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BIOELECTRIC FIELDS IN SEA WATER AND THE FUNCTION OF THE AMPULLAE OF LORENZINI IN ELASMOBRANCH FISHES

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13. ABSTRACT

The ampullae of Lorenzini, so characteristic of sharks and rays, have been examined by electrophysiological techniques, and were found not only very sensitive to thermal stimuli, but also remarkably responsive to weak mechanical and electrical stimuli. With these results, the ancient question about the function of these curious sense organs remained, however, unanswered.

Subsequently, Dijkgraaf and Kalmijn made a behavioral study of the electrical sensitivity of sharks and rays. They found 1. that the shark Scyliorhinus canicula and the ray Raja clavata react reflexly to to very weak electric fields in the surrounding sea water, and 2. that ampullae of Lorenzini are the sense organs by which these reflex actions are mediated.

To examine the aspect of how these sense organs respond in living animals to more natural stimuli, a method was developed by which the activity of the ampullary nerves could be recorded from live, free-swimming sharks. The preliminary results were promising , but, due to lack of experimental animals, this method could not be applied extensively in Utrecht.

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1. Introduction (o)

The ampullae of Lorenzini, so characteristic of sharks and rays, have been examined by electrophysiological techniques, and were found not only very sensitive to thermal stimuli (Sand, 1938), but also remarkably responsive to weak mechanical and electrical stimuli (Murray, 1957, 1960). With these results, the ancient question about the function of these curious sense organs remained, however, unanswered.

Subsequently, Dijkgraaf and Kalmijn (1962, 1963) made a behavioral study of the electrical sensitivity of sharks and rays. They found 1. that the shark Scyliorhinus canicula and the ray Raja clavata react reflexly to very weak electric fields in the surrounding sea water, and 2. that the ampullae of Lorenzini are the sense organs by which these reflex actions are mediated.

In the following years, Kalmijn (1966 and unpublished) investigated especially the biological significance of the electrical sensitivity. It was demonstrated that 1. the plaice Pleuronectes platessa produces electric fields in the surrounding sea water that are sufficiently strong to be detected by sharks and rays, and 2. that the sharks and rays do not only respond reflexly to these fields, but are also capable of using them in localizing the plaice, even if it has burrowed into the sand.

(o) For the literature cited, see:

Dijkgraaf, S. and A.J. Kalmijn, 1963. Untersuchungen über die Funktion der Lorenzinischen Ampullen an Haifischen. Z. vergl. Physiol. 47: 438-456.

Kalmijn, A.J., 1966. Electro-perception in Sharks and Rays. Nature, 212: 1232-1233.

To what extent do sharks and rays in their natural habitat employ their electrical sensitivity? In order to answer this question it was necessary 1. to perform a more extensive study of the electric fields occurring in sea water, and 2. to determine the role these fields play in the life of sharks and rays. The first half of the three month stay at Banyuls was spent in collecting data on these two topics.

What is the biological significance of the thermal and mechanical sensitivities of the ampullae of Lorenzini? Sand and Murray demonstrated the thermal and mechanical sensitivities in freshly killed specimens of which the ampullae of Lorenzini were partly or even completely severed from the rest of the animals. Moreover, they applied rather unnatural test stimuli. However, how do these sense organs respond in living animals to more natural stimuli? To examine this aspect, a method was developed by which the activity of the ampullary nerves could be recorded from live, free-swimming sharks. The preliminary results were promising, but, due to lack of experimental animals, this method could not be applied extensively in Utrecht. Therefore, the second half of the time available at Banyuls was reserved for these experiments.

2. Bioelectric fields in sea water

Bioelectric fields in sea water were measured with carefully prepared silver-silverchloride electrodes and a dc amplifier specially designed for this purpose (dc - 500 kHz). The ac component was registered directly, the dc component was determined by measuring with the recording electrode successively in the field and in a remote, indifferent position, and subtracting the potential readings so obtained. This procedure yielded reliable results even when the dc values were as low as a few microvolts, despite the electrode and amplifier drift inevitable in this range.

In previous experiments, it had become apparent that, in general, the configurations of bioelectric fields in sea water are rather complicated, and that surveying these fields is a time consuming process. Therefore, the electric fields of most experimental animals were determined only at a distance of one millimeter from the body wall. The so collected values gave a good idea of the strengths of the bioelectric fields, and made it feasible to compare the electric fields of various marine animals.

The measurements were performed on a total of about 120 experimental animals representing 60 species of 8 phyla. Thus, this research has to be considered as an initial endeavor, and, accordingly, the general validity of the results does not go further than "as far measured".

