THE ELECTRIC SENSE OF SHARKS AND RAYS

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INTRODUCTION

In 1917 Parker and van Heusen published their historic paper on the behavioural responses of the catfish, *Amiurus nebulosus*, to metallic and non-metallic rods. They found a blindfolded *Amiurus* to be remarkably sensitive to metallic rods, regularly responding to them even at a distance of some centimetres, whereas a glass rod did not elicit a reaction until it actually touched the skin of the animal. When much of the metal was exposed to the water, the fish swam away from it; when little was exposed, the fish turned towards the rod and often nibbled it. In a series of simple but convincing experiments Parker and van Heusen demonstrated that these responses were due to the galvanic currents generated at the interface between metal and aquarium water. The same responses could be obtained by sending a weak direct current into the water via two electrodes, kept 2 cm apart. In this case approach and nibbling were called forth by a current of a little less than 1 μA and the avoidance reactions by currents of 1 μA or more.

Parker and van Heusen did not realize the significance of their results, but in fact they were studying the electrosensitivity of fishes that have – as we now know – distinct electroreceptors. Curiously enough, the electroreceptors of *Amiurus* were not identified experimentally and investigated electrophysiologically until very recently (Dijkgraaf, 1968; Roth, 1968, 1969). Even now, we can only speculate about the biological meaning of the electrosensitivity of the catfish.

Long after the work of Parker and van Heusen, in the year 1951, a new impetus to the study of the electrosensitivity was given by Lissmann. He examined the electric discharges that *Gymnarchus niloticus* and other weakly electric fish almost continuously emit, and proposed the theory that they play an essential role in an electrosensory mechanism for object location. These fish would be able to detect a nearby object of an electrical conductivity different from that of the surrounding water by appreciating the distortion it causes to their electric field. Later on, Lissmann proved *Gymnarchus* to be indeed very sensitive to purely electrical stimuli as implied by his theory, and also showed the fish to be able to discriminate between objects of only slightly different conductivity (Lissmann, 1958; Lissmann & Machin, 1958).

Lissmann tentatively regarded the weakly electric fish as evolved from a pre-electric fish without electric organs but already sensitive to electric fields. He suggested that at this early stage the electrosensitivity might have been used to detect muscular potentials of prey, predators, members of the same species, and of the animal itself. Today,

such a hypothetical pre-electric fish is quite conceivable, for we now know two groups of living fishes that, likewise, are very sensitive to electric fields and lack electric organs, namely the catfish mentioned previously and the sharks that will be discussed next.

The suspicion of an electrosensitivity in elasmobranch fishes traces back to 1935 when Dijkgraaf, working on the shark *Scyliorhinus canicula*, noticed its sensitivity to a rusty steel wire (Dijkgraaf & Kalmijn, 1962). When the head of the shark was approached with such a wire, blindfolded specimens displayed orientated escape reactions at a distance of several centimetres. As in the experiments on *Amiurus*, a glass rod evoked an avoidance response only on coming into direct contact with the animal. On the analogy of the well-founded conclusions of Parker and van Heusen, Dijkgraaf assumed that the sharks also were stimulated by galvanic currents generated at the surface of the metal wire. A quarter of a century later, I tested Dijkgraaf's assumption and, principally following Parker and van Heusen's argument, proved it to be right (Dijkgraaf & Kalmijn, 1962). Moreover, similar behavioural reactions to weak electric currents were observed in the ray *Raja clavata*.

The sensitivity that *Scyliorhinus* and *Raja* exhibited to electric fields depended greatly upon the experimental conditions and on the kind of reflex action observed. Swimming sharks and rays escaped with fright from local direct current fields the moment they entered a region with a voltage gradient of roughly 1–10 μV/cm. Local square wave fields of 5 Hz were equally effective. Further, sharks and rays that had settled down on the bottom of the aquarium responded visibly to a homogeneous square wave field (5 Hz) with a voltage gradient of only 0·1 μV/cm, the sharks by contracting their eyelids, the rays by phase-shifting their respiratory rhythm. Finally the electrocardiogram of the ray, recorded by permanently implanted electrodes, revealed a temporary slowing down of the heartbeat even when the voltage gradient of the square wave field was lowered to 0·01 μV/cm (Kalmijn, 1966).

