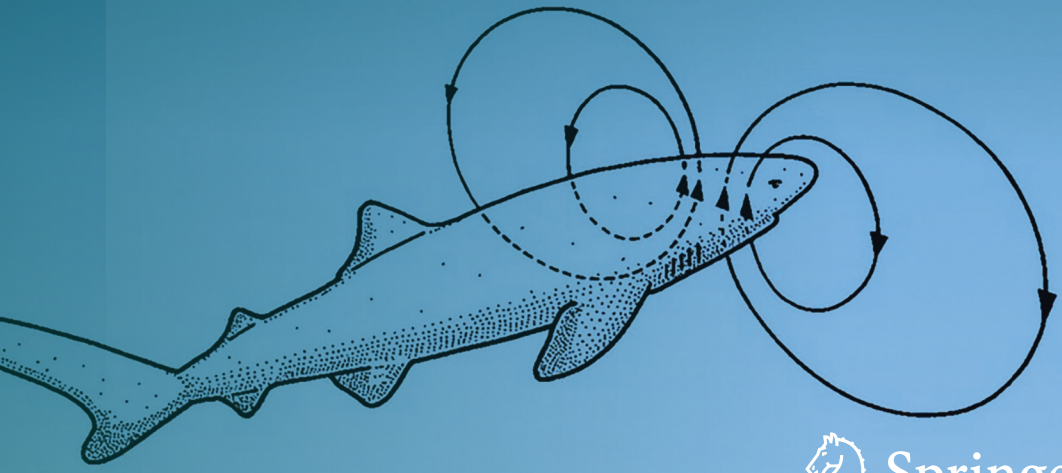
Adrianus J. Kalmijn

Theory of Electric and Magnetic Orientation in Sharks and Rays Revisited

Physical Principles, Biological Evidence, and Rebuttal of Misconceptions



Springer

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Physical Principles, Biological Evidence, and Rebuttal of Misconceptions

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In the high and pure philosophic desire
to remove error as well as discover truth —

Michael Faraday (1832)

Foreword

The author of this book, Dr. Adrianus Kalmijn, was a true pioneer with a unique understanding of biology and physics. This enabled him to arrive at conclusions, which no one before him had been able to deduce.

Since the first anatomical description of the mysterious tubes in the head of elasmobranchs, today known as Ampullae of Lorenzini, their function was a puzzle. These tubes were demonstrated to be sense organs, and they were proven to have great sensitivity to an array of stimuli. They are sensitive to changes in hydrostatic pressure, salinity, temperature, and electric fields, but for decades the biological significance was very uncertain.

However, a series of very well-planned experiments, best described by Kalmijn (1971), demonstrated that a dogfish could detect the presence of a plaice buried in the sand, only because of the electric fields from the respiratory movements of the operculum of the flatfish. These experiments immediately convinced the conservative and skeptical scientific world of their function.

Later Kalmijn designed experiments, in the open ocean and in tanks, which allowed him to conclude that the extraordinary sensitivity to weak electric fields allowed elasmobranchs to sense their swimming direction based on their movements in the geomagnetic field.

Kalmijn also made very significant contributions to the physics of hair cells in the lateral line and inner ear.

In 1984, I met Vera and Adrianus Kalmijn in San Diego during a research visit to the Scripps Institution of Oceanography. Their hospitality and friendly way to meet other scientists made us friends, and when I returned, with my family, to San Diego in 1986, we collaborated on experiments designed to disclose the sensitivity to hydrostatic pressure of the Thornback Guitarfish (*Platyrhinoidis triseriata*). We found that this ray could detect changes of less than 10 cm hydrostatic pressure in a shallow tank. Unfortunately, we never finished the experiments because I had to return to Denmark. But I was much impressed when I realized how strict Kalmijn was regarding control of the experiments. This was somewhat in contrast to what we see today, where many researchers hurry to publish preliminary results. Kalmijn never jumped to conclusions.

My family and I spent many good times together with Vera and Adrianus. We shall never forget the trips to the Anza Borrego desert, which they introduced to us.

