DOGFISH ELECTRORECEPTION AT UTRECHT UNIVERSITY 1966, A RETROSPECTIVE VIEW

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Half a century ago, Dijkgraaf and Kalmijn published a paper on dogfish electroreception, a contribution to the 'Festschrift' at the occasion of Karl von Frisch's 80th birthday. As was explained to the author at the time – and as is supported by Dijkgraaf's correspondence – the paper was a rush job, which did not fully meet the standards of a peer-reviewed experimental publication. The following should be considered a footnote to Dijkgraaf & Kalmijn's publication, and as a stage for serendipity and search images and their parts played in the discovery of the biological significance of the ampullae of Lorenzini.

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Karl von Frisch, Sven Dijkgraaf, Hans W. Lissmann, Peter E.P. Görner, Ad J. Kalmijn, Rob C. Peters, Arie Schuijf, Sir John Eccles, Yuri N. Andrianov, references, timeline

50 years ago – Karl von Frisch's 80th Birthday (1966)

'Karl v. Frisch zum 80. Geburtstag in Verehrung gewidmet'. In their paper *Versuche zur biologischen Bedeutung der Lorenzinische Ampullen bei den Elasmobranchiern* (Dijkgraaf & Kalmijn 1966), the authors summarize a number of characteristics of the ampullae of Lorenzini, found during their researches. These characteristics were: 1) the detection threshold of the ampullae, 2) the electrical sources to which they respond; at that time presumed to be muscle potentials, 3) the ability to learn to detect electrical dipoles hidden in the sandy bottom, and 4) the biological significance as derived from their being specifically sensitive to electrical stimuli.
At the time I worked as a student tutored by Ad J. Kalmijn at Dijkgraaf's lab. My task was to perform *in situ* electrophysiological recordings from the nerves innervating the ampullae of Lorenzini. And although I happened to make some publishable recordings, I was rather disappointed that my results were considered valuable enough to be presented in the 'Festschrift', but that acknowledgements were lacking. I had to understand that writing the paper had been a rush job because Professor Dijkgraaf received the invitation to write a contribution rather unexpectedly; he had two months only to write the paper and to have it accepted. Also I noticed that none of the contributions of the other students tutored by Kalmijn were acknowledged. The net result was that the success of my implantation experiment was balanced by the omission in the acknowledgements, allowing me to continue my existence in modesty.
During my major internship at Dijkgraaf's lab, I had the impression that the study on electroreception in dogfish knew a long tradition. To my surprise I noticed recently in the card-tray of Dijkgraaf's slide collection, that the ampullae of Lorenzini were filed under 'Mechanoreceptors' (fig. 1). This incited me to have a closer look at Dijkgraaf's involvement in ampullary research by digging in his legacy, conserved by *Stichting De Traditie.* The following is an elaboration of item 4 in the summary of the aforementioned publication of Dijkgraaf & Kalmijn (1966) on the biological significance of the ampullae of Lorenzini in dogfish.

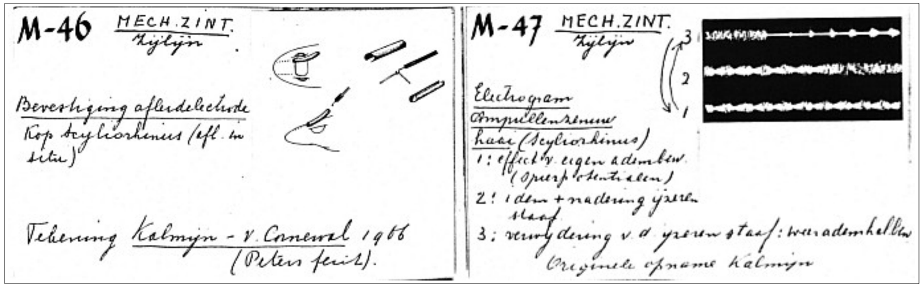


Figure 1. Two of Dijkgraaf's index cards of the collection of transparencies used for teaching. Both deal with electroreception and ampullae of Lorenzini, but are marked 'Mechanoreception'. M46 shows how a silver wire electrode is mounted around ampullary nerves in dogfish. M47 shows the response of an ampullary nerve bundle to an iron rod. Both illustrations are copies of figures of Dijkgraaf & Kalmijn 1966.

Enter: Sven Dijkgraaf (1932), Lorenzinian ampullae

According to Görner *c.s.* (1996), Dijkgraaf's first contact with the lateral line system took place in Vienna, at professor Abel's lab. However, rather soon Dijkgraaf moved to Karl von Frisch's in München, where he presumably had more freedom to choose the experimental approach. There he began to work on rheotaxis and the lateral line in minnows. The first evidence of his involvement with the ampullae of Lorenzini is a *Referat* on 24 February 1932, entitled *Bau und Funktion der Lorenzinischen Ampullen (Dotterweich-H 1932. Zool. Jahrb. Abt. Phys. 50, 347-418).*

After finishing his PhD thesis (1933), he follows a course on Comparative Physiology at Hermann Jordan's lab at Utrecht. Jordan was a proponent of conduction with decrement in invertebrate nerve fibers. As a consequence, we retrace Dijkgraaf not much later in the Zoological Station at Naples, fighting with a string galvanometer, trying to, but unable to, confirm Jordan's view on conduction with decrement. A manuscript on these findings was submitted to Pflügers Archiv, but rejected by editor Bethe. Stripped of some expletives, Dijkgraaf's reaction is given by the drawing on the rejection letter: *Aplysia Arbeit, Ruhe sanft* (fig. 2).