What are the receptors that make the sharks and rays so extremely sensitive to weak electric fields? For various reasons, the ampullae of Lorenzini seemed the most likely sense organs to mediate the electrical stimuli. (1) The ampullary organs form a rather complicated and extensive cutaneous sensory system. Yet, their function, although much debated, was in fact still unknown. (2) In sharks the ampullary system remains restricted to the head region, and only the head appeared to be sensitive to local electric fields. (3) Like the sense organs that Lissmann (1958) at the time already presumed to be electroreceptors in weakly electric fish, the ampullae of Lorenzini consist of sensory vesicles (the ampullae proper) that communicate with the water by a jelly-filled canal leading to an opening in the skin. (4) Finally, the strongest argument was given by Murray (1960, 1962), who studied the ampullae of Lorenzini electrophysiologically. He discovered that the ampullae are not only very sensitive to thermal and mechanical stimuli, but also respond to weak electric fields. In both *Scyliorhinus* and *Raja* a voltage gradient of only 1–2 μV/cm in the water adjacent to the animals produced at make and break a 10 % change in the impulse frequency of the afferent nerve fibres of the most sensitive mandibular ampullae.

To ascertain the electroreceptive role of the ampullae of Lorenzini, Dijkgraaf and I tested the behavioural responses of *Scyliorhinus* to local electric fields before and after partial denervation of the ampullary system. Although the ampullary fibres are mingled

with the lateral line (and, probably, the trigeminus fibres) up to their very ends, it still appeared possible, after a detailed morphological study, to discriminate between the different sensory systems. The results proved that the ampullae of Lorenzini, and only these, were responsible for the sensitivity of *Scyliorhinus* to the electric fields used as test stimuli (Dijkgraaf and Kalmijn, 1963). By accurate physical measurements on the ampullae, especially on the ampullary ducts, Waltman (1966) demonstrated, in addition, that their electrical properties meet the requirements of electroreceptors very well.

Can we conclude from the foregoing that sharks and rays have an electric sense and that the ampullae of Lorenzini are true electroreceptors? Possibly it is only a matter of definition, but I would like first to answer two other questions before making such a statement. (1) Are there electric fields in the natural habitat of the sharks and rays that can be detected by the animals? (2) If so, do the sharks and rays make a significant use of these fields? To answer the first question, I can refer to the bioelectric field of the flatfish *Pleuronectes platessa* that I previously found to produce a slowing down of the heartbeat in *Raja clavata* from a distance of 5–10 cm (Kalmijn, 1966). In the present article I will deal with the second question and describe a series of experiments designed to determine whether *Scyliorhinus* and *Raja* utilize the electric field of the flatfish to detect their prey.

MATERIALS AND PROCEDURE

The investigations were performed on fifteen specimens of the shark *Scyliorhinus canicula* (L.) and three specimens of the ray *Raja clavata* L., measuring from 30 to 60 cm in length. The animals were collected from the English Channel and the North Sea, and delivered to the laboratory by courtesy of the Netherlands Marine Research Institute at Den Helder and the Government Institute for Fisheries Research at IJmuiden. After the animals were gradually adapted to the temperature and the salinity of the aquarium water, they soon recovered from transportation and started feeding within 3 weeks. Their maintenance food consisted of whiting, *Gadus merlangus* L., which were stored in a freezer and cut into small pieces before use. During the study of their responses to living prey the sharks and rays were offered young specimens of the flatfish *Pleuronectes platessa* L., 8–15 cm in length. These prey were caught in the Waddenzee by local fishermen. Small flatfishes belong to the natural food of *Scyliorhinus* and *Raja* (Mizoule, personal communication).

The sharks and rays lived in circular, inflatable, all-plastic wading pools, 1·8 m in diameter, filled with natural sea water to a level of about 25 cm. On the bottom of the pools was a 2 cm layer of coarse sand. The temperature of the water ranged between 16 and 21 °C; the density was regularly adjusted to 1·025 g/ml. The wading pools had some important advantages over the ordinary aquaria used in earlier years: (1) the sharks, usually following the wall, could easily swim around uninterruptedly despite the relatively small size of the pools; (2) when occasionally bumping against the wall, the animals did not damage the rostrum, which contains many of the ampullae of Lorenzini; (3) and, very essential to the experiments, there were no metal parts to generate galvanic currents in the water. Moreover, the closed sea-water circuit, including a pump of synthetic material and a filter of pebbles and shells through which the water was returned to the pools, was electrically isolated from ground.

In most of the experiments the stimulus source – a living flatfish, some pieces of whiting, or a pair of electrodes – was enclosed in an agar structure (fig. 1), made of 30 g reagent grade agar dissolved in 1 litre sea water, and introduced into the experimental pool at least 12 h before use so that it would equilibrate electrochemically. The responses of the sharks and rays to purely electrical stimuli were studied, and the electrical conductance of the agar structure was tested with a dipole field generated by a current source and fed into the sea water through Ag/AgCl electrodes and sea-water bridges 1 m long so as to minimize the effects of polarization. The electric fields were measured with another set of Ag/AgCl electrodes and a high-impedance, differential d.c. amplifier. The technical problems of generating and measuring weak electric fields in sea water had been studied previously, and will be discussed elsewhere.