For the determination of the species and for the nomenclature the following text was consulted: W. Luther and K. Fiedler, Die Unterwasserfauna der Mittelmeerküsten; Paul Parey, Hamburg and Berlin, 1967.

CHORDATA : Vertebrata : Pisces : Osteichthyes

Boops salpa, Coris julis, Blennius gattorugine, Gobius spec., Scorpaena porcus, Lepadogaster lepadogaster.

In the surroundings of teleost fishes, three clearly distinguishable electric fields were recorded: dc fields, low-frequency ac fields (below 20 Hz), and higher-frequency ac fields (above 20 Hz).

The main dc fields occurred in the head and gill regions. The potentials in these fields were dependent on the condition of the experimental animals and could, in intact specimens, locally attain values up to 500 μV. In damaged animals, still higher values were measured in the vicinity of their wounds, even though the wounds were inflicted caudal to the gill slits.

The low-frequency ac fields were, just as the dc fields, the strongest in the head and gill regions. The potential fluctuations were synchronous with the respiratory movements, and when these movements became more vigorous, also the amplitude of the potential fluctuations increased. Thus, after a period of induced activity, the peak-to-peak values could run up to 500 μV and more.

The higher frequency ac fields were detectable only during contractions of the trunk and tail musculature. Judging from their time course, they consisted of stray fields of numerous muscle action potentials. At strong contractions, the peak-to-peak values were of the order of magnitude of some tens of microvolts.

CHORDATA : Vertebrata : Pisces : Chondrichthyes

Scyliorhinus canicula, Raja spec.

Also in elasmobranch fishes, dc and low-frequency ac fields were detected. However, these fields were a factor of ten weaker than in the teleosts. The highest dc potentials and the highest peak-to-peak values of the low-frequency ac potentials remained below 50 µV, even in excited sharks and rays. That these potentials appeared so much weaker than in teleost fishes is especially interesting in connection with the electroreceptive function of the ampullae of Lorenzini.

In elasmobranchs, the higher-frequency ac fields occurring during violent contractions of the trunk and tail musculature were about as weak as in teleosts.

CHORDATA : Tunicata

Phallusia mamillata, Halocynthia papillosa, Microcosmos sulcatus, Botryllus schlosseri.

The tunicates generated dc fields which were the strongest at the in- and outflow openings where the potentials attained values over 100 µV. Often, in closing these apertures, one or more slow, biphasic action potentials were observed having maximal peak-to-peak values of 120 µV and a duration of approximately 400 ms.

ECHINODERMATA

Antedon mediterranea, Marthasterias glacialis, Echinaster sepositus, Astropecten aurantiacus, Asterina gibbosa, Anseropoda membranacea, Ophioderma longicauda, Ophiotrix fragilis, Ophiura texturata, Dorocidaris papillata, Paracentrotus lividus, Echinus acutus, Spatangus purpureus, Holothuria forskåli, Stichopus regalis, Cucumaria planci, Leptosynapta inhearens.

The echinoderms generally produced only weak dc fields which appeared to be quite local and variable. The potentials in these fields normally were not higher than 10 μV. In some species, however, now and then values up to 80 μV could be measured.

Wounding was of little effect. Ac fields were not encountered in echinoderms.

CRUSTACEA

Palaemon serratus, Pagurus arrosor, Eupagurus prideauxi, Portunus holsatus.

The higher crustaceans, in undamaged state, showed dc potentials up to about 50 μV. Sometimes, also low-frequency potential fluctuations in the rhythm of the ventilation movements could be recorded, especially along the rim of the carapace.

Wounding the crustaceans had a striking effect. The dc injury potentials were invariably strongly negative and attained values as high as 1250 μV. When an animal died because of its wounds, the potentials diminished only slowly. After a full day, some of the cadavers still exhibited potentials of 200 μV and more.

MOLLUSCA

Haliotis tuberculata, Zyziphinus granulatus, Murex brandaris, Archidorus tuberculata, Mytilus galloprovincialis, Pinna squamosa, Avicula hirundo, Octopus vulgaris, Eledone aldrovandii.

Among the molluscs, the gastropods were the most electrogenic. Wounded or not, they locally produced dc potentials up to 100 µV. At the feet of creeping specimens, also slow action potentials were often recorded, showing peak-to-peak values up to 100 µV and a duration of about 400 ms.

