

A shark swimming through the earth's magnetic field induces electric fields giving the animal's compass heading (the horizontal component of the earth's magnetic field and the induced electrical currents are indicated). (From Kalmijn, 1974)

The Electric and Magnetic Sense of Sharks, Skates, and Rays

by Adrianus J. Kalmijn

Scientists must know the sensory world of an animal if they are to understand its behavior. Certainly most aquatic vertebrates have good eyesight, hear well, and are endowed with a sharp sense of smell and taste. Yet the physical characteristics of underwater light, sound, and odor fields are quite different from those on land. Moreover, animals use the sensory information in a variety of ways, depending on the particular interest of the species. Therefore, scientists cannot infer from man's own sensory experience how an animal perceives its environment but have to learn through behavioral tests and field observations. This point is dramatically emphasized by animals that have sensory capabilities that stretch man's imagination. One of the most interesting examples of this is the electromagnetic sensory performance of marine sharks, skates, and rays, commonly referred to as elasmobranch fishes.

In predation, sharks, skates, and rays cunningly cue in on the weak, bioelectric fields of their prey, even though it may be hiding under sand. These well-aimed feeding responses clearly demonstrate the remarkable acuity of the elasmobranchs' electric sense and testify to its biological significance in the animals' daily life. Recent research indicates

that the elasmobranchs also detect the electric fields they induce when swimming through the earth's magnetic field, and thus sense their compass heading. Obviously, the electric sense of these ancient fishes has reached a high degree of sophistication.

Last year, the author and his student collaborators initiated field experiments in Vineyard Sound off Cape Cod, Massachusetts, to verify the results of earlier laboratory studies on the electrical aspects of predation. After chumming with chopped herring, we observed the smooth dogfish *Mustelus canis* search the bottom and viciously attack a current source simulating the bioelectric fields of the shark's prey. Although attracted and motivated by odor, the predators made their final approach exclusively relying on their electric sense. Coming in with the sharks, the American eel *Anguilla rostrata* paid no attention to the fields, whereas in comparative tests the catfish *Ictalurus nebulosus* repeatedly dug at a current source hidden in the mud along the banks of a local freshwater pond.

The magnetic orientation studies have been conducted on the stingray *Urolophus halleri* at our land facilities, set up in the woods of the quiet Quissett Campus of the Woods Hole Oceanographic Institution. The stingrays

were trained to seek reward and avoid punishment by orienting to the earth's magnetic field. Between trials, the horizontal component of the magnetic field was reversed in a random order to eliminate the use of alternative orientational cues. These experiments have conclusively demonstrated the elasmobranchs' magnetic sensory abilities, which the author predicted on the basis of their acute electric sense.

Previous Studies

In 1917, G. H. Parker and A. P. Van Heusen published a historic paper on the curious behavior of *Ictalurus*, the common brown bullhead, with regard to metallic and non-metallic objects. They noticed that blindfolded specimens responded to the approach of metallic rods at distances of several centimeters, whereas a glass rod did not elicit a reaction until it actually touched the skin of the animals. In a series of simple but convincing experiments, Parker and Van Heusen demonstrated that these distant responses were due to galvanic currents generated at the interface between metal and aquarium water. Though very close to discovering the catfish's electric sense, these scientists did not realize the biological implications of their remarkable results.

In 1934, the Dutch biologist S. Dijkgraaf also observed a great sensitivity to metallic objects in the small shark *Scyliorhinus canicula*. A quarter of a century later, he suggested that the author, then his student in the Netherlands, investigate the possibility of electrical stimulation, as in the case of the catfish, and evaluate the biological significance of the response. A few years earlier, H. W. Lissmann in England had discovered that certain knife-fishes produce weak electrical discharges to probe their environment. Sharks, however, lack electrogenic organs; therefore, the main questions were: what might be the fields in nature that the sharks detect, and what could be the role of these fields in the animals' daily life?

Subsequent research soon revealed that marine sharks, skates, and rays are indeed extremely sensitive to weak electric fields. By recording the heartbeat of free-swimming specimens with implanted electrodes, the author established transient cardiac

decelerations when applying electric fields of voltage gradients as low as 0.01 microvolt per centimeter, which represents the highest electrical sensitivity known in the animal kingdom. In later behavioral tests, the frequency range of the animals' response appeared to extend from direct current (DC) up to about 8 hertz. Reception of these low-frequency, low-level electric fields was shown to take place by means of the ampullae of Lorenzini, delicate sensory structures in the protruding snout of the elasmobranch fishes (Figure 1).