In some of the experiments the flatfish was screened electrically by means of a polyethylene film. The electrical properties of the film were determined in sea water after an imbibition period of half an hour. This was achieved by applying d.c. and a.c. voltages (up to 100 kHz) with an amplitude of 10 V across the film and measuring the current through it.

The formal experiments were carried out by recording the behavioural responses of the sharks and rays towards specific stimulus situations in runs of half an hour. The responses were only counted if both people acting as observers independently judged them to be typical and unquestionable. The outcome of a half-hour session was taken for *positive* only if the five or six test animals observed at the same time scored together *at least twenty well-aimed responses*; the outcome was called *negative* only if the test animals showed *no definite responses at all*.

RESULTS

Behaviour of the sharks and rays in laboratory pools

When in good condition and well fed the shark *Scyliorhinus canicula* and the ray *Raja clavata* looked rather lazy, as do most bottom-dwelling fish. During the greater part of the day the animals lay dozing on the bottom of the pool, the sharks usually along the wall and close together, the rays barely discernible after having covered themselves with a thin layer of sand. Occasionally they moved slowly for short distances without apparent motivation and without really awaking. This state of inertness could be ended suddenly by tapping on the table upon which the pool rested, or by gently squeezing the tails of the animals. Following such a stimulus they normally darted away and kept restlessly swimming about for some time, mainly cruising just below the surface of the water or even with the head partly out of water.

Quite another type of behaviour appeared when the animals became hungry. They then spontaneously began to explore the pool, obviously searching for food, the sharks steadily swimming immediately above the sand, the rays walking on it by means of the leglike anterior parts of their pelvic fins. When a small piece of whiting was thrown into the sea water, the behaviour of the animals generally did not change within the first few seconds. However, as soon as the odour of the food reached them they began to swim very fast, excitedly circling around and snapping at the various objects, such as small pebbles and air stones, that they struck at the bottom of the pool. Yet, both the sharks and rays, although attracted by the odour from the food, could not find its

source until actually touching the piece of whiting or at least passing it closely. They then stopped abruptly at, or turned sharply towards, the food and swallowed it voraciously.

Responses to living prey

To see how the sharks and rays behaved in the presence of living prey in eight experiments a small specimen of the flatfish *Pleuronectes platessa*, the plaice, was introduced into the pool. As soon as it was released into the water, the plaice went to the bottom, and hid itself under the sand. If the sharks and rays had been fed shortly before, they were not visibly aroused by what happened in their surroundings, although certainly aware of it (Kalmijn, 1966). When swimming and accidentally coming across the plaice, they sometimes showed a weak approach or even an avoidance response to it. However, as time went by and the sharks and rays became hungry, they began to pay more attention to the plaice and after intermittently starting and chasing their prey, they finally devoured it, although often only after several hours.

For analysing the feeding behaviour, it was desirable to have the whole process intensified and shortened. This could be achieved by offering the plaice to sharks and rays that had not been fed for over a week. A more convenient method, however, was to put the plaice into the pool before the sharks and rays became hungry, and then, after the fish had settled down, to motivate the test animals by an odour stimulus. A few drops of whiting juice, diffusely spread throughout the water, were sufficient to produce a frenzied feeding behaviour, even if the sharks and rays had been fed only 2 days before.

When a shark was eagerly searching for food and passed a plaice at a distance of 15 cm or less, he generally exhibited a very clear feeding response, although the prey was almost entirely hidden from view by a thin layer of sand (Fig. 2a). The shark made a sudden, but smooth and well-aimed, turn towards the plaice and removed the sand over his prey by sucking it up and expelling it through the gill slits. Then the shark took the plaice between his jaws and swam away, wildly shaking his head to tear the prey into pieces small enough to swallow.

The feeding response of the ray differed in some respects from that of the shark. Moreover, because of the shape of the ray, it was difficult to determine the distance from which the prey was perceived. After detecting the plaice the ray pounced upon the prey and enclosed it under his body by pressing the flexible margins of the wing-like pectoral fins against the sandy bottom. In this case, too, the plaice was dug out by blow and suction, the sand, however, coming out from below the ray (the gill slits are situated ventrally; only the spiracles open dorsally). At the same time the ray also made jerky turning movements, as if to get the prey into the right position. The result usually became clear when the ray sooner or later lifted his head and swam away, for often the tail of the plaice was still protruding from his mouth. While swimming, the ray ultimately swallowed the plaice whole. If the plaice was too large for the ray, it was spat out again, alive and not damaged markedly.