In intact lamellibranchs, the dc potentials were less than 10 µV, and, in intact cephalopods even less than 1 µV. In wounded specimens, the values were appreciably higher.

ANNELIDA, SIPUNCULIDA, and ECHIUROIDEA

Aphrodite aculeata, Spirographis spallanzanii, Serpula vermicularis, Protula intestinum, Phascolion strombi, Bonellia viridis.

The worms belonging to the annelids, sipunculids, and echiuroids produced only weak to very weak dc potentials, never exceeding 10 µV, even not after being wounded.

COELENTERATA

Alcyonium palmatum, Eunicella verrucosa, Veretillum cynomorium, Pteroides griseum, Pennatula rubra, Anemonia sulcata, Bunodactis verrucosa, Calliactis parasitica, Pelagia noctiluca.

Also the coelenterates produced dc potentials which were weak to very weak, not more than 10 µV. Wounding had no detectable effect.

SPONGIAE

Tethya lyncurium, Suberites domuncula, Axinella damicornis.

The sponges did not show any potentials higher than 1 µV, whether damaged or not.

Summary of the potentials of 100 µV and more:

Dc potentials: in wounded crustaceans, up to and well over 1000 µV; in teleosts, up to and more than 500 µV; in some tunicates and gastropods, up to about 100 µV.

Ac potentials: in teleosts, potential fluctuations in the respiration rhythm up to and over 500 µV; in some tunicates and gastropods, slow action potentials up to about 100 µV.

3. The origin of bioelectric fields

Originally it was intended only to study the occurrence of bioelectric fields in sea water. In the course of the investigations, however, some attention was also paid to the origin of these fields, particularly in fish.

Tha higher-frequency ac potentials of fish were, as mentioned earlier, immediately recognized as muscle action potentials. The origin of the dc and low-frequency ac fields was not as readily obvious. Yet, after a few simple measurements, a notion could be formed about the sources of these fields. Recordings from fish anaesthetized in MS 222 (150 ppm) demonstrated that, in any case, the dc fields were not related to muscle activity. Although the higher- and low-frequency ac fields disappeared with the relaxation of the musculature and the cessation of the respiratory movements, the dc potentials persisted even in completely anaesthetized specimens.

As the dc potentials in the head and gill regions often were the highest just in front of the mouth opening and at the gill slits, respectively at the free rim of the operculum, it was logical to extend the potential measurements to the mouth cavity and the pharynx. In two live specimens of the teleost Boops salpa, potentials were recorded up to + 2.5 mV in the mouth cavity and up to - 7.5 mV in the pharynx. Measurements on Blennius gattorugine, Gobius spec., and Scorpaena porcus yielded similar results. Also in these fish, the potentials in the pharynx were in general negative compared with those in the mouth cavity.

After a close examination of the potential distribution, the conclusion seemed to be justified that the strong electric fields in the mouth cavity and the pharynx either were generated by the walls of these cavities (mucous membranes and gill epithelium), or were the result of electric currents leaving and entering the animal preferentially through these walls but having their origin somewhere else in the body.

As a necessary consequence of the potential distribution in the mouth cavity and the pharynx, electric currents must have strayed out through the mouth opening and the gill slits, thereby partially or even mainly producing the much weaker electric fields external to the cephalic and branchial regions of the animals. Conforming to this idea, the potentials measured in the mouth cavity and the pharynx of the relatively weakly electrogenic sharks and rays were much weaker than those in the teleosts.

That the dc potentials could have their origin somewhere else in the animals became especially apparent on encountering a local, but strong dc field in the vicinity of the anus of Blennius gattorugine. It is interesting that also in this case it was a mucous membrane that generated the potentials, or, at least, formed part of the electrical circuitry as could be concluded from the configuration of the field.

Originally it was supposed that the low-frequency ac fields occurring in the rhythm of the respiratory movements came directly from the gill muscles. Some of the measurements performed at Banyuls, however, made this assumption very doubtful. In the first place, during the rhythmic contractions of the trunk and tail musculature no appreciable low-frequency potential fluctuations were observed in addition to the higher-frequency potentials in the sea water adjacent to the corresponding body regions. Secondly, the respiration muscles appeared electrically so well screened that the action potentials of these muscles were not measurable in the sea water external to the head and gill regions of the animals. Thirdly, low-frequency potential fluctuations could also be obtained by passively moving the gill apparatus of anaesthetized specimens. On these grounds it was concluded that the low-frequency ac fields did not arise directly from the respiratory muscles, but resulted from the rhythmic fluctuations of the resistance ratios produced by the respiratory movements in the existing dc field. In other words, it was supposed that the alternating contractions and expansions of the mouth cavity and the pharynx, and the opening and closing the respiratory valves modulated the existing dc field and thus produced low-frequency ac fields.