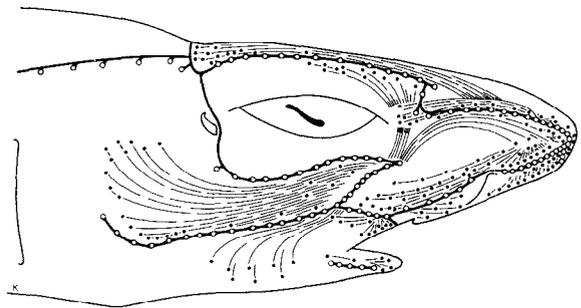


Figure 1. Ampullae of Lorenzini and mechanical lateral-line system in head region of the shark *Scyliorhinus canicula*. (Solid dots: skin pores of electroreceptors. Small circles: openings of lateral-line canals) (From Dijkgraaf and Kalmijn, 1963)

By measuring the electric fields in the laboratory habitat of the sharks and skates, it was found that aquatic animals produce direct-current and low-frequency electric fields in the water, which stem mainly from potential differences at the skin/water interface. In fish, for example, the mucous membranes lining the mouth and the gill epithelia in the pharynx give rise to steady DC fields, usually modulated by ventilatory movements. Externally, the bioelectric fields are of distributed dipole* configuration and, accordingly, fall off steeply with increasing distance. Yet the DC voltage gradients emanating from small fish and wounded crabs often measured over 0.01 microvolt per centimeter at distances up to 25 centimeters, which suggested the role of the elasmobranchs' electric sense in predation.

To elucidate the electrical aspects of predation, the author decided to analyze the feeding responses of the shark *Scyliorhinus*

*A field produced by equal but opposite electrical poles, usually separated by a small distance.

