

Elephant-Nose Fish

Gnathonemus petersii

Echolocation in Fish: The Electric Organ Discharge

Introduction

Electric fish played a significant role in the early history of neuroscience in that they figured in debates about animal electricity of Galvani and Volta's time. Fish of this sort interest neuroscientists today because of the extraordinary sensitive and precise system of generating, receiving, processing and responding behaviorally to electric signals.

Seven families of fish deliver appreciable voltage outside their bodies. Although a few predators kill prey electrically, investigators believe that the majority of weakly electric fish use this precise, highly specialized sensory guidance system for environmental navigation by echolocation much as bats and dolphins do. Such adaptations have obvious advantages for survival both offensive and defensive. Evidence also suggests that signals are used for communication including species and sex recognition in their low visibility environment.

Electrolocation operates on the following principle. By discharging the electric organ, the fish generates a current field which emanates from its anterior body and then converges on the tip of its tail. Electroreceptors on the anterior body surface monitor the local transepidermal current flow associated with the electric organ discharge (EOD). See Figure 1.

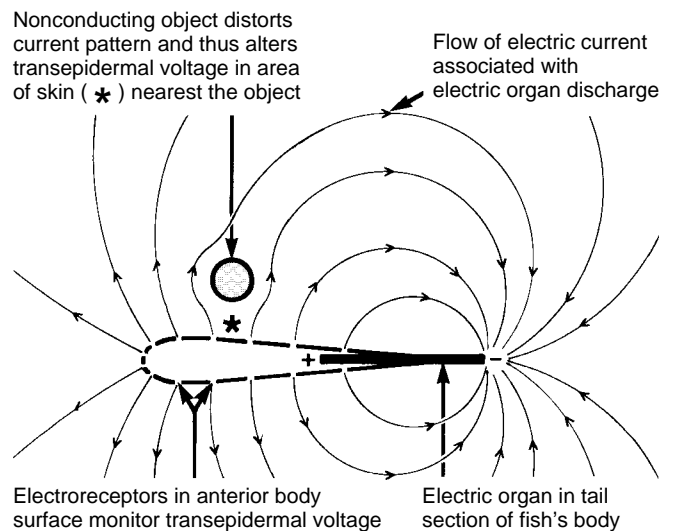


FIGURE 1. The principle of electrolocation. Longitudinal horizontal section through simplified electric fish indicates location of electric organ by *black bar*. Electroreceptors are found in pores of anterior body surface. (From Heiligenberg, 1977)

These fish continually probe their environment electrically. They test the conductivity of the water around them and locate variations by detecting distortions produced in their own electric field. An object that differs in impedance from the surrounding water distorts the electric field and alters the pattern of transepidermal current intensities in the area of the body surface closest to the object. By monitoring changes in electroreceptor activity, the fish perceives the presence and nature of such objects.

Electrolocation resembles **echolocation** in that the animal assesses its environment by actively emitting signals and receiving the feedback signal, rather than by passively exploiting extraneous energy sources such as sunlight. Because of this, electro- and echolocating animals can operate in darkness. This advantage, however, is paid for by the amount of energy exerted in continually emitting signals. In processing sensory information, both systems have to separate feedback associated with their own signals from interfering sensations caused by signals from other animals. This situation poses a number of challenging problems for neurophysiological research.

The Signal Generator – Electric Organ Discharge (EOD)

Electric organs, in most cases derived from muscle or nerve tissues. A few species, such as the electric eel, *Electrophorus*, can produce strong electric discharges of up to several hundred volts. However, the majority of species, including the one used in our exhibit, is limited to weak electric discharges in the range of millivolts to volts. Strong discharges are emitted infrequently to stun prey. Weak discharges are emitted continually for electrolocation and social communication.

The mormyrids, one of two groups of weakly electric fish, are a large African family living in fresh water. In all species, EODs are brief pulses separated by much longer and usually irregular intervals. In most genera, the organ discharge is very brief; less than 0.5 milliseconds in duration. See Figure 2.

