmstadt, Darmstadt, Germany
[2]Leibniz-Institute for Neurobiology, Magdeburg, Germany

Definition

The Australian platypus, *Ornithorhynchus anatinus*, and the two species of spine covered echidnas, *Tachyglossus aculeatus* and *Zaglossus brujnii*, are the only surviving species of ►monotremes. Among the three tribes of extant mammals, monotreme, marsupial and placental mammals, monotremes are the most primitive and limited to Eastern Australia, Tasmania, and New Guinea.

Since little is known about the role and function of the electric sense in echidnas this article focuses mainly on the platypus. The nocturnally diving platypus subsists entirely on live food caught during nightly dives in lakes and streams. With eyes, nostrils, and ear canals closed underwater, its ability to locate and catch mobile prey like crayfish, shrimp, and small fish is unlikely to depend exclusively on the remaining tactile sense of the bill which has long been known to be covered with mechanoreceptor organs. Behavioral experiments have shown that the platypus can detect weak electric fields. It locates small living objects and avoids large obstacles provided they generate such fields. The legendary sixth sense of the platypus was shown to be electrical. Several lines of evidence suggest that electroreception in monotremes has evolved independently from the corresponding senses in fishes and amphibians.

Characteristics

The platypus with a body length of about 45 cm is characterized by short legs, a flat tail, a dense fur with remnants of reptile scales, a duck-like bill of 15 cm length, small eyes, and a lack of pinnae. The male is slightly larger than the female. Aspects of its scull as well as its brain are reminiscent of those of reptiles. Its broad paws have five toes with sharp claws. A single poisonous hollow spur is exposed on the hind feet of the male. The urinal and genital tracts and rectum have a common opening (cloaca). Another unusual reptile-like characteristic of monotremes is that the platypus lays 2–3 eggs of about 2 cm. Embryos of 2.5 cm length hatch after a week, and are blind and nude. Their teeth are replaced by horn plates at a later stage of development. The platypus as well as the echidna are not endangered species, as their only natural enemies are snakes, crocodiles, marsupial foxes, and probably in former times the Tasmanian wolf.

The platypus lives in a self-made burrow, always near fresh water, which may be extremely long (10–20 m) and has its openings slightly above water level. It has adapted to catch small animals in water and roams about creeks and rivers in Eastern Australia and Tasmania. At dawn the animal swims and dives and then may stay under water for 5 min. It uses skin folds to close its eyes, ears, and nostrils, and relies totally on its somatosensory and electrical senses to feed on live prey, including several species of grubs, worms, decapod crustaceans, frogs, and small fishes. Typically the animal shows reflex-like head jerks when encountering transient electric fields in the millivolt range which may be generated by its prey.

Quantitative Description

Description of Structures, Processes, and Conditions

As recently as 1986 a German–Australian team of biologists from the Universities of Darmstadt and Canberra discovered that the large bill of the platypus is not only a