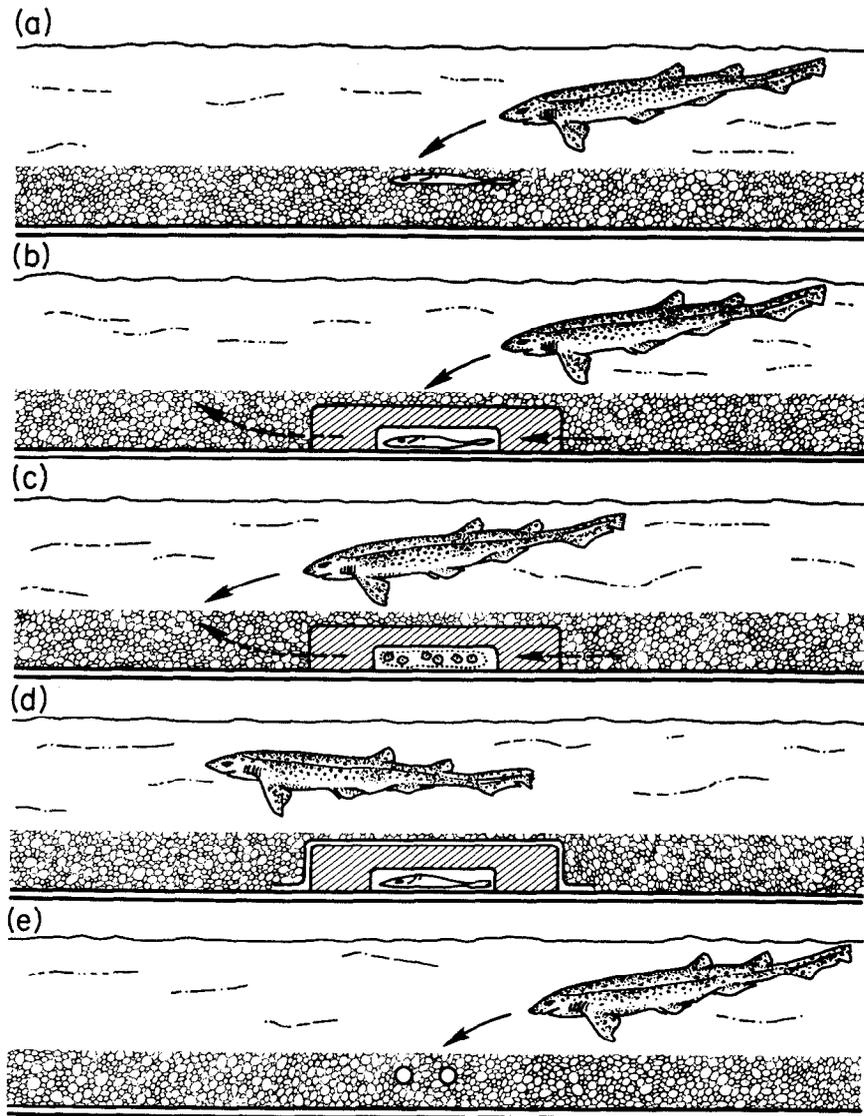


Figure 2. Feeding responses of the shark *Scyliorhinus canicula* to: (a) flounder under sand, (b) flounder in an electrically transparent agar chamber, (c) pieces of whiting in an agar chamber, (d) flounder in an agar chamber covered with an electrically insulating plastic film, and (e) electrodes simulating the bioelectric field of a flounder. Agar chamber not to scale. Solid arrows: responses of shark; dashed arrows: flow of seawater through agar chamber. (From Kalmijn, 1971)

canicula and the skate *Raja clavata* to small specimens of the flounder *Pleuronectes platessa*. The prey was cautiously introduced into the seawater habitat, and after it had hidden itself in the sand, a few drops of liquified whiting were diffusely spread throughout the water. Motivated by the odor, the sharks and skates began randomly searching the bottom of the pool. When coming within a distance of 10 to 15 centimeters from the flounder, they made well-aimed dives at their prey, uncovered it from under the sand, and devoured it voraciously (Figure 2a). Subsequently, the flounder was placed in a flat chamber made out of 3 percent agar in seawater, and positioned under the sand on the bottom of the pool. The chamber was aerated by a steady flow of seawater to keep the prey alive. The

purpose of the agar chamber was to conceal the flounder visually, chemically, and mechanically without impeding the animal's bioelectric field. Again, after odor motivation, the sharks and skates made their well-aimed feeding attacks from the same distance and in the same frenzied manner, as if the prey were not screened by agar at all (Figure 2b).

To prove that the 1-centimeter-thick roof of the agar chamber was really effective in attenuating odor stimuli, the live flounder was exchanged for pieces of whiting that had been frozen for several days (whiting was the regular food for the experimental animals). In this case, the predators did not show the slightest response to the food when swimming over the agar chamber, although they were strongly motivated by the odor of the seawater flow ventilating the chamber (Figure 2c). Whether

the agar was adequate to mechanically shield the live flounder was indirectly tested by repeating the original experiment, this time, however, with a thin, electrically insulating polyethylene film covering the agar chamber. Now, the sharks and skates no longer responded to the prey, although they eagerly searched about and often passed directly over it (Figure 2d). This drastic effect could not conceivably be due to the mechanical properties of the thin (10 micrometer) and extremely pliable polyethylene film, since even the stiff, 1-centimeter-thick agar roof to which the film was added did not noticeably weaken the feeding responses. Hence, the sharks and skates evidently were able to attack a flounder hiding in the sand without the aid of visual, chemical, or mechanical cues.

The results of these behavioral tests suggested that the sharks and skates *electrically* located the agar-screened prey. This would also explain the all-or-none effect of the polyethylene film, which offered an extremely high electrical resistance, whereas the agar layer did not distort the bioelectric field of the flounder to any extent. To provide direct evidence for the electrical hypothesis, the presence of the flounder was simulated by passing electrical current between two salt-bridge electrodes buried in the sand. After odor motivation, the predators displayed the same characteristic feeding responses to the electrodes (whether or not covered with agar) as they did to the actual prey (Figure 2e). They dug tenaciously at the source of the field, responding again and again when coming across the electrodes. These results proved that the electric sense of sharks and skates plays an important role in the animals' lives.

Field Observations on Cape Cod Sharks

Following the studies on captive sharks, we have sought to verify the results in tests on wild specimens, roaming freely in their natural habitat. The main problem, however, has been approaching the animals without introducing galvanic fields or other perturbations into the environment that might interfere with the fishes' normal behavior. Remember that the electrical sensitivity of catfish and sharks first revealed itself through the animals' unusual responses to metallic objects.