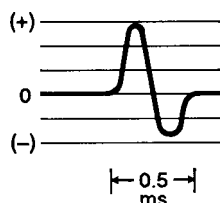


FIGURE 2. Single EOD from *Gnathonemus petersii*

In the majority of species, the interval between discharges (EODs) is long compared to the duration of the EOD itself. Discharges are thus widely spaced and audio-amplified records resemble patterns of neuronal firing. These pulsers, or “clickers”, differ markedly from a smaller number of wave species, or “hummers”,

which fire at intervals of approximately twice the duration of an EOD. Audio-amplified records of their EOD activity resemble continuous pure tones with a few harmonics. See Figure 3.

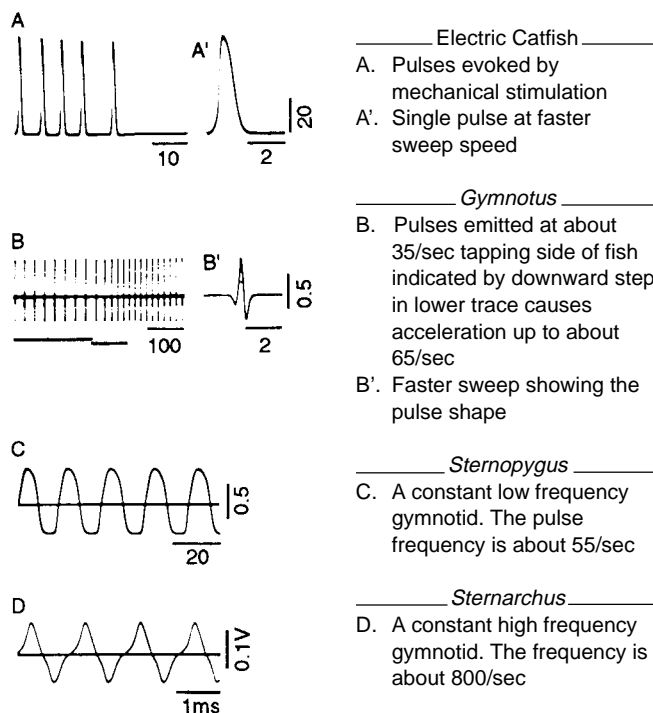


FIGURE 3. EODs from several species of electric fish (From Hoar and Randall, 1971)

In *Gnathonemus petersii*, our display species, the electric organ lies in the caudal peduncle; the thin part of the posterior of the body.

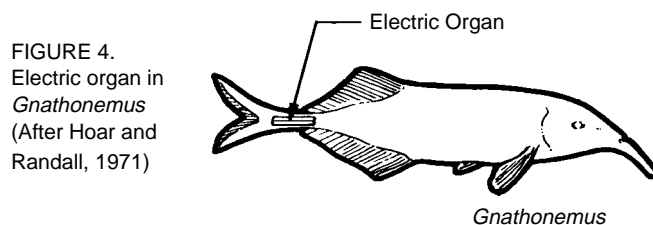


FIGURE 4. Electric organ in *Gnathonemus* (After Hoar and Randall, 1971)

It is innervated by a spindle-shaped nucleus of several hundred cells located in the spinal cord just anterior to the center of the organ. The spinal neurons are in turn innervated by a medullary nucleus of some 25 cells.

Electrocytes work on the same general principles as ordinary nerve and muscle cells; potentials are generated across membranes. In all known cases, the potentials result from selective permeability and passive movement of ions down their concentration gradients. When the membranes on opposite faces of the generating cells are at the same potential that at rest is the resting potential, no current flows.

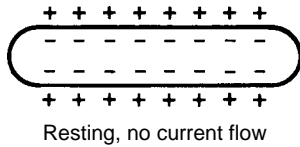


Figure 5a. Cell at rest
(From Hoar and Randall, 1971)

When the membranes are at different potentials, current flows in a circuit that involves the two membranes, the cell cytoplasm, and the external medium.

