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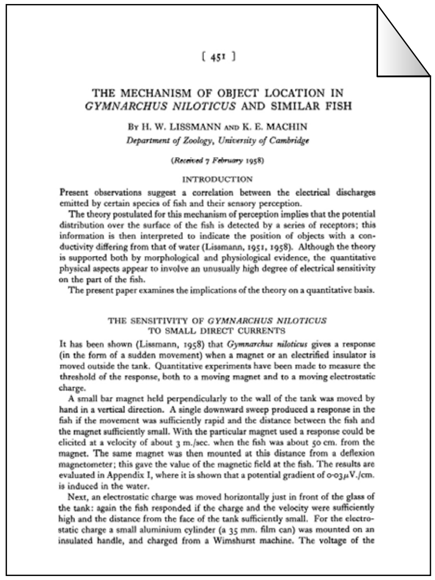
A NEW SENSE FOR MUDDY WATER



[451]

THE MECHANISM OF OBJECT LOCATION IN *GYMNARCHUS NILOTICUS* AND SIMILAR FISH

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INTRODUCTION

Present observations suggest a correlation between the electrical discharges emitted by certain species of fish and their sensory perception.

The theory postulated for this mechanism of perception implies that the potential distribution over the surface of the fish is detected by a series of receptors; this information is then interpreted to indicate the position of objects with a conductivity differing from that of water (Lissmann, 1951, 1958). Although the theory is supported both by morphological and physiological evidence, the quantitative physical aspects appear to involve an unusually high degree of electrical sensitivity on the part of the fish.

The present paper examines the implications of the theory on a quantitative basis.

THE SENSITIVITY OF *GYMNARCHUS NILOTICUS* TO SMALL DIRECT CURRENTS

It has been shown (Lissmann, 1958) that *Gymnarchus niloticus* gives a response (in the form of a sudden movement) when a magnet or an electrified insulator is moved outside the tank. Quantitative experiments have been made to measure the threshold of the response, both to a moving magnet and to a moving electrostatic charge.

A small bar magnet held perpendicularly to the wall of the tank was moved by hand in a vertical direction. A single downward sweep produced a response in the fish if the movement was sufficiently rapid and the distance between the fish and the magnet sufficiently small. With the particular magnet used a response could be elicited at a velocity of about 3 m./sec. when the fish was about 50 cm. from the magnet. The same magnet was then mounted at this distance from a deflexion magnetometer; this gave the value of the magnetic field at the fish. The results are evaluated in Appendix I, where it is shown that a potential gradient of 0·03 μV./cm. is induced in the water.

Next, an electrostatic charge was moved horizontally just in front of the glass of the tank: again the fish responded if the charge and the velocity were sufficiently high and the distance from the face of the tank sufficiently small. For the electrostatic charge a small aluminium cylinder (a 35 mm. film can) was mounted on an insulated handle, and charged from a Wimshurst machine. The voltage of the

R. McNeill Alexander writes about H. W. Lissmann and K. E. Machin's 1958 paper 'The mechanism of object location in Gymnarchus niloticus and similar fish.'

Electrophorus, the electric eel, can deliver electric shocks of several hundred volts. Its discharges, and those of the electric ray *Torpedo*, worried Darwin (1872). He did not see how their electric organs could have evolved, as his theory required, by natural selection of small variations. They appeared to be derived from muscles, which were already known to produce the weak electric pulses now known as action potentials, but what selective advantage could have driven the early stages of their evolution? A strong electric discharge would be a formidable defence, and possibly an aid to catching prey, but a weak one would be utterly useless for either of these functions.

Late in the nineteenth century and early in the twentieth, weak electric organs were discovered in several groups of freshwater fishes, notably the African Mormyridae and the South American Gymnotidae (reviewed by Lissmann, 1958). They produced pulses of a few volts, stronger than action potentials but much weaker than the discharges of the strong electric fishes. Various suggestions of possible functions were made, but none were convincing until Hans Lissmann and Ken Machin carried out the research that is the subject of this article.

Both these scientists had remarkable careers. Hans Lissmann (1909-1995) was the son of German parents living in Russia (Alexander, 1996). He and his family were interned as aliens during the First World War. After it, they set out on foot for Germany to escape the Russian Revolution, but after a 300 mile trek found themselves stuck in a refugee camp, still in Russia. Eventually they got to Hamburg, where Lissmann was able to train as a zoologist, obtaining his doctorate (on fish behaviour) in 1932. He worked briefly in Hungary and India, and (though not Jewish) was unwilling to return to Hitler's Germany. He wrote to James Gray in the Zoology Department at Cambridge, and was offered a post there. Gray was engaged on his pioneering research on animal locomotion. Lissmann worked closely with him on the locomotion of leeches, earthworms and amphibians, and independently on slugs and snails (summarised in Gray, 1968). In the Second World War, Lissmann was again interned as an alien, and was sent to Canada. He was allowed to return in 1943, and continued his career in Cambridge. He was elected to the Royal Society in 1954.

