A Biological Function for Electroreception in Sharks and Rays

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JEB Classics

A BIOLOGICAL FUNCTION FOR ELECTRORECEPTION IN SHARKS AND RAYS

THE ELECTRIC SENSE OF SHARKS AND RAYS

By A. J. KALMIJN

Carl D. Hopkins discusses Adrianus J. Kalmijn's 1971 paper entitled 'The electric sense of sharks and rays'.

A copy of the paper can be obtained from http://jeb.biologists.org/cgi/content/abstract/55/2/371

The discovery of a new sensory modality in animals is of great significance in the history of biology – akin to the description of a new species of bird or primate or the unearthing of a missing link in the fossil record. In this issue we celebrate one of the key papers in the discovery of electroreception in fishes (Kalmijn, 1971), which established a biological function for the ampullae of Lorenzini in sharks and rays. It has become a citation classic for *The Journal of Experimental Biology*.

Evidence for electroreception accumulated rapidly in the period between 1957 and 1971. First, there were behavioral studies that showed that weakly electric fish from Africa and South America could communicate with conspecifics (Möhres, 1957) and 'electrolocate' hidden objects in their environment (Lissmann and Machin, 1958). Electrolocation in electric fish had much in common with echolocation in bats that were using ultrasound to find their insect prey (Griffin, 1958). These fishes could sense objects that differed in conductivity from the water even when visual, chemical and mechanical cues were obscured. Shortly after Lissmann and Machin's behavior study in 1958 (Lissman and Machin, 1958), which is also a JEB Classic (Alexander, 2006), came electrophysiological recordings from electroreceptors (Bennett, 1965; Bennett, 1971; Bullock et al., 1961; Fessard and Szabo, 1961; Murray, 1959; Murray, 1960; Murray, 1962), anatomical studies on the receptor organs (Bennett, 1965; Bennett, 1971; Derbin and Szabo, 1968; Szabo, 1965) and neurobiological studies of sensory coding (Bullock and Chichibu, 1965; Hagiwara and Morita, 1963; Hagiwara et al., 1962; Hagiwara et al., 1965a; Hagiwara et al., 1965b).

Despite this rapid progress it was still unclear how the earliest electroreceptors evolved because there had been no study of the functional role of electroreception in species lacking weak electric organs. This included the non-electric sharks, skates and rays, and catfish and, as we now know, many others (Bullock and Heiligenberg, 1986; Bullock and Hopkins, 2005; Bullock et al., 2005; Hopkins, 2009). These electroreceptive but non-electric fishes were obviously the key to solving Darwin's (Darwin, 1859; Darwin, 1872) 'case of special difficulty' – the origin of electric organs in electric eels and Torpedo rays through a series of gradual adaptive modifications. If weak electric organs were useful for both communication and active electrolocation, it was possible to conceive of the intermediate steps that would lead to the evolution of stronger and stronger electric organs. But what was the function of electroreceptors if electric organs were absent, as they are in sharks and most rays?

In 1971 in one short paper, now a JEB Classic article, Adrianus J. Kalmijn from the University of Utrecht in The Netherlands found the answer. He demonstrated that these elasmobranchs could detect natural electric fields surrounding fish that were their natural prey, that they could orient to these electric fields, and that they could accurately attack them even when their prey was visually hidden – as occurred when the flatfish *Pleuronectes platessa* was buried under the sand. They could do so, at night, and even when chemical and mechanical cues were absent. The experiments were simple and clear, and the writing was direct. Furthermore, this paper had one memorable figure – a 'story board' for the six experiments performed in the study – that sticks in your mind like a Mozart melody. It lays out the evidence for a natural function for these electroreceptors (see Fig. 1 legend). By establishing a clear natural function for electroreception, Kalmijn did what Parker and van Heusen (Parker and van Heusen, 1917) had not done in their earlier account of experiments showing that catfish respond to metallic rods and galvanic currents. Prey capture was not simply a curious perceptual response of an