During the summer of 1976, we learned from longline fishing off Cape Cod that the smooth dogfish *Mustelus* regularly frequents the shallow, inshore waters of Vineyard Sound on its nightly feeding excursions. This predatory shark is a warm-season visitor, arriving at Woods Hole in May and leaving for the South again in late October or shortly thereafter. It is an active bottom hunter, preying on small fish as well as crustaceans and other invertebrate animals. The females reach an average length of 115 centimeters; the males are slightly smaller. The smooth dogfish is truly live-bearing; the new-born measure 29 to 37 centimeters.

To observe the sharks' feeding behavior, we worked from an inflatable rubber raft (Zodiac Mark II) free of any metal under the waterline. On station in 2.5 to 3.0-meter-deep water over a sand patch devoid of seaweed, we attracted the sharks by squeezing liquified herring through a long Tygon tube that ran from the raft to the bottom of the sea. The Tygon chumming tube was attached to a polypropylene line, suspended from a Styrofoam float and stretched over the ocean floor between two polyvinyl pipes anchored in low-profile cinder blocks (Figure 3). Starting after dark, we illuminated the area with a 100-watt, battery-operated underwater light. To break the water surface, we used a glass-bottom viewing box secured behind the stern of the raft.

Two pairs of agar-filled, salt-bridge electrodes were tied to the polypropylene line and positioned on the sand, one on either side of the odor source and 30 centimeters from it. Mekka underwater plugs with stainless steel pins and integral cables connected the thin, 30 to 90-centimeter-long Silastic salt-bridge tubes to the electrical equipment set up in the rubber raft. The use of a constant-current source virtually eliminated the adverse effects of polarization at the stainless steel/seawater interfaces. From the raft, we could conveniently vary the strength of the field and select the pair of electrodes to be energized, the other pair functioning as the control. The applied direct-current dipole moments ranged from 1 to 8 microamperes x 5 centimeters (dipole current x distance between electrodes), roughly corresponding to the bioelectric fields of small prey at a seawater resistivity of 20.0 to 20.5 ohm-centimeters and

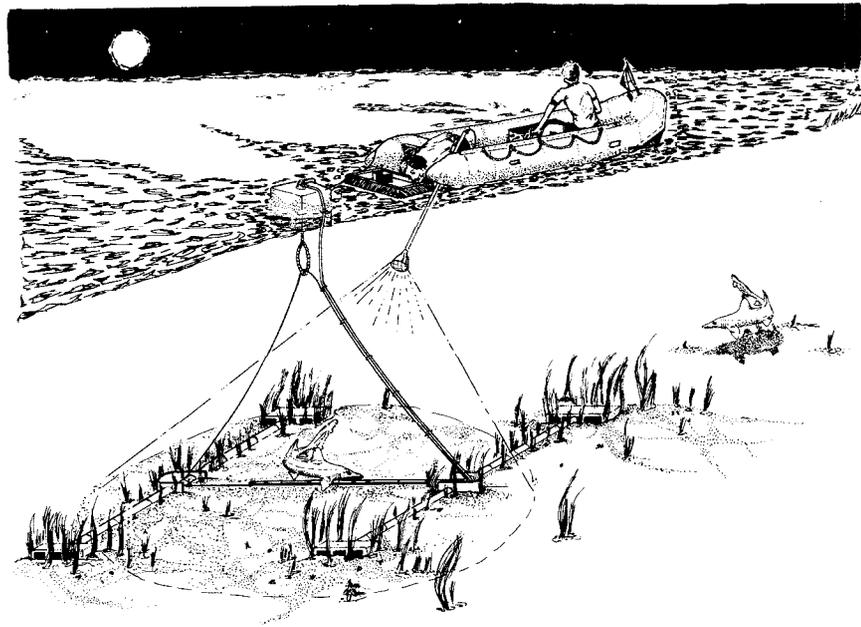


Figure 3. Field setup for observing the feeding responses of sharks to electrically stimulated prey. Though attracted by fish extract exuding from chumming tube, the shark *Mustelus canis zeroes* in on electrical dipole field in Vineyard Sound.

a temperature of 19 to 22 degrees Celsius.