The agar chamber

The object of this study was to determine whether, and to what extent, the sharks and rays were guided in their responses to the plaice by the electric field which emanates from it. In the preceding experiments the predators may have perceived their prey

by optical, chemical, mechanical, or electrical stimuli or by any combination of them. Vision was not expected to play a significant part, for *Scyliorhinus* and *Raja* seem not to rely much upon sight, and, moreover, the plaice was visually inconspicuous when buried in the sand. However, the relative importance of the other stimuli by which the place could have been detected remained difficult to assess. To discriminate between the various possibilities without affecting the condition of the sharks and rays, e.g. by depriving them of one or more of their senses, I first screened the plaice with 3 % agar in sea water. This was done by putting the plaice in what I shall call an agar chamber.
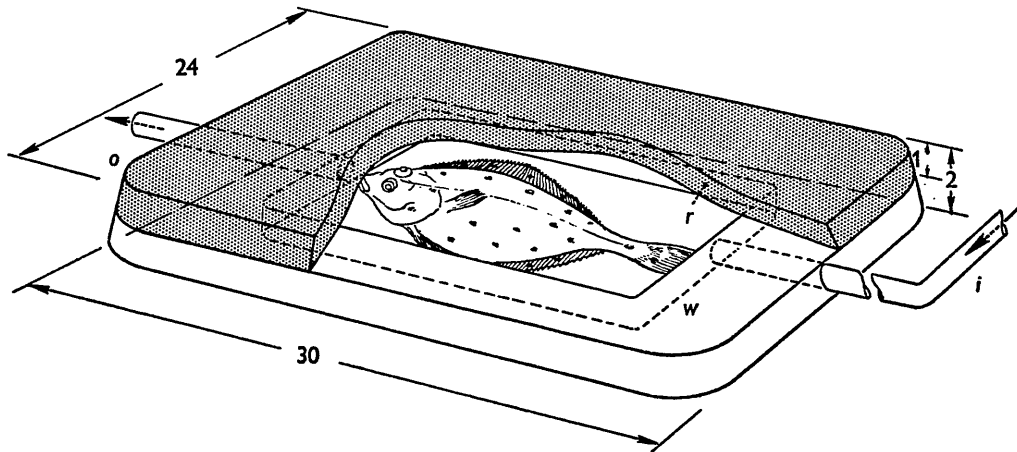

Fig. 1. Agar chamber with the plaice *Pleuronectes platessa*. *r* = foam-plastic stiffened roof, *w* = sidewall, *i* = inlet tube (connected with sea water reservoir), and *o* = outlet tube (freely opening into experimental pool). Dimensions in centimetres.

This chamber (Fig. 1) consisted of a flat cavity bounded by thick sidewalls and a thin roof stiffened with foam plastic. The plastic bottom of the pool, on which the agar structure was placed after locally removing the sand, functioned as the floor for the chamber. The cavity had just the right dimensions to hold a small plaice. The walls were fitted with an inlet and an outlet tube to circulate sea water through the cavity. After putting the plaice into the chamber, the sand was evenly spread over the bottom of the pool, thereby just covering the whole construction.

The idea of the agar chamber was to let the electric field of the plaice pass unimpeded, but to attenuate other stimuli as much as possible. To what degree the physical properties of the agar structure met these requirements will be discussed after describing the experiments carried out with it.

Responses to an agar-screened plaice

After the plaice was slipped under the agar structure and the sand levelled over the bottom of the pool, the sharks and rays were aroused and motivated to search for food by the odour of diffusely spread whiting juice. In some cases the animals were already hungry and searching spontaneously. When the sharks, eagerly swimming about, passed the agar-screened plaice at a distance of 15 cm or less, they still showed their characteristic, well-aimed turnings towards the animal (Fig. 2b). They also tried to dig up their prey, as was evident by the sand spurting out of the gill slits. The rays also swooped down on the agar-screened plaice in their usual way after perceiving the prey at a distance. When the sharks and rays found the plaice unattainable after some