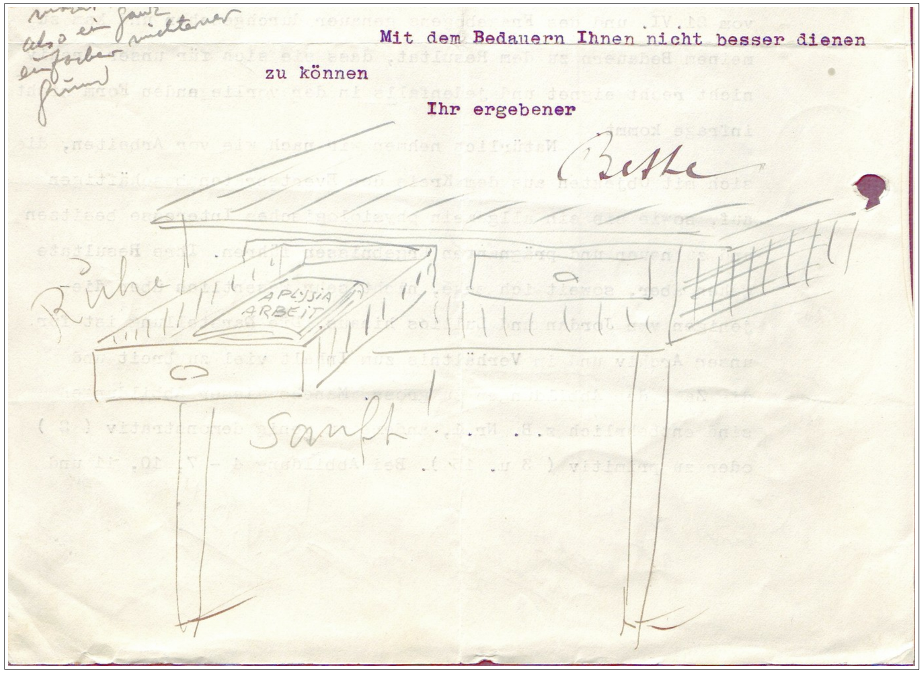


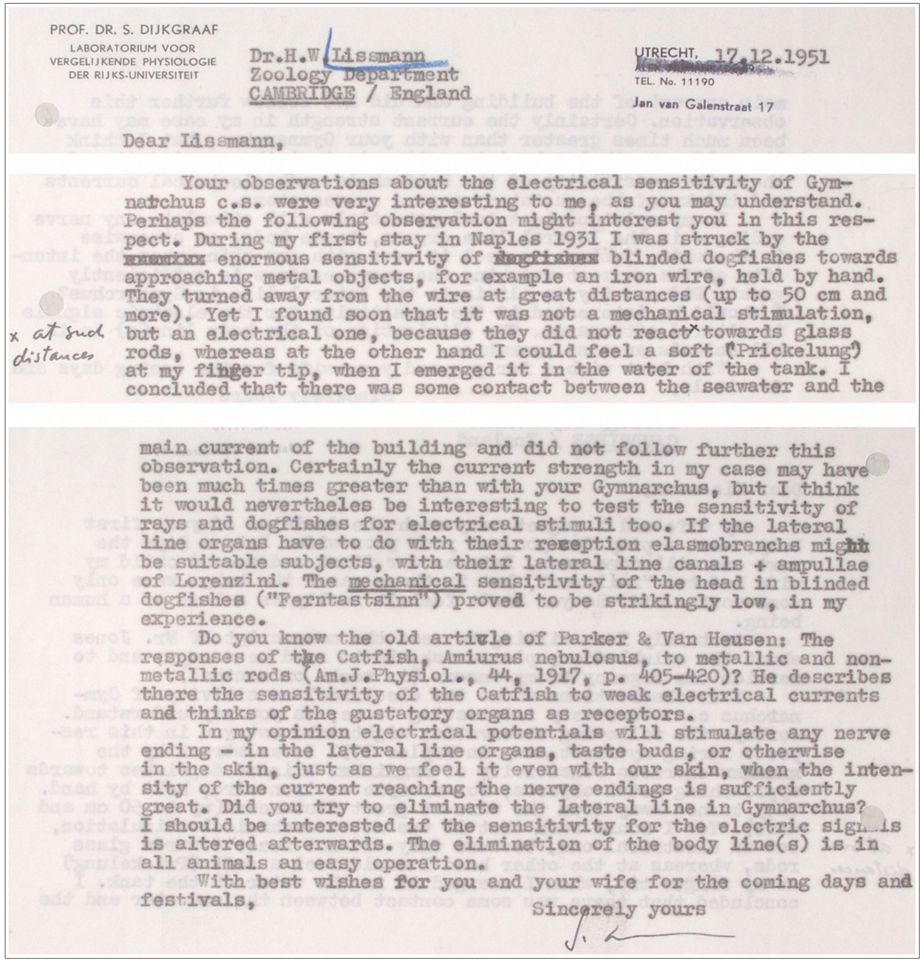
Figure 2. The drawing at the back of the letter in which Bethe explains why he cannot accept the manuscript for publication. The drawing is self evident: 'Ruhe sanft', and 'Aplysia Arbeit' makes citation of certain expletives unnecessary.

In the same notebook in which he made notes on the galvanometer experiment, experiments with *Scyllium* are described; lateral line experiments on the detection of water current. However, a note dated 14 June 1935 describes his observation of the reaction of *Scyllium* to iron wires. As he later wrote me, when I asked permission to publish his notes, he attributed the reaction to leakage currents from the mains. It is very likely that this period causes his undeniable future aversion of the string galvanometer. In 1936 he receives a teaching post at Groningen University at Engel Hazelhoff's lab to teach biology to medical students. His experimental notes at

Groningen reveal among other things the assistance of A.H.J. Vendrik in recording nerve impulses of the lateral line fibers in *Xenopus*. Incidentally this seems to be successful. Then comes WW2. In the mean time there are no involvements with ampullae of Lorenzini. After the war – 1948 - he is nominated professor of Comparative Physiology at Utrecht, Jordan's successor! B.J. Krijgsman (1940, 1947) is the local electrophysiologist who can handle the string galvanometer, who favours the oscilloscope, but who leaves to South Africa in 1950. The ampullae of Lorenzini remain unexplored at Utrecht, but the urgent need for an electrophysiologist who can study the lateral line system can no longer be denied.