After entering the area, the smooth dogfish began frantically searching over the sand, apparently trying to locate the odor source. Both young and mature sharks were observed, sometimes alone, sometimes in groups of two to five. Neither the raft nor the underwater light appeared to bother them. Most interestingly, when nearing the odor source, the animals did not bite at the opening of the chumming tube but from distances up to 25 centimeters turned sharply to the current-electrodes, viciously attacking the electrically simulated prey. After snapping the line with their teeth right at the position of the electrodes, the sharks usually attempted to rip them apart — and one night they succeeded. When the current was switched to the other pair of electrodes, the animals let go, circled around for awhile, and attacked again, but at the electrodes on the other side of the odor source. At the lower current levels, the sharks kept responding, though from increasingly shorter distances.

These observations convincingly demonstrate that odor-motivated sharks are capable of detecting and taking prey by the exclusive use of their electric sense, not only under well-controlled laboratory conditions, but also in their electrically more noisy, ocean habitat. Of course, other sense organs, in particular the fish's lateral-line mechanoreceptors, also can play an important part in predation. At short range, the electric fields appear to dominate in our experiments over the much vaguer odor cues that initially

attracted the sharks from a distance. Since the odor of wounded prey lingers long after the animal is gone, the sharks obviously need more precise directional cues to locate their prey accurately, enabling them to seize it with one quick move.

Behaviorally, elasmobranchs readily respond to direct-current fields. Electrophysiologically, however, the ampullae of Lorenzini are not true DC receptors, although they do detect frequencies as low as 0.1 hertz. That is, to sense a prey's DC field, elasmobranch fishes have to move relative to their prey, or *vice versa*. Alternatively, they may detect the low-frequency components that accompany the prey's ventilatory and body movements. Odor-motivated sharks and skates do zero in on DC, as well as low-frequency dipole fields of biological strengths. In their final approach, they aim directly at their prey, deriving its location from the spatial configuration of the animal's bioelectric field.

The American eels that visited our test area often nibbled at the opening of the chumming tube, but they *did not* pay any attention to the current-passing electrodes. The eels' behavior was particularly noteworthy because the fish had been reported to exhibit similar cardiac decelerations when subjected to weak electric fields, as previously observed in elasmobranch fishes. The eels' responses, however, have not been independently confirmed, nor are these fish known to have specific electroreceptors. In predation at least, they evidently are more chemically inclined.

Toward the end of the season, we conducted comparative tests on the common brown bullhead, which is endemic to the Cape's freshwater ponds. With small pieces of beef liver, we lured the fish into shallow water, and offered them direct-current dipole fields of 0.5 to 4.0 microamperes passed between two salt-bridge electrodes with openings 1 centimeter apart buried in the mud. Along the banks of the pond, the resistivity of the water measured 19 kilohm-centimeters at a temperature of 20 degrees Celsius. As with the sharks, the catfish repeatedly dug at the source of the field in apparent attempts to devour the electrically simulated prey.

Although we primarily conceived this field work with the undisturbed bioelectric sensory world of the sharks in mind, the results of our tests also indicated that attacks on humans and underwater gear may be elicited and guided by electric fields resembling those of regular prey. The human body, especially when the skin is damaged, creates DC bioelectric fields that sharks in the ocean may detect from distances up to 1 or 2 meters. The galvanic fields of metallic objects on the body may be even stronger. In this connection, we expect that the U.S. Navy's polyvinyl anti-shark bag, which is suspended from an inflatable floatation collar and designed to visually and olfactorily conceal a mariner in distress, electrically screens the person as well. Sidetracking the sharks to alternative sources of electricity that secondarily release a discouraging agent may, under certain circumstances, be another means of warding off electrically evoked shark bites. It should be emphasized here that the electrical aspects of the animals' environment should be taken into account in all behavioral studies on elasmobranchs and, if possible, left undisturbed.

Evidence of Geomagnetic Orientation

When cruising through the earth's magnetic field, marine sharks, skates, and rays induce electric fields that are well within the dynamic range of their highly-sensitive electroreceptor system. As the induced voltage gradients depend on the direction in which the animals are heading, they may form the physical basis of an electromagnetic compass sense in these fishes. To substantiate the biological feasibility of this novel orientation mechanism, the

author has endeavored to collect hard experimental evidence of the elasmobranchs' magnetic abilities predicted from the animals' known electric sense and the theory of electromagnetic induction.

Our first, most simple magnetic tests were performed on the leopard shark, *Triakis semifasciata*, in outdoor, all-fiberglass pools on the bluffs of Scripps Institution of Oceanography's campus at La Jolla, California. With the fish swimming steadily along the circumference of their circular habitat, we introduced a local magnetic field by passing an electrical current through a small induction coil (20 centimeters in diameter) held external to the tank. The field was switched on when the sharks were at the far side of the pool. Then, seconds later, upon completing their lap and swimming into the imposed field, the sharks suddenly veered off to the center of the tank, although the coil current did not distort the earth's ambient magnetic field by more than 25 percent.