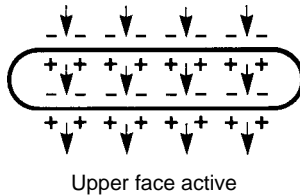


Figure 5b. Cell during discharge
(From Hoar and Randall, 1971)

Electric organs are generally gelatinous, and a large fraction of their volume is extracellular space. They contain a considerable amount of connective and other accessory tissues as well as blood vessels and motor nerves that control the discharge.

Electric organs function as follows: The serially stacked electrocytes are excited in synchrony by spinal nerve signals to generate small voltage gradients. Since each stack is surrounded by insulating tissue, the voltage adds linearly, similar to small batteries. The electric organ is driven by a command center in the medulla. The spinal nerves supplying the electric organ are adapted to insure synchronous arrival of the pacemaker signal at the electrocytes of the organ. The current flow and field that an electric fish sets up around itself can be large since many cells in series and parallel are active at the same time.

Since several hundred generating cells are involved, considerable precision in their firing is achieved. Moreover, each cell generates a diphasic signal due to successive activation of the two principle faces. These signals would tend to cancel out if added together only slightly out of phase.

Close electrotonic coupling of the medullary and spinal neurons contributes to the firing precision. Within each nucleus the cells are connected by thick dendritic bridges that appear to provide cytoplasmic continuity. Membranes separate the two cells and in the region of apposition there are areas where the cell membranes appear to be fused. Comparison with other tissues indicates these are gap junctions which are the morphological substrate of electrotonic synapses. (See Grass calendar, April, 1976.) Protein units in each membrane form a channel between cells that allows small ions to flow. In the mormyrid, the electrotonic synapses effectively tie the coupled cells

together so that an impulse in one cell very rapidly propagates to its neighbors. The transmission is more rapid than possible at chemical synapses at which there is always a relatively long delay between pre- and postsynaptic responses.

Electroreceptors

Electroreceptors are derived from lateral line organs and are supplied by lateral line nerves. Two classes of receptors are commonly distinguished. Ampullary organs respond to low frequency electric signals and serve in the detection of extraneous fields. These are also called tonic receptors. These organs are also in species of nonelectric fish such as sharks, rays and catfish. Tuberous organs, called phasic receptors, respond to high frequency signals and are tuned to the spectrum of the animal's EOD. These organs monitor transepidermal current flow associated with EODs and thus are essential for electrolocation and electrocommunication with conspecifics.

In mormyrids, the electroreceptors are of three kinds termed large, medium and small, although there is some overlap in size of the different kinds. They are found over the entire head and along the dorsal and ventral surface, but they are absent on the sides of the body and caudal peduncle.

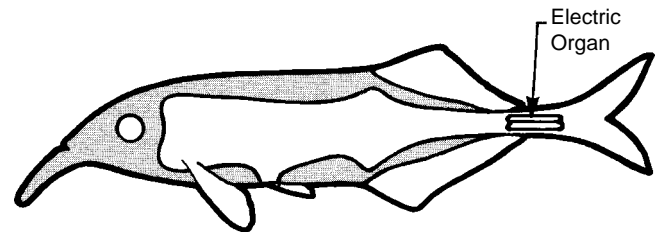


FIGURE 6. Areas containing electroreceptors in *Gnathonemus petersii*. The gray sections contain receptors. The electric organ is located just anterior to the caudal fin. (After Hoar and Randall, 1971)

The receptors are innervated by either anterior or posterior lateral line nerves. The head region is innervated by the anterior lateral line nerve. The dorsal strip of receptors is innervated by both medial and dorsal branches of the posterior lateral line nerve. The ventral strip of receptors is innervated by only the medial branch. Ordinary lateral line organs are found at the level of the medial branch and are innervated by it.

In freshwater electric fish, electroreceptors are generally visible under a dissecting microscope as specialized regions on the surface of the skin. They are easily seen on heavily pigmented skin. Investigators study individual receptors by isolating a single active fiber in the lateral line nerve and then establish its response to gross stimulation.