Enter: Hans W. Lissmann (1948), electric fish

In 1948, shortly after Dijkgraaf's nomination, Hans Lissmann from Cambridge seeks contact with Dijkgraaf in order to visit the sea aquarium of the laboratory at Utrecht. A rather intensive correspondence takes place. In 1951, Lissmann's paper appears on the electrical signals from the tail of a fish, after which Dijkgraaf writes to Lissmann about his peculiar observation of dogfish responding to iron rods in Naples, and about the unexplained electrical sensitivity of catfish to weak electrical currents described by Parker and van Heusen (1917). In this letter to Lissmann, Dijkgraaf dates his famous observation in 1931, but Dijkgraaf's 'Versuchsprotokollen' show a different year: 1935. He also writes that it would be very interesting to test the sensitivity of the ampullae of Lorenzini to electrical stimuli, because they seem to be very insensitive to mechanical stimuli (fig. 3. Dijkgraaf to Lissmann: 17 December 1951). In 1952, student Peter F. Elbers, later professor of Electron Microscopy, starts with electrophysiological recordings on the lateral line of *Xenopus.* It would take a couple of years extra, and the efforts of two more students – A.C.J. Burgers and A.M. Stadhouders – to gain publishable results (Dijkgraaf 1956).



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LABORATORIUM VOOR
VERGELIJKENDE PHYSIOLOGIE
DER RIJKS-UNIVERSITEIT

Dr.H.W.Lissmann
Zoology Department
CAMBRIDGE / England

UTRECHT, 17.12.1951
TEL. No. 11190
Jan van Galenstraat 17

Dear Lissmann,

Your observations about the electrical sensitivity of Gymnarchus c.s. were very interesting to me, as you may understand. Perhaps the following observation might interest you in this respect. During my first stay in Naples 1931 I was struck by the enormous sensitivity of blinded dogfishes towards approaching metal objects, for example an iron wire, held by hand. They turned away from the wire at great distances (up to 50 cm and more). Yet I found soon that it was not a mechanical stimulation, but an electrical one, because they did not react× towards glass rods, whereas at the other hand I could feel a soft ("Prickelung") at my finger tip, when I emerged it in the water of the tank. I concluded that there was some contact between the seawater and the

× at such distances

main current of the building and did not follow further this observation. Certainly the current strength in my case may have been much times greater than with your Gymnarchus, but I think it would nevertheles be interesting to test the sensitivity of rays and dogfishes for electrical stimuli too. If the lateral line organs have to do with their reception elasmobranchs might be suitable subjects, with their lateral line canals + ampullae of Lorenzini. The mechanical sensitivity of the head in blinded dogfishes ("Ferntastsinn") proved to be strikingly low, in my experience.

Do you know the old article of Parker & Van Heusen: The responses of the Catfish, Amiurus nebulosus, to metallic and non-metallic rods (Am.J.Physiol., 44, 1917, p. 405-420)? He describes there the sensitivity of the Catfish to weak electrical currents and thinks of the gustatory organs as receptors.

In my opinion electrical potentials will stimulate any nerve ending - in the lateral line organs, taste buds, or otherwise in the skin, just as we feel it even with our skin, when the intensity of the current reaching the nerve endings is sufficiently great. Did you try to eliminate the lateral line in Gymnarchus? I should be interested if the sensitivity for the electric signals is altered afterwards. The elimination of the body line(s) is in all animals an easy operation.

With best wishes for you and your wife for the coming days and festivals,

Sincerely yours

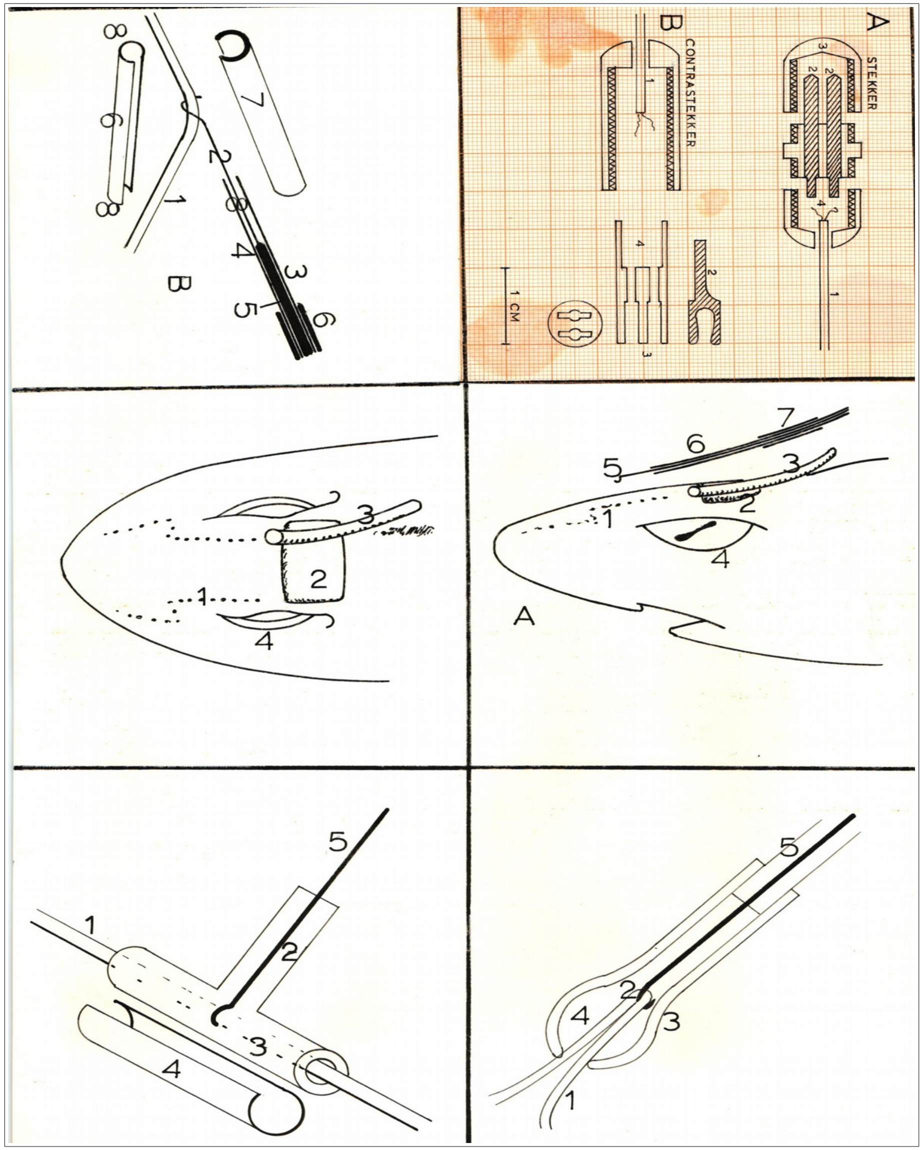
Figure 3. Sections of a carbon copy of the letter by Sven Dijkgraaf to Hans Lissmann. The lower section is the back of the letter (*verso)*, the top two sections are the front (*recto*), minus a few personal lines. Apparently Dijkgraaf realizes the electrosensitive potential of the Lorenzinian ampullae, but somehow he does not seem to have plans to tackle the problem himself electrophysiologically.