4. Sharks, rays, and the electric fields of their prey

The shark *Scyliorhinus canicula* and the ray *Raja clavata* feed on all sorts of bottom fishes, crustaceans, molluscs, and worms (Dr. Robert Mizoule, personal communication[o]). Of these animals, the higher fishes (wounded or not) and the crustaceans (only when wounded) produced the strongest electric fields in the sea water. In Utrecht, it had already been demonstrated that sharks and rays utilize the electric fields of the plaice *Pleuronectes platessa* in localizing their prey. To gather more information on this subject, the responses of the sharks *Scyliorhinus canucula* and *Scyliorhinus stellaris* to the small bottom fish *Lepadogaster lepadogaster* and to the crustaceans *Palaemon serratus*, *Portunus corrugatus*, and *Pagurus arrosor* were briefly analyzed at Banyuls.

During the experiments, the sharks were motivated to search for food by a few drops of octopus or fish juice dispersed in the aquarium water. In the first series of trials, the prey was presented to the sharks simply by releasing it on the bottom of the aquarium. In a second series, the prey was placed in a small chamber of which the walls and the roof were made out of 5% agar in sea water. This chamber was superficially buried in the sand on the bottom of the tank. The agar roof,

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[o] Dr. Robert Mizoule, biologist CNRS, Laboratoire Arago, Banyuls-sur-Mer, based his data on an extensive survey of stomach contents in sharks and rays. He also made many observations in the natural habitat of these animals.

reinforced with foam plastic, formed an excellent optical, chemical, and mechanical screen, but permitted the bioelectric fields emanating from the prey to pass through almost without any attenuation, as had been proved in the experiments on the plaice.

The only specimen of the strongly electrogenic fish Lepadogaster lepadogaster available for the first series of experiments, was located and devoured whole by a passing shark within the shortest possible time. Likewise, another Lepadogaster placed in the agar chamber immediately elicited well-aimed feeding responses from sharks coming within a distance of about 5 cm from the prey.

Intact specimens of the prawn Palaemon serratus (relatively weakly electrogenic) were found and eaten by the sharks only after a long period of time after being released in the experimental tank. The sharks had to come very close or even to touch the prawns before they snapped at them. Prawns that had been damaged at their abdomen (strongly electrogenic) were, however, localized by the sharks from distances of more than 5 cm, and consumed within a very short time. A wounded prawn in an agar chamber appeared to be as attractive and as easy to localize for the sharks as were the wounded specimens which could move freely throughout the aquarium.

The results of the experiments with the swimcrab Portunus holsatus, as far they could be carried out, were analogous to those obtained with the prawn Palaemon serratus.

Abdomens of hermit crabs freshly severed from the body (strongly electrogenic) were presented as food, first uncovered, half buried in the sand on the bottom of the aquarium, and then enclosed in an agar chamber. In both cases, the abdomens were very attractive to the sharks, and could be located accurately from a distance of several centimeters.

The results of all these tests clearly show that bioelectric fields emanating from strongly electrogenic prey or from prey in a strongly electrogenic state are used by sharks in searching and localizing their prey.

Also many weakly electrogenic animals such as worms and molluscs, wounded or not, and intact crustaceans form part of the diet of *Scyliorhinus canicula* and *Raja clavata*. Judging from the behavior of the sharks and rays, these weakly electrogenic animals are probably detected not so much by their bioelectric fields as by the chemical and mechanical stimuli they produce.

5. Electrophysiological investigations pertinent to the function of the ampullae of Lorenzini

It has been demonstrated electrophysiologically that the ampullae of Lorenzini are sensitive to test stimuli of quite different modalities. In short, the ampullae appeared even to respond to: 1. a temperature change of 0.05 centigrade (Hensel, 1955), 2. a force of 1 mg exerted on the jelly in the ampullary pores (Murray, 1960), 3. an electric field of 1 μV per cm in the surrounding sea water (Murray, 1962), and 4. a salinity change of the sea water from 3.2 to 3.3 percent or *vice versa* (Murray, 1962). For details, see the original papers.