It is a great pleasure for me to recommend this book. While it may be a challenge to read, I am sure that it will be an essential road map for scientists and teachers interested in the biology of elasmobranchs or general animal orientation. It really is a most important text in this field, and we are lucky that Adrianus Kalmijn spent so much time to clarify his thoughts. We also owe much gratitude to Vera Kalmijn and their children who helped move this work to publication.

Aarhus, Denmark
2023

Jørgen Mørup Jørgensen

Preface

Dear reader, you are welcome to delve into the just completed monographic treatise on motional electric orientation in sharks and rays, if you have the courage, but be aware, it was not written with you personally in mind. The author does not know your scientific background nor what you hope to learn from his discourse. You may very well consider it scholarly gibberish and put it aside. Actually, he wrote the article in an endeavor to explain to himself what he has been asserting for half a century about sharks and rays orienting in the oceans' electric and magnetic fields, with the ultimate goal to ascertain whether at his age he really understands the intricacies of his lifetime scientific endeavor. The present version is not intended as a final statement but as a platform for further discussion. Hence, if you find errors or disagree, as you certainly will here and there, or despite great effort cannot follow his concise reasoning, he would greatly appreciate you letting him know, so that together we can discover the truth and lay a firm physical biology foundation for future generations of scientists.

The art of biological science is to ask the animals experimentally the right questions, using the right methods, and properly to interpret their behavioral answers. Certainly, sharks gave the author many invaluable hints. Actually, to grasp their sensory world, he endeavored to view their underwater habitat as if he were a shark himself. As a result, he not only gained insight into the animals' electric and magnetic sense, but also got now and then rather vicious, especially when encountering scientists in his field of research who have not made a serious effort to inform themselves of the rich legacy of our trusted forefathers, Faraday, Maxwell, and Einstein, upon which the present author has founded his hard-wrought contributions to science. With regard to well-versed inquisitive readers, though, he wishes them great success in science, in the hope and expectation that physics will start making sense to shark biologists and for physicists shark biology will become an animated field of research.

Though I wrote the article to the best of my abilities in the crowning years of my career, I sincerely hope that it inspires you, the reader, to further this exciting field of research. However, I shall warn you in advance, the initial highlights, which lay bare the physics bedrock of the motional electric orientation theory, are very

concise. Furthermore, the first section is rather grueling with lots of nitty-gritty physical intricacies, many of which have escaped the attention of my predecessors. The second section, on the exploratory movements sharks must make to detect the electric and magnetic fields, is still exacting but may be more appealing biologically. The last section is not nice at all, for which I feel regretful. I wish I would not have had to include it. However, it is the obligation of a scientist not only to state what he considers right, but also to state what he considers wrong and to do so in clear scientific terms. I have tried my very best, even though I realize that my scientific adversaries, who I mention by name on some of the darker pages, may be displeased, for which I apologize.

Perhaps, my earlier writings on the topic are more palatable to start with. Instead of aggravating you with the present harrowing narrative, I merely aspired to relive my line of thoughts concerning the theory of electric and magnetic orientation in sharks and rays as it evolved from reading Faraday's Lecture on magneto-electric induction (1832), perusing von Arx's Physical Oceanography textbook chapter (1962) on towed electrodes to measure the velocity of ocean currents, and scrupulously equation-by-equation analyzing the classic foundational article of Longuett-Higgins, Stern, and Stommel (1954), while I was still a biology and physics student at the University of Utrecht in The Netherlands, followed by years of reflection and experimentation at the Woods Hole Oceanographic Institution, Massachusetts, and at the Scripps Institution of Oceanography, California, leading by good fortune to my present position as an Emeritus with return to active duty, enjoying the use of my Scripps biophysical laboratory and marine research facility. I feel strongly urged to complete my lifetime scientific endeavor by filling the voids I left behind and correcting my mistakes, for the sake of my own fulfillment and in deference to my teachers, our venerable scientific forefathers and, above all, the awe-inspiring sharks and rays.