Enter: Peter E.P. Görner & Ad J. Kalmijn (1959), electrophysiology

The need for an experienced electrophysiologist is high. Dijkgraaf falls back on his Münchener background, and finds in Peter Görner the man who can continue the electrophysiological experiments on *Xenopus*, The Utrecht Philips-Voigtlander oscilloscope camera is transported from Utrecht to München, and when Görner sends his first scuccessful recordings of the lateral line organs of *Xenopus*, a position in Utrecht is created. Görner begins at Utrecht in 1959. All efforts are focused on he mechanoreceptive function of the lateral line system, for which Görner receives assistance from a student, Ad J. Kalmijn. He further creates a sound basis for the instruction of electrophysiological recording techniques. In 1959 we see, finally, for the first time continuation of electrophysiological research by students. In the internal annual of Utrecht University of 1959/1960, students are listed who work on the electrophysiology of the lateral line (W. Berendsen), and on the ampullae of Lorenzini (A.J. Kalmijn). Students working on the electrophysiology of the ampullae of Lorenzini are also mentioned in the annual of 1961/1962, but are absent in that of 1962/1963. The latter annual mentions students who are going to work on the electrophysiology of the Crustacean eye (R.C. Peters), frog labyrinth (J. Atema), chemoreception in flies (L. Schouten), and Crustaean statocysts (H.G. Gallé). In the mean time H. Hensel (1955, 1956) has been investigating electrophysiologically the effects of mechanical and thermal stimulation on the ampullae of Lorenzini, and R.W. Murray is performing electrophysiology on *Xenopus* lateral line organs and also ampullae of Lorenzini in dogfish (1957, 1959, 1960, 1962). It is Murray (1962) who finds moreover an extreme sensitivity to electrical stimulation. This must have been an unpleasant surprise for the Utrecht student whose task it was to perform electrophysiology on the ampullae of Lorenzini. On the other hand, the biological significance of the ampullae remained still an enigma, because of the sensitivity to both thermal, mechanical, and electrical stimuli. It is Lissmann again who suggests tentatively that muscle potentials of other fish might be the relevant stimuli to the ampullae (Lissmann 1958, p. 183). Muscle potentials, because dogfish have no electric organ like Lissmann's *Gymnarchus.*

Enter: Rob C. Peters, *in situ* recordings (1966)

My internship at Comparative Physiology began in 1963 as assistant of the 3rd year practical. I was scouted by Jelle Atema and more or less pressed to sign a working contract. Supervisor of the muscle and nerve physiology part was Ad J. Kalmijn, who succeeded Peter Görner as teacher of electrophysiological techniques.
My first recollection of the work at the lab was the battery operated electrical stimulator, specifically designed by Kalmijn for field work on the electrosensitivity of dogfish. Kalmijn's proposal for my internship was to spend the first weeks of my internship at the lab in order to get a feeling of what was needed to perform electrophysiological experiments successfully. Then I should do a 6 months minor in physics with, among other things, electronics and theoretical electricity, after which I could return to Comparative Physiology to finish my 12 months major. This turned out to be a very profitable study program, which later helped me to survive in the academic environment. During the last part of my major, I was redirected to the electric sense in dogfish. The question of the biological significance mentioned in Dijkgraaf & Kalmijn (1962) was still not answered. Electrophysiological experiments had demonstrated sensitivity of the ampullae of Lorenzini to mechanical, thermal, and electrical stimuli, but behavioural evidence for a specific natural biological use was still missing. I got the task to record spikes from the nerves innervating the ampullae of Lorenzini *in situ*, without damaging the ampullary capsules, to investigate the ampullary responses under conditions as natural as possible. The procedure outlined by Kalmijn was straightforward. Anesthetize the dogfish with MS222 – which he introduced as a central anesthetic – expose the ampullary nerves which would not be affected by the anesthetic, implant a silver wire electrode after having established a provisional response, and have the animal recover to swim around freely. There were, of course, some minor difficulties to overcome. Kalmijn's idea was to make a T-piece of perspex in which the electrode and nerve could be mounted. The mechanics workshop considered this task too cumbersome, so that I had to spend many hours behind the lathe myself. After having tested these T-pieces and other structures on nerve fibers of frogs, eventually a simple piece of insulation



< Figure 4. Drawings made in 1966 by the author to be copied into the typewritten report (1966). Remember that at the time the Lab did not have a Xerox machine; the figures had to be photographed manually first. The figures show how the silver electrode wire was attached finally to the nerve bundle (top left), and the drawing of the custom made waterproof connector (top right) The middle row shows the position and size of the adhesive patch on the dogfish's head. The bottom row shows a drawing of the custom made pespex T-piece (bottom left), and a simple polythene cannulae (bottom right), both intended as insulation compartments for the recording site. The legends of the figures are omitted here. Copies of these originals were pasted into the carbon copies of the report. See also figure 11.

Figure 5. Photograph of the anesthetized dogfish with two insulation stockings glued on its head. Only after hardening of the glue, the skin in front of the stockings was opened in order to expose the underlying nerve bundles of the ampullae of Lorenzini. Size of the dogfish about 50 cm TL.