Do these data prove that the ampullae of Lorenzini could operate as thermo-, mechano-, electro-, and chemoreceptors? If that is the case, the question arises as to whether the function of these sense organs can be determined electrophysiologically, or whether it would be more instructive to approach this problem from a behavioral point of view. Certainly, a behavioral approach can be profitable as has been shown previously. On the other hand, it would not be correct to pass judgement about the function of the ampullae of Lorenzini merely on grounds of their sensitivities. For the same reason, the unsuitability of the electrophysiological method for solving this problem has not yet been established.

How can we evaluate the functional significance of the sensitivities obtained? In my opinion, the only sensible way is to compare the sensitivities with the strengths of the stimuli that act upon the sense organs in nature. It goes without saying that such a comparison is only of value if the test stimuli applied reaches the sensory epithelium in a natural way, and if the sensitivities are not influenced by experimental conditions.

From the foregoing it follows that we are still far from a functional assessment of the electrophysiological data. In the first place, it has not been determined to what extent killing the experimental animal and partial or complete dissection of the ampullae influenced the properties of the sense organs and the way in which the test stimuli acted upon them. In the second place, until recently, no serious effort had been undertaken to examine systematically the thermal, mechanical, electrical, and chemical stimuli occurring in the natural habitat.

To avoid the difficulties and uncertainties outlined above, I planned to apply the electrophysiological method in a more direct way, namely, by registering the activity of the ampullary nerve fibers not in preparations but in live, free-swimming sharks. That means not by first determining the sensitivities to test stimuli and then comparing them with the strengths of the natural stimuli but by having the natural stimuli act directly upon the ampullae of Lorenzini.

The nervus ophthalmicus superficialis innervating the ampullae in the rostrum appeared to be the most suitable for these experiments. A silver-wire electrode was subcutaneously fitted around one of the bundles of which this nerve is made up. The electrode was connected to the amplifier by a thin cable anchored on the head of the animal. The nerve activity was registered on a tape recorder and later written out on a chart recorder both directly and also via an integrating circuit.

6. The effect of electric fields on the activity of the nervus ophthalmicus superficialis

The nervus ophthalmicus superficialis showed a spontaneous activity consisting of numerous, small action potentials and less numerous, large action potentials. The small action potentials could be suppressed by weak electric fields, but not by water currents directed against the head. Thus, the small action potentials seemed to represent the activity of the ampullary fibers. On the other hand, the large action potentials just responded to water currents, but not to weak electric fields which indicated that they had their origin from the ordinary lateral-line fibers.

Although it was possible to distinguish the two kinds of action potentials from each other, it was endeavored to work with lateral-line free recordings as much as possible. Such recordings could, however, only be obtained by chance because of the intermingling of ampullary and lateral-line fibers.

Seldom, even in resting animals, was the activity of the ampullary fibers nicely constant. In most cases, the nerve activity appeared to be more or less modulated in the rhythm of the respiratory movements, most likely as a result of the low-frequency potential fluctuations accompanying these movements (see section 2).

That these respiratory variations really were alterations in the activity of the ampullary fibers could be demonstrated by applying weak, artificially generated electric fields. By switching on a sufficiently strong dc field of appropriate polarity all nerve impulses were suppressed for several seconds. If this field was left on, then adaptation occurred and the modulated activity returned gradually. Switching off the field caused a temporary increase in the number of impulses per second, thereby masking the respiratory modulations. After this break response, the original activity level was restored and the respiratory modulations became again apparent. It has to be noted that no changes in the amplitudes of the respiratory movements could be observed, neither at the beginning nor at the end of the stimulus.

Also with weaker electric fields, switching on and off had pronounced effects on the activity of the ampullary fibers, but without influencing the respiratory modulations as drastically. In other experiments, the electrical stimuli were applied in a more natural way, namely by having a dc field move relative to the shark or the shark relative to the dc field. The results of all these experiments were in complete conformity to those obtained previously in Utrecht.

In the most informative trials, the ampullae of Lorenzini were directly stimulated by bioelectric fields. From a distance of 5 cm, the low-frequency respiratory potentials of the fish Boops salpa appeared to produce impressive modulations in the activity of the ampullary fibers of the shark. Furthermore, characteristic changes in the activity of the ampullary fibers were observed when the shark swam at a level of several centimeters through the dc field of an anaesthetized Boops salpa. Similarly, the dc field of a severed abdomen of the hermit crab was strongly stimulating.

The results of the latter experiments demonstrate that the ampullae of Lorenzini of free-swimming sharks respond to natural electric fields normally occurring in the natural habitat of the animals. In my opinion, this is the most important information that the electrophysiological method can furnish us if we want to evaluate the electrical sensitivity of the ampullae of Lorenzini from a functional point of view.

