

SENSING THE ENVIRONMENT

Detection and Generation of Electric Signals

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Detection and Generation of Electric Signals in Fishes: An Introduction

BA Carlson, Washington University in St. Louis, St. Louis, MO, USA

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Further Reading

Glossary

Active electrolocation The ability of weakly electric fish to orient and detect objects based on their electric sense.

Electric field A spatial gradient in electrical potential. In animals, these can be actively generated by an electric organ or passively generated due to the uneven distribution of ions between the inside of the animal and the surrounding water. Direct current (DC) fields are steady, whereas alternating current (AC) fields are changing.

Electric organ An organ specialized for generating external electric fields. Myogenic electric organs are derived from skeletal muscle and are composed of individual cells called 'electrocytes'. Neurogenic electric organs are derived from neuronal axons.

Electric organ discharge (EOD) Electrical discharges resulting from the summed excitation of the cells (electrocytes) of the electric organ of electric fishes that

function both in communication and in locating nearby objects. Short (100 ms to several tens of milliseconds) electrical pulses of various voltages (a few millivolts to several hundred volts) are generated at various rates (a few to over 1000 times per second).

Electrocommunication Communication based on electric signals.

Electroreceptor A sensory cell specialized for the detection of external electric fields. Ampullary electroreceptors are sensitive to low-frequency fields up to ~50 Hz, whereas tuberous electroreceptors are sensitive to high-frequency fields up to tens of kilohertz such as those produced by an EOD.

Electrosense The ability to detect electric fields. A passive electrosense is one in which external electric fields are detected, whereas an active electrosense is one in which self-generated electric fields are detected.

Humans have been familiar with the special abilities of strongly electric fish since antiquity. Egyptian tombstones depict images of the electric catfish *Malapterurus electricus*. Ancient Arabic texts refer to both *Malapterurus electricus*

and the torpedo rays *Torpedo* spp. as 'thunderer' or 'trembler'. The ancient Romans used the shocks of these fish as therapeutic treatments for a wide range of medical ailments. However, it was not until the eighteenth century

that the painful, numbing sensations caused by these fish were convincingly demonstrated to be caused by electricity. This discovery of animal electricity set the stage for the famous experiments of Luigi Galvani, in which he demonstrated that frog leg muscles could be made to contract by connecting nerves of the muscle in series with two different metals and the spinal cord. Galvani incorrectly attributed this effect to a unique form of electricity – an innate vital force housed within animal tissue that was released by the metal. His contemporary, Alessandro Volta, disagreed. Volta maintained that the contractions were not due to intrinsic electricity, but extrinsically generated current provided by contact between the two different metals. Volta ultimately proved correct, but the experiments of Galvani provided the first direct evidence of the electrical basis for nervous and muscular activity in all animals. The controversy engendered by these experiments led to the invention of the first battery to produce a reliable, steady electrical current – the Voltaic pile – which Volta created as an artificial model of an electric organ by stacking alternating disks of two different metals separated by cardboard soaked in brine.

When Darwin published *On the Origin of Species* in 1859, he devoted an entire chapter to problems with his theory of natural selection, which he entitled ‘Difficulties on theory’. One area of concern was the evolution of electric organs, of which Darwin remarked “The electric organs of fishes offer another case of special difficulty; it is impossible to conceive by what steps these wondrous organs have been produced. . .” By that time, anatomists had discovered several groups of fish with relatively small organs similar in structure to the electric organs of *Malapterurus electricus*, *Torpedo* spp. and the electric eel *Electrophorus electricus*. Some of these were shown to generate electric fields, but they were far too weak to serve as any kind of a weapon, leading Du Bois-Reymond to dub them pseudo-electric. Because of morphological similarities between skeletal muscle and electric organ, Darwin correctly concluded that electric organs likely evolved from muscle, with strong electric organs evolving from weaker versions. Due to the absence of any apparent common ancestor, he further concluded (again, correctly) that the electric organs found in different groups of extant fish must have evolved independently. The problem, as Darwin saw it, was explaining how a weak electric organ could serve any adaptive function. Not for another century did Lissman and Möhres provide convincing experimental evidence that weak electric organs are used for communication (electrocommunication) as well as for navigation and orientation (active electrolocation). Such behaviors require a specialized sensory structure – an electroreceptor – for detecting electric fields.