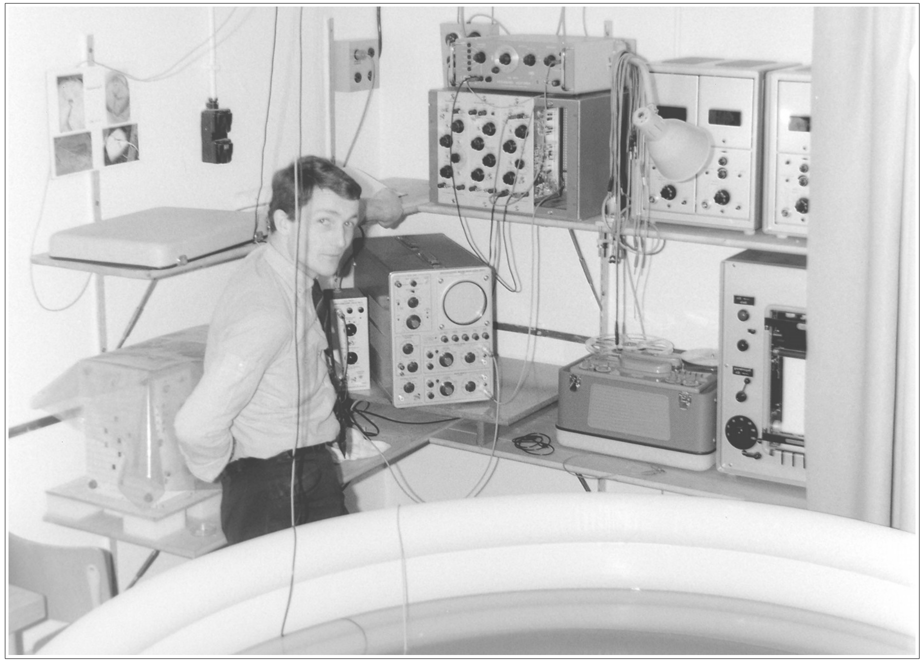


Figure 6. Impression of the equipment in use at the Laboratory of Comparative Physiology at Utrecht in 1966. Demonstrator is enthusiastic and expert Jelle Atema. Close to Jelle the Tektronix 502A Oscilloscope, and behind him the Tektronix 122/125 Pre-amplifier. The tape recorder to the right is a Revox G36 for the recording of action potentials and gross activity. Next to the Revox stands the Hellige Helgoscript He86 paper chart recorder. Above the Hellige recorder, its two pre-amplifier stages. In front, part of the plastic wading pool in use for dogfish and rays.

stocking proved the best solution, more or less as described in Delgado (1964, p. 122). Another problem was the mechanical fixation of the electrode wire onto the skin of the dogfish. At the time we choose for a rather new two component adhesive that seemed non-toxic. Hardening however took more than an hour. For the implantation procedure the dogfish was put on the table top (fig. 5), and provided the fish was kept moist with seawater, its oxygen exchange through gills and skin

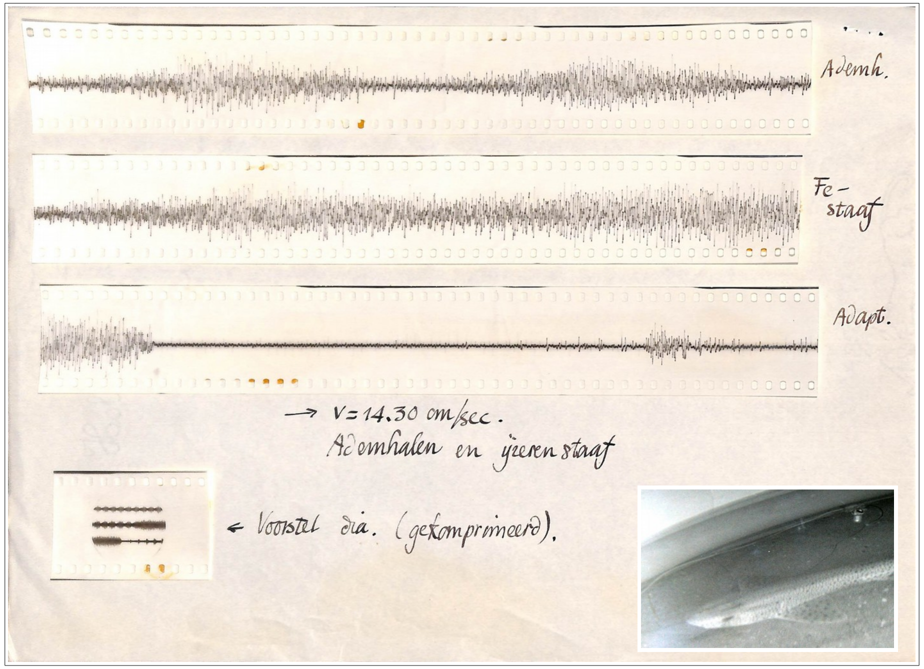


Figure 7. Recording of the approach of an iron rod to the ampullae of Lorenzini. Before writing my final report on the research period at Kalmijn's, I was asked to make some pictures that could be used for the Karl von Frisch Festschrift. Also I should write a preliminary report with my results briefly summarized, for the same purpose. Inset: picture of the dogfish in the plastic pool. The recordings were filmed with a Philips-Voigtlander oscilloscope camera type FE106-5500 ; for the picture of the dogfish with its floating connector attached I used my Exa Ia camera

proved sufficient to have the animal survive the 3 hours needed for the operation. After having anesthetized the dogfish, I tried to record table top wise from the nerves, but the only responses I got were trains of spikes that might be related with respiration, as well as 'contact' responses on touching with a metal pin. On the whole a very disappointing result. I made two or three of such unsuccessful operations.