The article was written and checked in several stages over a long period of time. The main text is interspersed with mini-essays, personal opinions, and bold statements. Some elaborations are put in appendices and a scholium, so as not to interrupt the flow of the discourse. Vital issues are discussed more than once in different contexts, since electric and magnetic misbeliefs have led to widespread persistent but badly-off instances of alternative interpretations. In short, the manuscript offers a mélange of honed utterings, repeatedly hammering on a variety of fundamental anvils. Deplorable enough, the author now and then lashes out in exasperation, feeling overwhelmed by the piles of road clutter along the challenging path to the truth. Rather than being formal and conventional, he often writes in personal terms to pour out his heart and soul in an attempt to break the deadlock in the exciting field of research he initiated. Why should I hide my personal emotions in presenting my scientific data and thoughts behind the stifling reporting constraints? I am not a robot.

Admittedly, I am a lone scientist, scientifically feeling most at ease with my revered teachers of the past, who I yearly meet—in imagination—for a chat on a fallen tree trunk in my holy woods in The Netherlands. From very early on, I enjoyed Galileo's conversational writings about relativity, Newton's hypotheses *non fingo*,

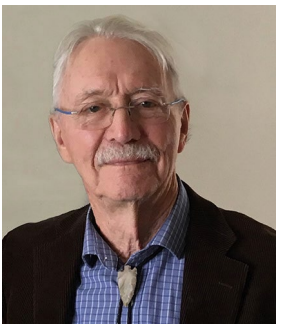
Faraday's magneto-electric transduction of a ship passing on the surface of the water, Maxwell's exacting treatise (1891), Heaviside's genius understanding and blunt criticism, my compatriot Lorentz's namesake force, and Einstein's insights in the nature of physics, especially his 1905 motional electric view. If I unwittingly imitate any people, they are these old-time scientific heroes of mine. Concerning my academic education, I am indebted to Dr. S Dijkgraaf and to Dr. T. H. Bullock, who gave me the opportunity to conduct my Ph.D. research, though—by my fault—I was too physics-minded for further joint efforts with them. I agree with them that I am a difficult person. Nevertheless, we remained trusted friends for all the remaining years. Concerning my tenacious perseverance, I must thank my outspoken adversaries, too many to name.

Unfortunately or not, I have one stubborn drawback in that I am reluctant to write many short articles for the sake of promotion or for securing contracts and grants. Yet, I feel strongly urged to write comprehensive articles when I feel scientifically ready for them, not because of the trite saying "publish or perish." Fortunately, I survived anyhow. Future will tell whether I made the right choice. Beside the present discourse, I have written a companion motion-electric rebuttal manuscript that will be submitted. Furthermore, I have prepared fresh translations of the old Italian and Latin texts on the ampullae of Lorenzini of sharks and rays and on the lateral line of fishes in general. I believe them biologically to be more accurate than earlier translations, having worked on the topics myself for many years. Yet, I will not tell you which further manuscripts I am working on until I am sure that they are ready for publication—deo volente. Life on earth is so long as it is, no longer. Luckily enough, legacies last. Hence, they had better be well-founded.

Since English is not my native language, I do not claim consistently to be correct grammatically and idiomatically. It is not the British English I learned in the Dutch high school either. It is some kind of Californian English without the "real good" instead of "really well." My proud Dutch accent is well known and immediately noticed after I speak three words or even fewer. I have been blamed that my writings are all about me, overly autobiographic. Not true, they all are about what the sharks and rays generously shared with me concerning their keen electric and magnetic sense, behaviorally, electrophysiologically, anatomically, and theoretically. No hearsay, all pure physics and biology conquered by me over the years, based upon the foundations laid by my scientific forefathers. I am merely the fascinated intermediary, seeking to explain what my forefathers discovered not too long ago, yet the venerable sharks and rays have practiced for millions of years.