Ken Machin (1924–1988) took a BA in physics, followed by a PhD in radio-astronomy. After that, in a remarkably astute move, Gray appointed him to a post in the Cambridge Zoology Department. His role was to collaborate with the zoologists on the physical aspects of their research. He worked with Pringle on the asynchronous flight muscles of insects, showing how they will drive any resonant system at its natural frequency of vibration (Machin and Pringle, 1959). This and his work with Lissmann were Machin's finest scientific achievements.

Before Machin joined the Zoology Department, Lissmann had been sent a living specimen of *Gymnarchus*. Despite the similarity of name between this African fish and the South American gymnotids, *Gymnarchus* is not related to them, but to the mormyrids. Lissmann became interested in its weak electric discharges, pulses of 3–7 volts. He wondered whether they could be the basis of a previously unknown sense, which might enable the animal to detect objects in the water around it (Lissmann, 1951). The story told in Cambridge was that the first clue to the electric sense had come when a student combed her hair near its tank, and the *Gymnarchus* went wild. This may have been a myth, but Lissmann did indeed find that the fish reacted to electrostatic charges outside its tank (Lissmann, 1958). More generally, he showed that the fish was sensitive to any change in the electric field around it.

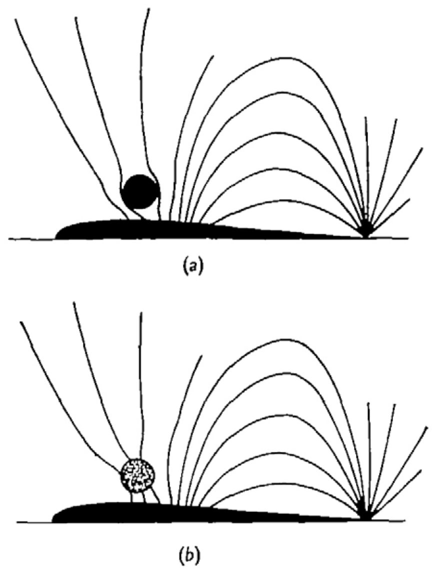

Fig. 1. Diagrams showing how the electric field around *Gymnarchus* is distorted by objects of (a) lower and (b) higher electrical conductivity than the water. The lines represent the flow of electric current. From Lissmann and Machin (1958).

The first *Gymnarchus* died, but others were obtained, and Machin joined forces with Lissmann. I was a research student, sharing a laboratory with Machin, so I was well placed to watch their progress. To test Lissmann's hypothesis, they needed to show that objects in the water around the fish would affect its electric field in ways that could provide information about the objects' positions, and that the fish was sensitive enough to detect these changes in its field.

Fig. 1 shows how the field would be affected (a) by objects of lower electrical conductivity than the water, for example rocks; and (b) by objects of higher conductivity, such as other fish. They would change the distribution of electrical potential along the fish's body. Was the fish sensitive enough to detect the changes?

They needed to show that the fish could tell the difference between objects that were indistinguishable by sight, touch, smell or any other known sense. They chose porous earthenware pots with contents of different electrical conductivity. They eventually showed that the fish could distinguish a pot filled with aquarium water, from an identical pot containing 75% aquarium water plus 25% distilled water. They also showed that it could distinguish between pots filled with aquarium water, with and without a glass tube of 2 mm diameter down its centre. It could not, however, distinguish between a pot of diluted aquarium water and an electrically equivalent pot of undiluted aquarium water with a glass tube in it.

While Lissmann concentrated on training the fish to make ever-finer discriminations, Machin built an electrical model of it. This model had a Perspex body immersed in a shallow tank of tapwater. Two electrodes on the long axis of the body were used to establish an electric field like the one produced by the fish. Recording electrodes around the edge of the body proved capable of recording distortions of the field like the ones shown in Fig. 1, when objects of higher or lower conductivity were placed in the water. There was a feeling of rivalry between Machin and the fish; which could make the finer discriminations? The fish won hands down, but the experiments with the model showed that the postulated mechanism for object location was feasible.

Gymnarchus lives in extremely turbid rivers. Lissmann (1958) showed that the weakly electric gymnotid fish, which are active mainly at night, have similar sensitivity to electric fields. The value of a non-visual means of locating objects is evident, both in turbid water and in darkness.

Lissmann and Machin had discovered and explained a new sense, utterly unlike anything that we humans can experience. Here was something at least as remarkable as the echolocation of bats, a discovery of the previous decade (see Griffin, 1958). It has generated a huge and diverse literature, both before and after Moller's (1995) book. Physiologists have shown in great detail how the electric organs and electroreceptors work. Neurobiologists have investigated the processing of receptor output in the brain. Researchers in animal behaviour have shown how fish use the electric sense in their natural environments, and how they interact with neighbouring electric fishes to avoid being confused by their signals. Electrolocation has been shown to be a remarkably refined sense, enabling fish to discern the shapes, distances and, to some extent, the composition of objects (von der Emde, 2004). We can now appreciate the major part it plays in the lives of the two large groups of fish that possess it.

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