Enter: Arie Schuijf (1966), slide show of Arie on Safari

The last time I tried to implant an electrode was on March 23, 1966. At the end of another apparent failure, I put the dogfish back into its tank, with the intention to have a quick meal, and then to return to the lab in order to check the treated dogfish before attending the slide show by Arie Schuijf. Arie had made a beautiful series of transparencies during a holiday trip through Africa, which was referred to as the Tombuctu and Kilimanjaro trip: Arie on Safari! I did not want to miss it. When I returned to the lab, I was happy to see that the dogfish had recovered fully from its anesthesia and was swimming around actively. So I decided to skip the first part of Arie's talk, and check the implanted electrode, just in case a miracle would have happened. To my surprise, a miracle did have happened. When I connected the implanted electrode wire to the Tektronix 122/125 pre-amp, a loud noise of recorded gross nerve activity filled the room (figs. 6, 7, 8, 9). I never had seen such beautiful responses before. I wondered what the cause of this unexpected activity might be;

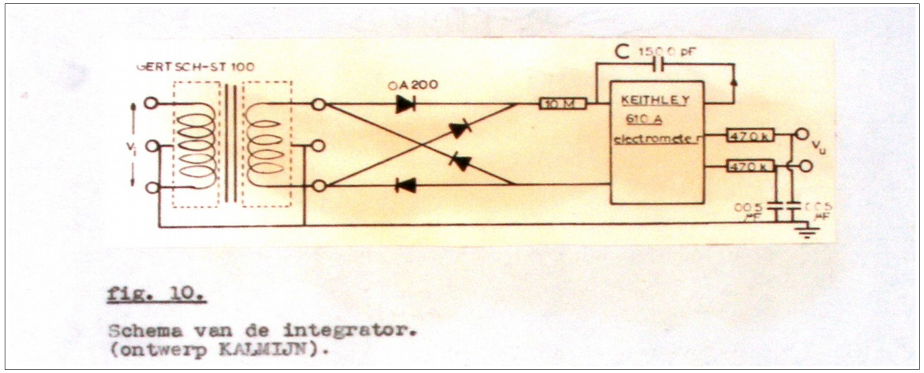


Figure 8. Integrator circuit, designed by Kalmijn, to measure the overall power of the gross nerve activity recordings, for better presentation and evaluation. The integrated signal matches better the auditive impression, than does the original recording.

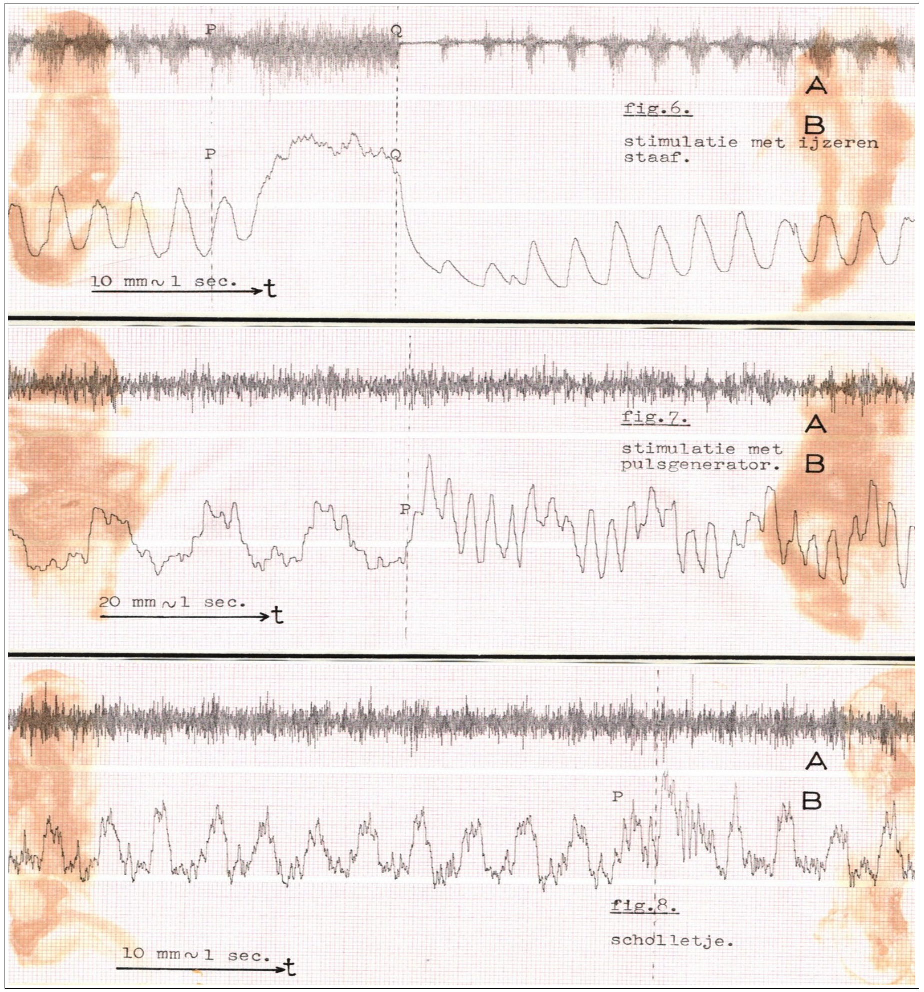


Figure 9. Recordings of the ampullary nerve bundle on 23 March 1966. A – taped signal; B – Integrated signal (cf. fig. 8). Top: response to the approach of an iron rod. Middle: response to 5Hz square wave stimulation. Bottom: response to a burying plaice. The recordings were copied from Rob Peters' report. The brown stains are the result of 50 years of non acid-free glue.