What do I hope to achieve with the present article? I certainly do not expect all scientists interested in the electric and magnetic sense of sharks and rays to digest my discourse in its ghastly details. It may not be needed either. Yet, I am eagerly looking forward to learning of a few scientifically accomplished readers who publicly dare to concur with the article, if necessary after clarifying some issues and, where needed, correcting some minor or even major mistakes in discussion with me. I hope, these experts will in writing support the hard-wrought conclusions of my research to assure those readers who are not trained to scrutinize the exacting

physical and biological particulars of my treatise. Scientists are mortal, but science will evolve forever, however long that may be.



San Diego, CA Adrianus J. Kalmijn

Acknowledgments

My husband, Adrianus J. Kalmijn, devoted his life to understanding and explaining the electric and magnetic orientation in sharks and rays through a deeply rooted and exacting physics approach. He developed this manuscript over several years and we worked together on proofreading and editing it to the last days of his life in 2021. One of Ad's last wishes was that this work would be published and he entrusted me with shepherding the manuscript through the final steps. With profound respect and admiration for Ad's lifelong devotion and contribution to science, my sons, Jelger and Sander Kalmijn, and I prepared this manuscript for publication. I would like to express our gratitude to Scripps Institution of Oceanography at the University of California San Diego, especially to Dr. Douglas Bartlett who has been influential and a great support in getting this monograph published.

Ad received lifelong support from the Office of Naval Research and funding from the W.M. Keck Foundation and the Office of Naval Research for the Electromagnetic Research Facility.

Vera Kalmijn, verakalmijn@gmail.com

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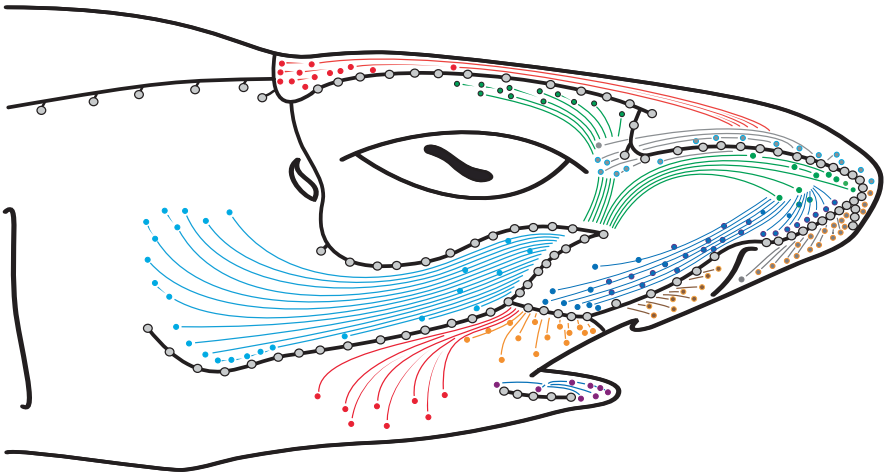
Chapter 1
Introduction



The principal characters Scyliorhinus and Torpedo
Ampullae of Lorenzini and lateral-line canals sensory systems of sharks and rays

In the shark *Scyliorhinus canicula*, the ampullae of Lorenzini are clustered in three paired capsules deep under the skin, the rostral, infra-orbital, and the small mandibular capsule, from where the subcutaneous ampullary canals spread over the head in virtually all directions. The proximal ends of the colored traces indicate the positions of the capsules from which the canals originate. The distal ends of the traces indicate where the ampullary canals open to the outside through the skin pores, the solid dots, densely populating the head of the animal. The small circles are the pores of the subepidermal lateral-line canals, in black. Also indicated in black are the naris, mouth, eye, spiracle, and the first gill slit.