vigorous trials, they moved away, leaving an open patch in the sand over the agar chamber. This cleared spot always appeared to be just over the head region of the plaice. In other words the sharks and rays detected the plaice in the agar chamber from the same distance, and tried to feed on it in the same way, as if there were no agar at all. (Six runs of half an hour, all definitely positive according to the strict criteria mentioned under 'Materials and Procedure'.)
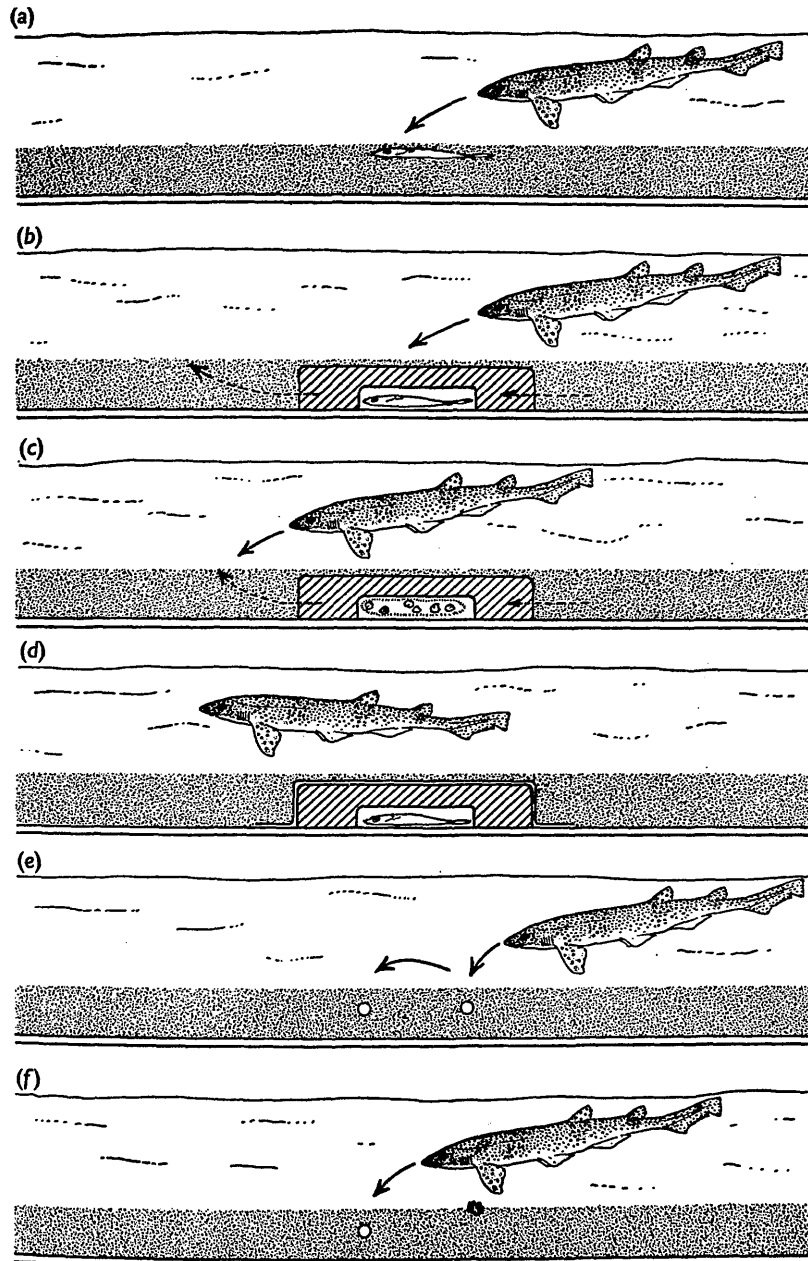

Fig. 2. Feeding responses of the shark *Scyliorhinus canicula* to (a) plaice under sand, (b) plaice in agar chamber, (c) pieces of whiting in agar chamber, (d) plaice in agar chamber covered with plastic film, (e) electrodes producing electric dipole field, and (f) piece of whiting and electrodes (only one shown). Agar chamber not to scale; compare with Fig. 1. Solid arrows: responses of shark; dashed arrows: flow of sea water through agar chamber. For discussion, see text.

That the sharks and rays did not respond to the agar chamber itself or to the effects of the sea water flowing through it, was ascertained by control experiments. (Three runs, all absolutely negative.) To prevent the animals from losing interest in the agar-screened plaice after too many fruitless feeding attempts in succession, now and then small pieces of whiting were given at a place sufficiently remote from the agar chamber not to interfere directly with the responses to the living prey. In this way these and similar experiments in which feeding responses to simulated prey were studied could be carried out three to six times a week and for several months (at least eight) without any appreciable decline in the behavioural reactions of the sharks and rays to the test objects.

Optical, chemical, and mechanical stimuli

In the foregoing experiments the agar chamber kept the plaice completely out of sight. Therefore, the sharks and rays proved, as was expected, not to need visual contact with the plaice to perform a normal feeding response to it.