most likely the electrode had been displaced and made better contact with the nerve. At least that is what I thought at that moment. So without any further delay I took a piece of iron and brought it in the vicinity of the dogfish's snout. The response was enormous (fig. 7). A further conspicuous feature was that the responses were heavily modulated in the rhythm of the gill movements. The only other thing I could do at the time was to stimulate the ampullae electrically with Kalmijn's battery operated square wave generator; square waves of 5 Hz. Then I realized that a plaice was lying in the same pool, and since the objective of my internship was to find out to what kind of stimuli the ampullae of Lorenzini responded under 'normal' circumstances, I spent about half an hour to manipulate the dogfish above the plaice just in time to have it respond to the burying movements of the plaice (fig. 9). Remember that Lissmann (1958) had suggested that muscle potentials might be a biologically relevant stimulus source for the ampullae of Lorenzini. To see if under these conditions the ampullae also responded to temperature changes, salt concentrations, and mechanical stimulation, I poured warm seawater into the pool, tap water, and I tapped the snout of the dogfish with a plastic rod. All to no avail, *i.e.* I did not recognize audible responses, whereas, the square waves, the iron rod, the respiration movements, and the burying place yielded clearly audible modulations in the gross activity. All this took about one hour, so in the break of Arie's talk I invited professor Dijkgraaf, Kalmijn, and of course my fiancée Tonny Gest, downstairs in the basement to enjoy these unexpected findings. I demonstrated the iron rod trick again, and we all returned happily afterwards to Arie's slides.

On Kalmijn's request I wrote a quick report to be used by Dijkgraaf for the von Frisch paper, and a more elaborate one as the final report of my internship. In both I tried to describe dutifully the procedure followed, but did not dwell on the discrepancy between my unsuccessful experiment the afternoon, and the successful recording that same evening. I just took the success for granted. This was – my view - partly due to Kalmijn's rather imperative and detailed way of editing my reports.

At the time nobody asked how it came that the recording of such beautiful responses had been impossible in the afternoon. Nobody realized that MS222 blocked the synapses of the ampullary system, and that the procedure I had described could never have yielded proper responses during anesthesia. It was my guess then, as unexperienced electrophysiologist, that the electrode had been moved somehow, with better recording conditions as the result. When Kalmijn went to Banyuls in the fall of 1969 to repeat my experiments more in depth himself, he discovered to his chagrin, that it was impossible to get decent responses under MS222 anesthesia. He told me that it took him at least a couple of weeks before he realized that MS222 also blocks the ampullary synapses. I have tried to recover in vain why he thought MS222 to sedate the central nervous system *selectively*; in the literature MS222 was simply described as a *general* anesthetic. I was further very disappointed that Kalmijn did not accept the responses to the burying plaice as responses to electrical stimuli. According to him, they were mechanosensory lateral line responses. I reluctantly adapted my report according to his instructions, but I have been always convinced that these responses were electrosensory, mainly because I could not evoke responses by tapping the ventral skin with a plastic rod (*cf.* Dijkgraaf & Kalmijn 1966, summary nr. 4). And last but not least, neither Dijkgraaf nor Kalmijn were there when I made this recording.

Enter: Sir John Eccles (1969), Direct Current stimuli

Sir John Eccles does not need an introduction. However, what is not generally known, is his contribution to the understanding of the biological significance in electrosensitive fish without electric organs. Somewhere in 1969 he visited Utrecht to give a lecture on what I remember as the evolution of the visual arts[1]; at the same occasion he visited Dijkgraaf's lab, and was introduced to Kalmijn's dogfish work (personal communication by Kalmijn, and later by Dijkgraaf). At the time it was still not known to what electrical stimuli the ampullae of Lorenzini responded under natural conditions. The most promising sources were muscle potentials of other fish, as suggested by Lissmann. It was Sir John Eccles who provided an alternative: strong

1 Up till now I was unable to pinpoint the exact date of his visit.

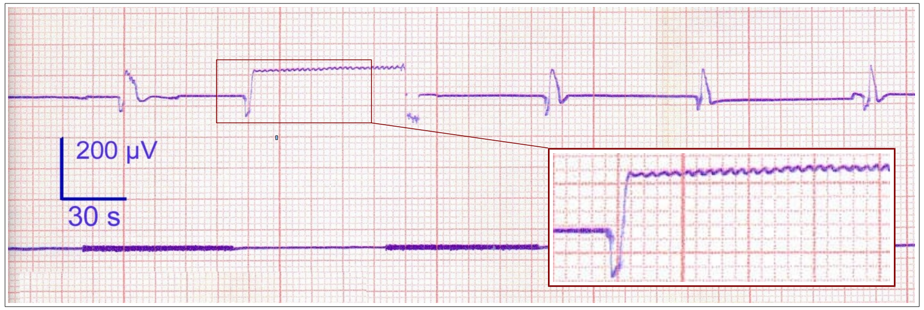


Figure 10. DC field of a freshwater catfish, *Ameiurus nebulosus* LeS, recorded by having the fish swim in a shuttle box connected by a plastic tube. The recording electrode was in the middle of the bottom of the tube, and the reference electrode outside the tube. The fish was forced to swim from the left compartment to the right one, and vice versa, by switching on lights (bottom trace). Every now and then, the fish stopped swimming in the middle of the tube so that the DC character of its electric field could be appreciated. Note that the respiratory potentials are only a small fraction of the total DC component. See inset for respiratory fluctuations. (Peters et al., 2001, 2002).

DC-potentials in the pharynx of fishes (fig 10). It was this suggestion that induced Kalmijn (1972) to look successfully for DC sources in the Banyuls aquarium in 1969.

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Enter: Yuri N. Andrianov 1991

The nature of the neurotransmitter in the ampullary system is in my experience strongly connected to the person of Yuri N. Andrianov. In 1966 we knew little of the pharmacology of the ampullae of Lorenzini. Dijkgraaf used most of the time urethane solutions if he wanted to anesthetize or immobilize lower vertebrates or invertebrates. When I started in 1963, MS222 became fashonable, and proved a very convenient anesthetic: fast in and fast out. As we know today by the investigations of several authors, ampullary nerve endings have glutamatergic synapses (see e.g. review by Akoev & Andrianov 1993). Many years later we had the privilege to start cooperations with among other people Hans Braun (Marburg), Klaus Schäfer (Stuttgart), and Yuri Andrianov (St. Petersburg), experts on the ampullary system. Only this time we did not work on ampullae of Lorenzini, but on the micro-ampullae in freshwater catfish. For single unit recordings in catfish we injected sometimes a muscle relaxant, but most of the time the steroid Saffan, a mixture of alphadolon and alphaxolon. Eventually, on recommendation of Kirsty Grant (Gif-sur-Yvette), we used etomidate added to the water as sedative to immobilize the catfish. In this way, even single unit activity of ampullary organs could be recorded non-invasively in immobilized catfish receiving artificial respiration, thus providing an excellent system for teaching sensory neurophysiology. After a successful pilot experiment with unexperienced students, tutored by analyst Wim J.G. Loos, ampullary electroreceptor organs in catfish have been used at Comparative Physiology at Utrecht University for more than 20 years in all practicals on neurophysiology (Peters *et al.* 1988). Dijkgraaf's accidental observation on dogfish in 1935 had evolved into an elementary instruction experiment in 1988.