7. The effect of mechanical stimuli on the activity of the nervus ophthalmicus superficialis

After having studied the electrical sensitivity of the ampullae of Lorenzini, it was determined to what extent these sense organs responded to mechanical stimuli in free-swimming sharks. From lateral-line free registrations showing pronounced responses to weak electric fields, the ampullae of Lorenzini appeared to be completely insensitive to 1. strong water currents directed against the head, 2. strong, fast changing whirlpools just in front of the head, and 3. mechanical vibrations all through the experimental tank. That these mechanical stimuli were, in fact, relatively strong, was proved in control experiments by the vigorous reactions of the lateral-line fibers to such stimuli. Therefore, it seems to be justified to conclude from the electrophysiological results that the ampullae do not serve a "distant touch" like the lateral-line sense organs.

In lateral-line free registrations, responses to mechanical stimuli occurred only when the skin of the rostrum came into direct contact with solid objects. Conceivably, these responses really represented a mechanical sensitivity of the ampullae of Lorenzini. There are, however, other possibilities: 1. the action potentials originated from the ampullary fibers, but the ampullae were stimulated by the electrical effects accompanying the mechanical stimuli as, for instance, the modulation products of the existing dc field of the shark, 2. the action potentials did not originate from the ampullary fibers but from trigeminal fibers innervating the skin of the rostrum and sensitive to tactile stimuli. Thus, the results of the electrophysiological investigations do not yet exclude a tactile function of the ampullae of Lorenzini, although the lateral-line system is much more sensitive to tactile stimuli and also the trigeminal fibers are responsive to them.

It was striking that the lateral-line fibers, in addition to their sensitivity to water currents, showed themselves to be extremely sensitive to all kinds of mechanical vibrations. The lateral-line organs of the rostrum responded not only to vibrations throughout the whole experimental tank, but also to light stroking of the denticles of the dorsal skin and to gentle tapping of the tail. The latter stimuli did apparently not move the water relative to the sense organs, but the sense organs relative to the water. It is notable that all these vibrations to which the lateral-line system is so sensitive generally produce vigorous startle responses in dozing sharks. In order to evaluate the functional significance of their sensitivity to vibrations, it would be necessary to know more about the mechanical stimuli that act upon the lateral line in nature. The most direct way to obtain this kind of information is, in my opinion, registering the lateral-line nerve-fiber activity of free-swimming sharks in the ocean.

8. The effect of thermal, chemical, and compound stimuli on the activity of the nervus ophthalmicus superficialis

Thermal and chemical stimuli were applied by having sea water of different temperatures and different salinities respectively flow against the rostrum of the experimental animal. To both types of stimuli the ampullary fibers showed gradual but distinct activity changes. The rather slow onset of the response has to be explained by the way in which the stimuli reached the sensory epithelium.

The results of the older electrophysiological studies suggest that, in the experiments just described, the thermal stimuli acted directly upon the sensory epithelium of the ampullae of Lorenzini and the chemical stimuli via the electrical effects accompanying them. Due to lack of knowledge about the thermal and chemical stimuli in the natural habitat of the sharks, it is not yet possible to assess the functional significance of the sensitivities in question.

In preliminary experiments in Utrecht, it had already been noticed that, when a shark surfaced and thrusted its head completely or partly out of the water, the electrical activity of the nervus ophthalmicus superficialis increased greatly. After a more detailed examination, it appeared that this activity originated not only from the lateral-line and ampullary fibers, but also from the respiratory, trunk, and tail musculature.

When the head of the animal came above the water and, thereby, the shortcircuiting action of the surrounding sea water was partially lost, stray fields of muscle action potentials penetrated directly into the registrations as could be demonstrated by inserting an electrode under the dorsal skin of the head without bringing it into contact with the nerve.

It seems to be obvious that upon surfacing the lateral-line organs were stimulated mechanically. The responses of the ampullae of Lorenzini could have been elicited either by the mechanical or the electrical effects of breaking the water surface. The electrical effects could again be explained as modulation products of the existing bioelectric dc fields of the shark itself. The best place to measure the strength of the effects would be directly across the sensory epithelium of the ampullae of Lorenzini.

I wish to thank the director and the staff of the Laboratoire Arago for the hospitality and the services rendered during this study. Thanks are also due to Mr. Loos, Mr. Schönhage, and Mr. van de Zalm for their help in preparing the equipment and Mr. van Rhijn for his qualified assistance during the experiments.