About this Demonstration

Our demonstration attempts to monitor the EOD of *Gnathonemus petersii*, a freshwater African mormyrid. Recording this signal simply involves placing two gold disc electrodes in the water along with the fish — a noninvasive recording.

Connection of the electrodes is made differentially to a Grass AC preamplifier. The amplified and filtered EOD signal is connected to PolyVIEW®, digital data acquisition system, and a Grass AM10 audio monitor for visual and auditory presentation.

Changes in the EOD frequency can be shown by tactile stimulation. Alterations in the discharge waveform morphology and amplitude can be demonstrated by moving the electrodes closer or further away from the fish.

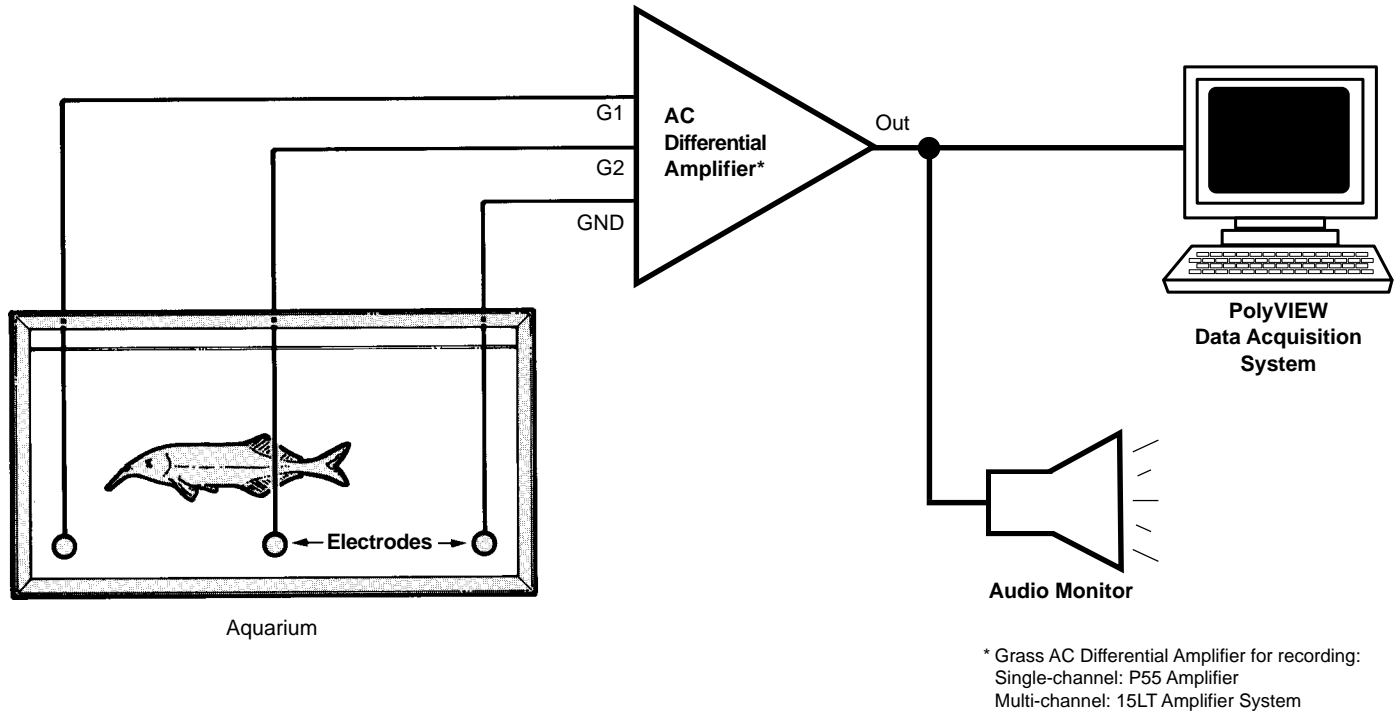


FIGURE 7. Recording scheme

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