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Electroreception

ELECTRORECEPTION is the sensory ability of some species of animals to detect weak, naturally-occurring electrostatic fields in their environment. It is found in the most ancient lineages of fishes, and survives today in about 10% of all vertebrate species -- all of which are aquatic. Electroreception was lost in evolution when vertebrates crawled onto land, so we humans can only imagine the perception of an electrical world with this sixth sense. For reasons unknown to biologists, electroreception was also lost among the ancestors of the modern fishes only to reappear in two separate lineages of ray-finned, or teleost fishes. The sense also appeared independently with the evolution of the monotreme mammals such as the platypus and echidna. All electroreceptive species possess sensitive electroreceptor organs in their skin that can detect electric fields as weak as a fraction of a microvolt per centimeter. These electroreceptors exhibit a low-resistance pathway for current to flow from the external environment to a sensory epithelium containing cells with voltage-sensitive ion channels in their membranes. As these sensory cells are depolarized they activate nerve fibers to send action potentials to the brain. The oldest lineages of fishes with electroreceptors have ampullary organs that can sense D.C. fields. This allows then to detect and capture prey in the dark or in murky water. The more recently-evolved teleosts with electroreceptors have tuberous organs that can sense A.C. fields, an ability that is useful for social communication and for active object-location if it is combined with discharges from an electric organ. Terrestrial animals have no use for electroreception because the high resistance of the air prevents the flow of electric current.

There have been very few investigations searching for electroreception among invertebrates although there a few studies which report on electric sensitivity of crayfish and worms, but the behavioral thresholds are so high (more than 3 V/cm in the worm, *Caenorhabditis elegans*), that it is doubtful that natural fields would ever activate them. For comparison, sharks and rays, which have the most sensitive ampullary receptors, have thresholds as low as a 0.02 microvolts per centimeter, the equivalent of an electric field set up between one pole of a 1.5 volt battery in San Francisco Bay and the other pole connected to the ocean near Los Angeles.

Even though humans lack electroreceptors, we can perceive strong electric currents from batteries, static generators, and other sources if we make direct contact with them or establish indirect contact through a conducting medium such as water. The perception is unpleasant because electric currents stimulate sensory and motor nerve fibers indiscriminately, producing a tingling sensation at threshold levels, and painful sensations and muscle twitch at higher levels. Human thresholds are in the 1 milliamp current range, which translates into electric fields of 0.1 to 1 Volts/cm in freshwater. Our threshold for sensing an electric field in air is more than 4 kV/cm, a perception that originates with the mechanical displacement of charged dermal hairs in electric fields.

DISCOVERY. Electroreceptor organs were first identified physiologically in the early 1960's from weakly electric fish by the American Neuroscientist, Theodore H. Bullock and colleagues, and French scientists Thomas Szabo and A. Fessard. The existence of electroreceptors had been anticipated in the late 1950's by Hans W. Lissmann from Cambridge University who was the first to discover continuous "weak" electric discharges from an electric organ the tail of the African fish, *Gymnarchus niloticus*. By

1958 he had demonstrated the reason for the discharge by showing that these fish could detect the presence of glass and metal rods or other conducting or non-conducting objects at distances of 10 centimeters or more, even in the absence of visual, mechanical, or chemical cues. Lissmann postulated that they were sensing the distortions of their own electric organ discharges as electrical shadows on their skin. Lissmann correctly guessed that there were dermal electroreceptors in these fish. He called their behavior "electrolocation" after the well-know ability of bats to echolocate objects by detecting returning ultrasonic echoes from their calls.

In the 1960's Dutch scientists Sven Dijkgraaf and Adranius Kalmijn established that sharks and rays, which have dermal sense organs called Ampullae of Lorenzini, could sense weak electric currents from their prey organisms such as flatfishes even when they were buried under sand. They showed that the Ampullae of Lorenzini were essential to this behavior, which was entirely based on electrosensory cues. They also showed that prey have weak D.C. electric fields surrounding their gills, gut, and skin wounds that gave away their presence to the sharks. When given a choice between a prey fish covered with plastic wrap and a pair of wire electrodes connected to a prey fish in another tank, the shark preferred to dig up the wires. Kalmijn and colleagues called this ability "passive electrolocation" in contrast to the "active electrolocation" ability of *Gymnarchus niloticus* discovered by Lissmann.