Next, we noticed that the leopard sharks each morning before dawn gathered in the northern area of the tank. To eliminate the possibility of visual orientation, we covered their pool with a large sheet of black plastic. We also took all objects out of the water and even rotated the whole tank. Surprisingly, this did not change the sharks' early-morning orientation. However, when we roughly neutralized the earth's ambient magnetic field by passing electrical current through two large induction coils diametrically attached to the outside of the tank, the animals lost their positional preference and distributed randomly.

Although the outcome of these preliminary tests was consistent with the idea of geomagnetic orientation, none were fully conclusive. The avoidance reactions proved the sharks' sensitivity to fields of geomagnetic strength but were not of obvious biological significance. The spontaneous orientation was biologically more interesting, but at that time we were not technically prepared to reverse the field in order to verify the magnetic nature of the response.

In the meantime, the author moved to Massachusetts to pursue his magnetic studies at the Woods Hole Oceanographic Institution. To scale down the technical problems of controlling the ambient magnetic field, we

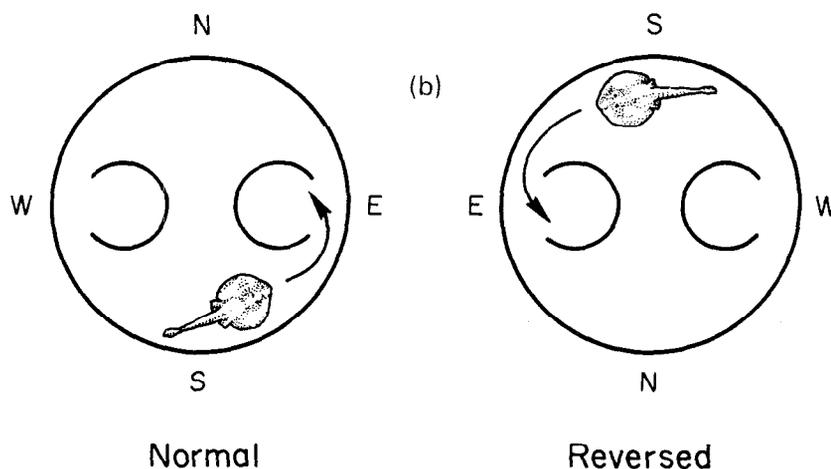
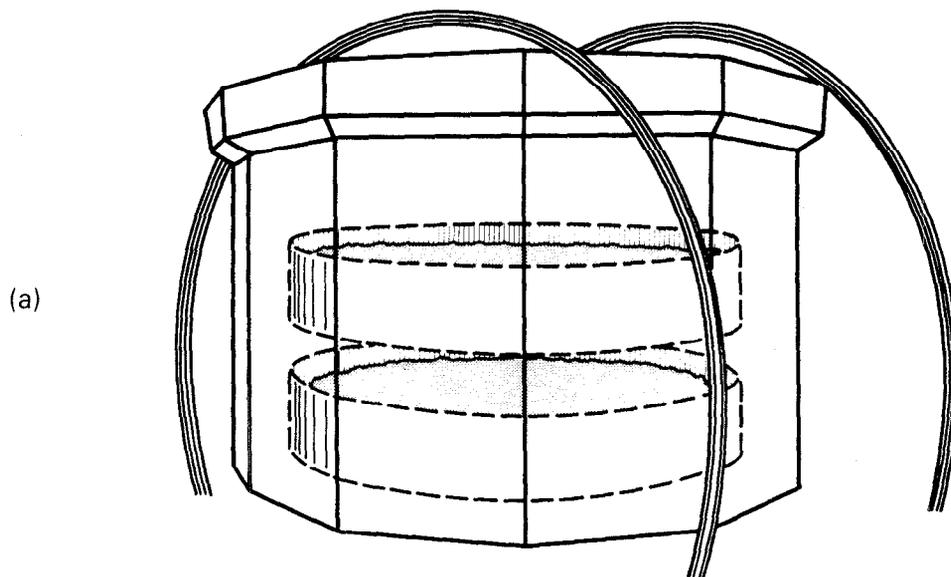


Figure 4. Magnetic test facility on the Quissett campus of the Woods Hole Oceanographic Institution (a). The round stingray *Urolophus halleri*, swimming toward the east enclosure to secure food, under normal and reversed field conditions (b).

looked for a good experimental animal of smaller size, which one of the students found in the round stingray *Urolophus halleri*. The round stingray is a hardy, very alert and active elasmobranch of subtropical and tropical seas, reaching an average span of 25 centimeters. To fit our tanks, we selected five specimens measuring only 15 to 20 centimeters.