What did the results of the experiments tell about olfaction? In answering this question caution had to be exercised, because the sharks and rays have a very acute sense of smell. Yet there was strong evidence that the feeding responses to the agar-screened plaice were not directed by smell. First, the predators responded to the plaice at once after its introduction into the agar chamber, while a possible odour substance would have required considerable time to diffuse out through the agar roof. Secondly, the major part of the possible odour substance must have been carried off by the sea water flowing through the agar chamber. Nevertheless, the sharks and rays scarcely paid any attention to the opening of the outlet tube. To confirm the latter argument, I carried out another experiment. The plaice in the agar chamber was exchanged for a small bag of loose Nylon tissue, containing pieces of whiting. In this situation the sharks and rays eagerly tried to find their food at the end of the outlet tube, and did not show even the slightest response when swimming just over the agar roof (Fig. 2c). (Two runs, one with and one without diffuse odour stimulus, both to the outlet positive and for the agar roof negative.)

Finally, to what extent did the agar chamber screen the plaice mechanically? Sharks and rays have well-developed lateral line and labyrinthine organs, and can certainly perceive other animals by the mechanical disturbances they make in their surroundings. The plaice lying under the sand must also have made such disturbances, e.g. by the movements of the gill apparatus and the sea water currents resulting from them. With the agar chamber I hoped to attenuate the mechanical stimuli emanating from the plaice sufficiently to preclude the possibility that the sharks and rays used these stimuli to detect their prey. Whether the agar chamber fulfilled this condition was tested in an indirect but safe and simple way. For this purpose, I repeated the original experiments after changing the mechanical properties of the setup only slightly, but the electrical properties severely as will be discussed in the next paragraph. The agar chamber was spread with a very thin sheet of polyethylene film (thickness about 10 μ) before covering the whole structure with sand. After the test animals had been motivated with whiting juice they searched intensively all over the bottom of the pool, but did not notice the plaice any longer, although they often passed it very closely (Fig. 2d). (Two runs with plastic film, both negative, each followed by a control run without

plastic film, both positive.) The attenuation offered to the mechanical stimuli by the 10 μ-thick plastic film could not be so much higher than the attenuation offered by the agar roof, stiffened with foam plastic, as to explain the dramatic effect of it on the outcome of the experiments. Thus, the well-aimed responses to the agar-screened plaice were likewise not due to purely mechanical disturbances produced by the prey.

Electrical stimuli

Since the sharks and rays did not detect the position of the agar-screened plaice by visual, chemical, and mechanical stimuli, it seemed to be a logical inference that they located their prey electrically. However, such an indirect conclusion may indicate only a limitation of the human imaginative faculty if not tested thoroughly and affirmed by more direct evidence. Therefore I had first of all to determine whether the electrical hypothesis could explain the results of the previous experiments.

Did the agar chamber really, as supposed, not seriously affect the bioelectric field of the plaice? To test the agar chamber electrically, especially its foam-plastic stiffened roof, a 1 Hz sine wave current with an amplitude of 120 μA was fed into the sea water via two salt bridges, positioned on the bottom of the pool and ending 5 cm apart. (The open ends of the sea-water bridges will be referred to as the electrodes.) The resulting dipole field was plotted, first without, and after that with, the agar structure over the electrodes. The potentials in the successive fields appeared to differ no more than the 3 % limit of the accuracy of the measurements. The agar chamber was, therefore, virtually transparent to electric currents. As mentioned above, the feeding responses of the sharks and rays were directed to the head region of the agar-screened plaice. This observation is consistent with the electrical hypothesis, for the bioelectric field of the prey mainly originates from the head region of the fish and passed the agar shielding without appreciable distortion.

On the other hand, did the 10 μ-thick polyethylene film attenuate the electric field of the plaice sufficiently to account for the total lack of responses after it was spread over the agar chamber? The film had a resistance as high as 10^{12} ohm.cm^2 and a capacity of less than 200 pF.cm^{-2}; the resistivity of the sea water was, however, only 19–23 ohm.cm. Consequently, the plastic sheet effectively prevented the d.c. and low-frequency a.c. fields (to which the searching sharks and rays could have responded[*]) from straying out of the agar chamber, and was appropriate indeed to make the plaice electrically undetectable by its predators.

Finally, I proved directly that the sharks and rays actually are able to detect the source of such an electric field as produced by the plaice. To that end, the 1 Hz sine wave current was fed into the sea water once more. Now, however, the sea-water bridges were buried in the sand, and the amplitude of the current was lowered to 4 μA so as to obtain a field strength of the same order of magnitude as in the case of a living plaice. Although the pure sine-wave dipole field was only a poor simulation of the a.c. part of the bioelectric field of the plaice, the sharks and rays reacted to the electrodes, after arousal by smell, in the same way as to a real plaice (Fig. 2e). (Three runs, all positive.) Also by simulating the d.c. part of the bioelectric field of the plaice with a direct current of 4 μA, apparently natural feeding responses could be elicited.