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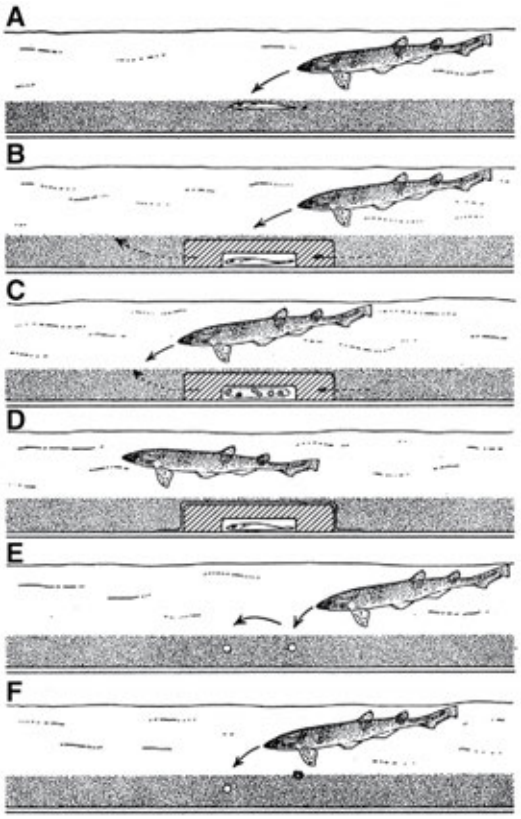

Fig. 1. Kalmijn's behavioral experiments revealed the importance of electroreception in passive electrolocation of prey (Kalmijn, 1971). The studies were conducted in captivity, and the spotted dogfish shark *Scyliorhinus canicula* detects and accurately attacks its natural prey, a flatfish, *Pleuronectes platessa*, buried under the sand (A). The shark also attacks when the flatfish is covered both by sand and a chamber molded from agar made with seawater (B). The sand blocks visibility of the prey while the agar chamber impedes mechanical cues due to water motion and limits diffusion of chemicals but it has the same electrical conductivity as the seawater. By pumping water through the chamber to an exit tube some distance away, Kalmijn tested the importance of chemical cues carried in from the water flow (Kalmijn, 1971). The shark attacks the chamber, not the outflow. Chopped fish bait under the agar chamber redirects the shark's attack to the outflow tube (C). Electrically insulating the agar chamber with thin plastic sheeting blocks the flatfish's inevitable bioelectric signals and muscle potentials and the shark is disoriented (D). As proof that the shark is guided by the electric signal, electrodes buried in the sand replace the prey, and when they are connected to a low frequency 4 μA current source emitting signals that are close in amplitude to natural bioelectric emissions (*ca.* 120 μV 5 cm^{-1}, 1 Hz sine wave) the shark attacks (E). Finally, the sharks show a preference for attacking the electrodes even if a piece of fish bait is presented on the surface (F). Reprinted from fig. 2 from Kalmijn (Kalmijn, 1971).

animal in an experimental set-up but a natural sensory response essential to its survival. Hence, it was a new sense organ.

Why was this paper so compelling, given that most of the basic anatomy of electroreceptors was known by 1971, and most of the functions already established? Perhaps it was the care with which the laboratory studies were linked to relevant field conditions, or the clarity of the figure, or the economy of the writing, which summarized data without tables or statistics.

I first met Ad Kalmijn in Ted Bullock's laboratory at Scripps Institution of Oceanography in San Diego, CA, USA, shortly after this paper was published. It was a good time to be a post-doc there, as the Bullock lab was thriving with several students and post-docs actively at work on electroreception and other aspects of comparative neurobiology. Walter Heiligenberg had just arrived to study the Jamming Avoidance Response, and Joe Bastian was trying to understand the large cerebellum of electric fish. Kalmijn was busy setting up large tanks for testing sharks and rays. He helped Eric Knudsen, a beginning graduate student, to study electroreception and the geometry of electric fields from weakly electric fish. Knudsen later made electrophysiological recordings of sensory maps for electric field vectors in the torus semicircularis of catfish. Several years later Kalmijn wrote influential papers on the use of electroreceptors in the detection of the Earth's magnetic field (Kalmijn, 1974), which he alluded to in his JEB paper; and he was influential in understanding the physics of electric and hydrodynamic fields in water (Kalmijn, 1997). It was an exciting time to work on the many aspects of this new sensory modality, and it is gratifying to see how far electric fish have come, from those early beginnings to become a great model system in neuroethology (Bullock et al., 2005).

I often return to Kalmijn's 1971 paper in my teaching. I show Fig. 1 and tell the story of how we learned the function of early electroreception in fishes.

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