In the late seventeenth century, Stefano Lorenzini described in detail a series of pores and associated canals distributed throughout the body of *Torpedo* spp. that were later found in many species of aquatic vertebrates, the so-called ampullae of Lorenzini. In 1773, John Walsh, the first person to detect actual sparks from an electric fish (an electric eel), provided the first direct evidence for an electric sense. Walsh found that an electric eel would approach a pair of recording electrodes and discharge its organ whenever the electrodes were short-circuited, leading him to conclude that eels could detect electrical conductors. Du Bois-Reymond, consistent with his opinions on weak electric organs, believed that the ampullae of Lorenzini served no useful function. Physiological experiments from the 1930s through the 1960s led various researchers to conclude that the ampullae were used for thermoreception, mechanoreception, chemoreception, and eventually electroreception. The latter was ultimately confirmed through clever behavioral experiments by Kalmijn, which conclusively demonstrated the existence of a passive electrosense in sharks and rays that was used to locate prey. Concomitant to these developments, the discovery of electrocommunication and active electrolocation by Lissman and Möhres had inspired an intensive effort to identify and characterize the necessary receptor cells. This culminated in the discovery of electroreceptive units in the lateral line nerve by Bullock and colleagues that were sensitive to much higher frequencies than the low-frequency ampullary receptors, making them well suited to detecting the specialized discharges of weak electric organs.

Today, research in the field is as varied as the diversity of organisms possessing an electrosense. Molecular biologists, electrophysiologists, neuroanatomists, mathematical modelers, and evolutionary biologists continue to study this distinctly foreign sensory system to ask broadly relevant questions ranging from information processing by sensory systems and the neural organization of motor output to the evolution of animal communication and the process of speciation. The section begins with an overview of electroreceptors (**see also Detection and Generation of Electric Signals: Morphology of Electroreceptive Sensory Organs**) by Jørgen Mørup Jørgensen, who describes the morphology of ampullary electroreceptors used for passive electrolocation and tuberous electroreceptors used for detecting actively generated electric fields for the purposes of active electrolocation and social communication. Jørgensen also summarizes the basic patterns of electroreceptor evolution across vertebrates, highlighting their multiple, independent origins. Michael Hofmann goes on to describe the physiology of ampullary electrosensory systems (**see also Detection and Generation of Electric Signals: Physiology of Ampullary Electrosensory Systems**), while Maurice J Chacron and Eric Fortune describe the physiology of tuberous electrosensory systems (**see also Detection and Generation of Electric Signals:**

Physiology of Tuberous Electrosensory Systems; in both cases, the authors focus on the peripheral encoding of sensory information and mechanisms for the detection of behaviorally relevant stimuli within the central nervous system. Gerhard von der Emde and Jacob Engelmann describe how tuberous electrosensory systems are used in active electrolocation (see also **Detection and Generation of Electric Signals: Active Electrolocation**) for the detection and analysis of objects in the environment. This behavior relies on the active generation of electric fields, and Angel Caputi describes in detail the morphology of the electric organs (see also **Detection and Generation of Electric Signals: Electric Organs**) that generate these fields, paying special attention to the relationship between structure and function. Masashi Kawasaki, discussing the generation of electric signals (see also **Detection and Generation of Electric Signals: Generation of Electric Signals**), describes how the central nervous system controls the timing of electric organ output. Kawasaki considers both the general principles of electromotor circuits as well as the evolutionary variation in these pathways as it relates to differences in electric signaling behavior. The section ends with a description of the development of electroreceptors and electric organs (see also **Detection and Generation of Electric Signals: Development of Electroreceptors and Electric Organs**) by Frank Kirschbaum and Jean-Pierre Denizot. Despite the diversity of approaches and interests, readers will recognize throughout this section an appreciation for comparative approaches to biological problems, as well as a common bond that holds the field together: a deep interest in the amazing capabilities of these animals and the fundamental insights they provide into the origins and operations of our own biology.

See also: **Detection and Generation of Electric Signals: Active Electrolocation; Development of Electroreceptors and Electric Organs; Electric Organs; Generation of Electric Signals; Morphology of Electroreceptive Sensory Organs; Physiology of Ampullary Electrosensory Systems; Physiology of Tuberous Electrosensory Systems. Sensory Systems, Perception, and Learning: Shocking Comments: Electrocommunication in Teleost Fish.**

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Relevant Websites

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- <http://biology4.wustl.edu> – Homepage of Dr. Bruce A. Carlson in the Department of Biology at Washington University in St. Louis.
- <http://www.nbb.cornell.edu> – Homepage of Dr. Carl D. Hopkins in the Department of Neurobiology and Behavior at Cornell University.
- <http://www.psy.jhu.edu> – Homepage of Dr. Eric S. Fortune in the Department of Psychological and Brain Sciences at Johns Hopkins University.
- <http://people.virginia.edu> – Homepage of Dr. Masashi Kawasaki in the Department of Biology at the University of Virginia.
- <http://www.medicine.mcgill.ca> – Homepage of Dr. Maurice J. Chacron in the Department of Physiology at McGill University.
- <http://alumnus.caltech.edu> – Movies of electromotor behavior and computer simulations of weakly electric fish.
- <http://www.scholarpedia.org> – Scholarpedia article on electrolocation.
- <http://video.google.com> – Video of electric eel.
- <http://en.wikipedia.org> – Wikipedia article on electric fish.