The stingrays were tested in a circular, fiberglass pool, 1.8 meters in diameter, which rested on Teflon blocks to insulate it from ground. The pool was filled with natural seawater to a depth of 15 centimeters. Coarse sand covered the bottom, and two airlifts maintained a slow, internal circulation. We surrounded the pool with a lighttight, twelve-sided hut devoid of any ferromagnetic materials. The seawater was kept at 20 degrees Celsius by regulating the air temperature in the hut. Outside the hut, two large Helmholtz

coils, each 5 meters in diameter, were mounted along the north-south axis to control the horizontal component of the earth's magnetic field in the tank (Figure 4a). We chose for our tests a magnetic induction of 0.34 gauss, corresponding to the horizontal component of the Southern California region from where the animals were taken.

During the 1 to 2-hour training sessions, twelve concealed lights illuminated the ceiling over the tank to produce an even, low-level light distribution. For the rest of the day, the lights were programmed to simulate the sunshift and daily variation in brightness of the sky in accordance with the direction of the ambient magnetic field. Lights, heaters, and coils were DC-powered from distantly located voltage and current sources. The wiring was tightly twisted and judiciously installed to prevent unwanted electric and magnetic fields

from straying into the animals' habitat.

Each morning, two observers ran a series of 15 to 20 trials after first turning on the lights, shutting off the airlifts, and checking the direction of the horizontal component of the magnetic field (either normal or reversed). Then, they simultaneously introduced two circular enclosures into the pool, one with the opening to magnetic East, the other with the opening to magnetic West (Figure 4b). After positioning the enclosures, the observers stepped back to watch the behavior of the animals from behind a black, felt screen. When one of the three participating stingrays entered either the east or west enclosure, both observers blocked off the openings by lowering a gate. If the animal entered the east, by definition the correct enclosure, it was rewarded with a small piece of herring; if the animal entered the west or incorrect enclosure, it was gently prodded with a blunt Plexiglas rod as a form of punishment. Eventually, the enclosures were moved to the magnetic North and South of the pool, and the animal was set free for the next trial.

Although it took the animals awhile before they learned to rely on the magnetic field in deciding which side to avoid and where to go for food, after catching on, two of the stingrays made the highly significant scores of 56 and 164 correct choices out of 78 and 248 trials, respectively ($P < 0.001$). The third ray was disqualified because it was not fast enough to compete and was actually losing weight. After the initial training, the stingrays' orientational performances did not significantly change further, either during individual sessions, or from day to day. This, we felt, allowed us to treat the trials as independent choices, despite the fact that the field was reversed only once a day; that is, after each series of 15 to 20 trials. In

a follow-up series, we changed the direction of the field again on a daily basis, but this time in random order. Under this regime, our most active stingray, without further training, made 120 correct choices out of 184 trials ($P < 0.001$) within a period of 15 days.

In earlier tests, frequent field reversals appeared to confuse the animals. Yet we recently began a series in which we randomly reversed the horizontal component of the magnetic field from trial to trial so as to provide the strongest possible evidence. In these experiments, the field is set by a third person, while the two observers do not know whether to feed or punish until after the animal has made its choice. At this writing, our fastest performing stingray has scored 101 out of 154 correct choices, which proves our case ($P < 0.001$) and makes the magnetic orientation of *Urolophus halleri* a fact. Since these results were anticipated as a logical consequence of the animals' keen electric sense, it seems justified to assume that the proposed electromagnetic detection mechanism holds true.

Usually, animals are magnetically tested to explain such remarkable performances as long-distance migration and homing. Thus, a magnetic sense has been established in migratory birds and homing pigeons, though without any indication of the underlying physical principles. In our case, however, we started with sensory structures of unknown function — the ampullae of Lorenzini — and inched our way to discover the electric and subsequently the magnetic sensory world of the elasmobranch fishes.

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