[*] The bioelectric fields of the plaice and other sea animals, and the frequency range of the electrical sensitivity of the sharks and rays, will be dealt with in a subsequent paper.

(Three runs, all positive.) The accuracy with which the animals tried to dig out their imaginary prey became evident when they swam away leaving the electrodes uncovered and clearly visible. That the sharks and rays actually responded to the electric fields and not merely to the electrodes, was easily demonstrated by control experiments without electric current. (Three runs, all negative.)

How strongly the sharks and rays were attracted by the dipole fields roughly simulating the plaice was obvious from the results of an experiment in which I laid a small piece of whiting on the bottom of the pool at a distance of 5 cm from the electrodes, forming with them the angular points of an equilateral triangle. After a while, the sharks and rays were aroused by the odour of the piece of whiting and began searching eagerly. When coming into the vicinity of the food, they showed their typical feeding responses, but, curiously enough, not to the whiting, but to the electrodes, although they were covered by sand (Fig. 2f). Often they swam just over the piece of whiting to reach the site of the electrodes; often they swam away, after digging at the electrodes, without finding the piece of whiting. From these observations, it followed that the electric fields acted as a much stronger directive force for the sharks and rays than did the visual and chemical stimuli of the piece of whiting. After accidentally touching the food, however, the animals immediately bit into it, as they also did with small pebbles and the like.

DISCUSSION

The experiments described in this paper demonstrate that the shark *Scyliorhinus canicula* and the ray *Raja clavata* make a biologically significant use of their electrical sensitivity. Thus, *all criteria mentioned earlier now have been satisfied to accredit the animals with an electric sense and to designate the ampullae of Lorenzini as electroreceptors.* The apparently normal feeding responses to a plaice of which all but the electrical stimuli are attenuated tell us how much the sharks and rays rely on their electric sense. Moreover, the smooth and well-aimed dives towards such a prey show how well they appreciate the spatial potential distribution of the bioelectric field as sensed by their ampullary system.

The bioelectric fields that animals produce in sea water are stray fields of which the voltage gradients rapidly fall off with distance. Therefore it is quite understandable that the sharks and rays can perceive the animals electrically only at a rather short range. However, within this range, the electric sense is surprisingly effective, even if the animal to be perceived has burrowed into the sand.

Unlike the electric fields, an odour field – of a wounded prey for example – spreads out farther and farther, and as time goes by attracts the sharks and rays from a large area. On the other hand the odour fields are easily distorted by local water currents, and in consequence are often too vague for an exact location of the prey. Thus the electric sense and the olfactory sense of the sharks and rays seem to complement each other remarkably well. For the literature on the part the other sense organs play in the feeding behaviour see Gilbert (1963).

Now that the sharks and rays have been shown to detect a plaice electrically, it is tempting to presume that they also use their electric sense to perceive animals with which they have other relations. Even more challenging is the question of whether they can distinguish different kinds of animals electrically, or possibly sense their moods or

intentions. However, first of all, more data are needed on the frequency range of the electric sense and on the occurrence of bioelectric fields in sea water in order to get a better idea of the animals that are to be considered.

Besides the bioelectric fields there are several types of potential gradients of inanimate origin in sea water. To give our speculations about these fields a real basis, I will mention one interesting and relatively well-documented instance. As already foreseen by Faraday (1832), all water movements crossing the lines of the earth's magnetic field give rise to potential differences by the process of electromagnetic induction. Thus (1) the ocean currents, forming a worldwide system to which the Gulf Stream also belongs, (2) the tidal currents, most conspicuous along the continents, and (3) the water movements associated with the waves all produce electric fields. The voltage gradients resulting from the ocean currents in the Atlantic were systematically measured by von Arx (1962). They typically range from 0·05 to 0·5 μV/cm.* The voltage gradients of the rather strong tidal currents in the English Channel reach twice a day maxima up to 0·25 μV/cm (Barber & Longuet-Higgins, 1948). All these values are well above the threshold of 0·01 μV/cm found for medium-sized specimens of the ray *Raja clavata*. Larger sharks and rays with longer ampullary tubes can be expected to be even more sensitive to homogeneous electric fields. Subtle behavioural studies will be required to determine whether or not the sharks and rays in fact use the information that is potentially available. While it is true that the ampullae of Lorenzini are not really sensitive to direct current fields, the animals can theoretically detect both the strength and the direction of the electric field in which they find themselves simply by turning to one side or the other.