Serendipity, search image, prejudice, and the open mind

Dijkgraaf's observation of the dogfish turning its head away from an iron wire (1935), was more or less coincidence, as was Sir John Eccles' passage through the Netherlands in 1969. Both events provided nevertheless essential keys to the elucidation of the biological significance of the electrosensitivity of the ampullae of Lorenzini. My own *in situ* recordings of the ampullary nerve are perhaps also a typical example of serendipity: after having already accepted the failure of making a successful implantation, I found beautiful responses to electrical stimuli, whereas I had only the intention to check whether or not the dogfish had survived my surgery. It is rather confronting to recognize that expertise can lead to particular search images, which may turn out to be prejudices, hampering the discovery of what one is looking for. Because Dijkgraaf's *search image* was that the lateral line system was mechanoreceptive, it took him a very long time to enter the world of

electroreception. Also Kalmijn's expectation that the *general* anesthetic MS222 was a *central* anesthetic only, which would leave the synapses of the ampullary system untouched, took time that could have been used to investigate the responses of the Lorenzinian ampullae to pieces of food and prey under 'free-swimming' conditions.
It is also revealing that in the world of sensory physiologists, electrical potential differences belong to the world of nerve and muscle fibers, whereas the standing DC potentials, mentioned by Sir John Eccles, belong to the expertise of chemical physiological transport scientists. Apparently roaming and scavenging through the sciences is a 'must' for innovation.
Halfway the 19th century, the eminent physiologist Johannes Müller wrote about the senses: *The manifestation of different objects to each other cannot express the nature of light ; that it renders objects visible to us depends merely on our having an organ of vision with vital properties. And in this way many other agents have the same power of rendering objects manifest: were we endowed with as delicate an organic re-agent for electricity as for light, electricity would have the same influence as light in rendering manifest the corporeal world* (Müller 1842, p. 1068).
A whole century later, the search image for the ampullae of Lorenzini was still traditional. The simple idea that there could exist sensory organs typically adapted to very weak electrical stimuli was too far fetched. Even after successful electrophysiologcal recordings (e.g. Hensel 1955, 1956; Murray 1957, 1959, 1960, 1962), the biological significance remained enigmatic. Sir John Eccles' advice to have a look at standing DC potentials in the pharynx of fishes, marks in my view the turning point in the understanding of the biological significance of the ampullae of Lorenzini. After Sir John Eccles' suggestion, von Uexküll's trininy (1909) could be completed: 1) the physiology of the sensory organ was pretty well understood, 2) appropriate electrical stimuli had been recognized, and 3) behaviour contributing to survival had been described. Looking back: It took some time, but it was fun!

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Appendix

Figure 11. About two decennia later another type of waterproof connector was used: a piece of an Amphenol strip connector and vaseline turned out to be both a waterproof, and an easy and good connection (Coen Ballintijn, Groningen, personal communication). The adhesive used to glue the connector to the skin hardened in about 10 minutes. Reference: Peters-RC, Evers-HP 1985. Frequency selectivity in the ampullary system of an Elasmobranch fish (*Scyliorhinus canicula*). J. Exp. Biol. 118, 99-109.

Ampullary essentials – abbreviated timeline

yyyymmdd

19320223	Dijkgraaf presents 'Referat' on the Lorenzinian ampullae in München
19350614	Dijkgraaf observes the sensitivity of dogfish to corrosion currents
19511217	Dijkgraaf writes to Lissmann about his observation and about the electric sensitivity of catfish, as discovered by Parker & van Heusen.
19530924	Dijkgraaf correponds with Hensel about the biological significance of thermo- and mechanosensitivity of dogfish
19600712	Dijkgraaf asks Murray about plans re electrophysiology and behaviour
19600714	Murray writes that he already found electrosensitivity for the ampullae
19611016	Murray-RW 1962. The response of the ampullae of Lorenzini of elasmobranchs to electrical stimulation. J. Exp. Biol. 39, 119-128
19620525	Dijkgraaf-S, Kalmijn-AJ 1962. Verhaltensversuche zur Funktion der Lorenzinischen Ampullen. Naturwiss. 49, 400.
19630425	Dijkgraaf determines electrical detection threshold for dogfish in Villefranche
19630704	Dijkgraaf to Lissmann: found in Villefranche that ampullae are electroreceptors
19640201	Dijkgraaf-S 1964. Electroreception and the ampullae of Lorenzini in Elasmobranchs. Nature (London) 201, 523.
19661210	Kalmijn-AJ 1966. Electro-perception in sharks and rays. Nature (London) 212, 1232-1233.
19660323	Rob Peters records ampullary activity in freely swimming dogfish
19660414	Lindauer invites Dijkgraaf to write a paper for 'Festschrift von Frisch'
19660606	Manuscript for Festschrift accepted: Dijkgraaf-S, Kalmijn-AJ 1966. Versuche zur biologischen Bedeutug der Lorenzinischen Ampullen bei den Elasmobranchoern. Z. vergl Physiol. 53, 187-194.
19680520	Dijkgraaf to Lissmann on inadequacy of ampullae as electroreceptors, as suggested in J. Exp. Biol. 135, p 183.
19680522	Lissmann to Dijkgraaf about reasons to consider muscle potentials as putative biologically adequate stimuli
1969	Sir John Eccles suggests pharynx DC potentials as adequate stimuli