EVOUTION and ANATOMY OF ELECTRORECEPTORS. Electroreception first apears in crainates among lampreys which have epidermal "end-bud" organs innervated by the lateral line nerve. The end bud receptors are sensitive to weak, low frequency (DC to 50 Hz) electric fields. Among the earliest jawed vertebrates we see the first ampullary electroreceptors embedded in the skin or at the base of a long conducting canal leading from the skin surface to a specialized patch of modified sensory epithelial cells in the case of Ampullae of Lorenzini. The sensory epithelial cells resemble hair cells of the lateral line or inner ear and the nerve fibers connecting them to the brain travel in the same nerve bundles with the lateral line nerves. The cells lining the ampullary canals are packed tight to make a high resistance insulator around the low resistance canal lumen which is composed of a salty gelatinous matrix. Like an insulated wire, this arrangement is ideal for conducting electric currents to the sensory cell membranes. All vertebrate electroreceptors follow this basic design.

Electroreception is shared by all of the primitive aquatic vertebrates, including some aquatic amphibians, but it was lost in the Amniotes as they made the transition to a terrestrial existence. It reappears in monotreme mammals in which the sense reappears, derived from modified mucous glands on the bill or snout. These mucous glands have low resistance canals leading from water to bare nerve endings of the trigeminal nerve. Electroreception is absent in the majority of modern fishes including (bowfins, gars, and teleost fishes) except that it appears in two independently evolved lineages of teleosts, first as ampullary receptors among catfishes and independently among notopterid knife fishes of Africa. Remarkably, tuberous or AC-sensitive electroreceptors appear in electrogenic species belonging to both lineages – the gymnotiforms among the Ostariophysi, and the mormyroids among the Osteoglossomorpha. They are the South American gymnotiform fishes, related to the electric eel, and the unrelated mormyroid or elephant-snouted fishes from Africa. Members of both groups use their tuberous organs for active electrolocation of objects and for electrical communication. There are sufficient anatomical and physiological differences between teleost electroreceptors and the ancient Ampullae of Lorenzini so that biologists conclude they were derived secondarily. The molecular basis for electrosensory transduction is unknown for electroreceptors.

FUNCTIONS of ELECTRORECEPTION. Ampullary electroreceptors are used for passive electrolocation of the DC electric fields from prey organisms, predators, or conspecifics. The ability to sense other animals gave these fishes a decided advantage in navigating in the dark or in turbid water. Tuberous electroreceptors, which are found only in the two independent lineages of teleosts already mentioned, are used for sensing the AC electric fields from electric organs, either in the context of active electrolocation of objects, or for social communication. Electric communication signals from electric organs can be quite elaborate and varied. There is a rich repertoire of electric signals used for signaling threats, submission, alarm, and courtship and for some of these fish there are electric signals for sex, species, and individual recognition.

PERCEPTION. Because humans lack electroreception and words to describe it we can only imagine what this sense must be like for other animals. For those with true electroreceptors, the sensation is probably nothing like the unpleasant feeling we associate with electric shocks. To understand what an animal perceives we can only do behavioral tests, make physiological recordings, and examine behavior of animals with sensory deficits, and even so we will never experience what the animal feels. We imagine that electroreception must resemble the touch since both modalities have receptors distributed over the body surface and both have sensory maps of the body surface in the brain. However electroreception is also like the thermal sense since electric currents flow in vague and diffuse pathways and never create sharp boundaries. But there are also similarities between electroreception and hearing since both modalities are encoded by frequency-tuned receptor cells resembling hair cells and both use time encoding to represent time varying stimulus waveforms. Electroreception is also similar to vision since multiple receptor types are distributed over the skin surface like in the retina, and in both modalies there are local regions where receptors are extremely dense, creating a fovea of acute spatial resolution. Whether electroreception is perceived more like we perceive touch or hot or cold or hearing or seeing is unimportant to the scientists who strive to describe the sensory experience in terms of physical attributes of the stimulus, electrophysiological properties of sensory afferents, or central neurons, or the behavioral performance during natural behavior and trained discrimination. An animal's perception will remain unknown to us. Nevertheless, the widespread appearance of electroreception among aquatic vertebrates and the multiple cases of its evolution suggest that this sense, although foreign, is an extremely important part of the evolutionary history of our vertebrate lineage.

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Further Readings

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