Scyliorhinus is only a small animal compared with the sharks that are dangerous to men. It is, in fact, a harmless kind – to humans at least – and even looks tame. Thus *Scyliorhinus* does not immediately make one think about shark hazard. However, my observations may be relevant to this problem. When working on shark repellents it is highly desirable to know about both the sensory capacities of the predators and the stimuli emanating from their prey. Because the ampullae of Lorenzini are a general characteristic of sharks and rays, it can be expected that the dangerous species also live in an electrical world. Therefore, the bioelectric as well as the inanimate electric fields that men produce in sea water must be taken into consideration in studies on shark attacks. To obtain some information about the electrical activity of human prey, I investigated briefly the bioelectric fields of men standing in the middle of a sea-water tank, 8 m in diameter and filled to a level of 1·5 m, and found that the d.c. gradients at 1 m from the body can measure as much as 0·02 μV/cm. By wounding a test person slightly, or by introducing metallic objects into the water, the d.c. fields became even stronger. The a.c. fields of muscles, including the heart, appeared to be negligibly weak as they are in the flatfish and many other sea animals (Kalmijn, in preparation).

I am aware that my reflections on a possible electrical orientation in the open sea and on shark attacks directed by electric fields, although based on real data, are speculative. Of course, what is true for *Scyliorhinus* and *Raja* need not be so for other species. Moreover, how sharks and rays behave in electric fields depends largely upon both the

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* Von Arx has informed me that the values given in his textbook *An Introduction to Physical Oceanography* (fig. 9–11, p. 262) are in error by a factor of ten.

presence of other stimuli and on the internal state of the animals. Yet, now that we know of the existence of an electric sense in sharks and rays, we can expect exciting new results.

SUMMARY

1. Previous experiments have demonstrated that (a) the shark *Scyliorhinus canicula* and the ray *Raja clavata* are extremely sensitive to weak electric fields; (b) their electrical sensitivity is due to the ampullae of Lorenzini; (c) the sharks and rays can be stimulated by the bioelectric fields emanating from the flatfish *Pleuronectes platessa*.

2. When hungry, *Scyliorhinus* and *Raja* perform well-aimed feeding responses to flatfish, even if the prey have covered themselves with sand. The object of the present study was to determine whether the sharks and rays use the bioelectric fields of the flatfish to detect the position of their prey.

3. To analyse the feeding responses of the sharks and rays, a flatfish was put into an agar chamber. The predators responded to the so screened prey from the same distance, and tried to feed on it in the same way as if there were no agar at all. As the flatfish in the agar chamber was completely hidden from view, the sharks and rays were thus shown not to need visual contact to locate the prey.

4. If the agar chamber was filled with cut-up pieces of whiting, the sharks and rays did not respond to the food, although the odour of whiting juice normally attracts them strongly. Therefore, the sharks and rays did not detect the position of the agar-screened flatfish by smell.

5. The feeding responses to the flatfish could be entirely abolished by covering the agar chamber with a very thin sheet of plastic. The mechanical attenuation offered by the plastic film was too weak to explain its dramatic inhibitory effect, and, thus, a purely mechanical detection of the agar-screened flatfish without plastic film was also ruled out.

6. As the responses to the agar-screened flatfish were not merely due to visual, chemical, or mechanical stimuli, it was tentatively concluded that the sharks and rays perceived the prey electrically. This conclusion was fully in agreement with the results of the experiments, for the agar chamber did not appreciably distort the bioelectric fields of the flatfish, and the electrical impedance of the plastic film was extremely high.

7. Further, the bioelectric field of a flatfish was simulated with a pair of electrodes, buried in the sand. Now, the sharks and rays displayed exactly the same feeding responses to the electrodes as they did previously to the real prey. This crucial experiment confirmed the electrical hypothesis in a very direct way.

8. The experiments described demonstrate clearly that the shark *Scyliorhinus canicula* and the ray *Raja clavata* make a biologically significant use of their electrical sensitivity. Therefore, *we now are justified in accrediting the animals with an electric sense and in designating the ampullae of Lorenzini as electroreceptors*.

9. When the sharks and rays were offered a piece of whiting in the vicinity of two electrodes simulating a flatfish, they were attracted by the odour of the food but usually performed their well-aimed responses to the electrodes. Thus, at short range, the electric fields act as a much stronger directive force than do the visual and chemical stimuli. Only direct mechanical contact dominates over the electrical stimuli.

10. Theoretically, the sharks and rays can detect the electric fields resulting from oceanic and tidal currents. Whether they make use of the available information for orientation in the open sea is not yet known. Furthermore, the observations and measurements described indicate that, in studying shark attacks, the electric fields of the prey and the electric sense of the predators should be taken into account.

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