A. J. Kalmijn, *Theory of Electric and Magnetic Orientation in Sharks and Rays Revisited*, https://doi.org/10.1007/978-3-031-58445-9_1

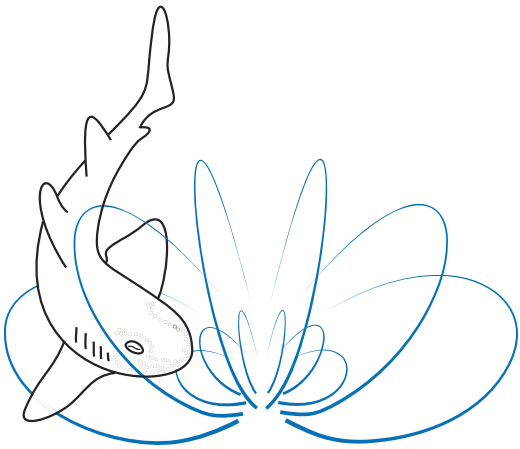
Differential pair of ampullae proper, ampullary canals, skin pores, and afferent nerve fibers

aaaaa, &c. Sono i canali fin quì descritti, che terminano nella pelle.
bb, Luogo dove i canali suddetti con l'altra estremità vanno ad unirsi a i globi di sopra descritti.

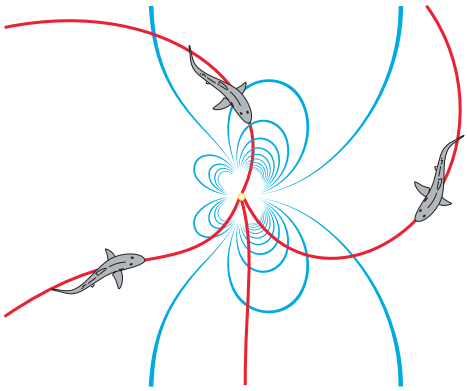
Figure four of Table one, in which: aaaaa, etc. are the *canali* described thus far, which terminate in the skin. bb, the place where the above-mentioned *canali* at the other end join the globes described above.

Stefano Lorenzini (1678). Osservazioni intorno alle Torpedini

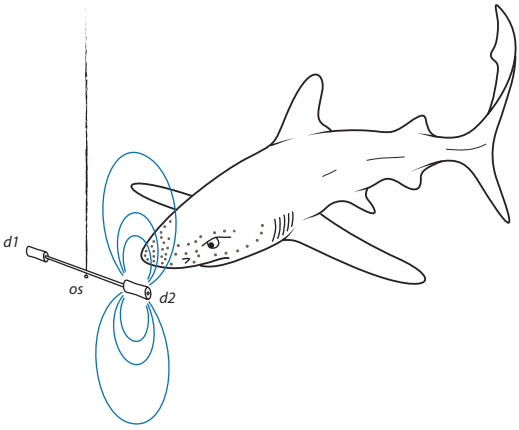
Pictorial of fundamental observations



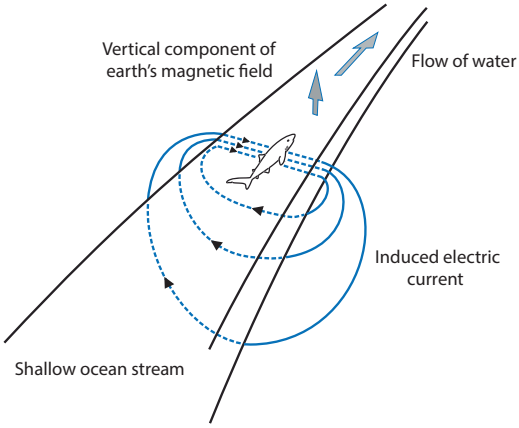
Bottom dwelling dogfish *Scyliorhinus canicula* orienting in bioelectric field of prey



Guided by approach algorithm sharks zero in on quadrupole source simulating prey



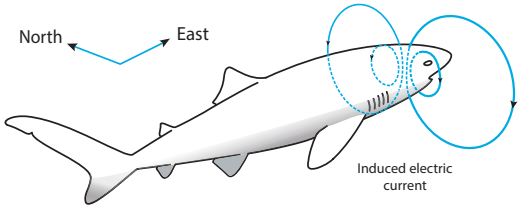
Pelagic blue shark *Prionace glauca,* roused by odor, attacks prey simulating dipole source



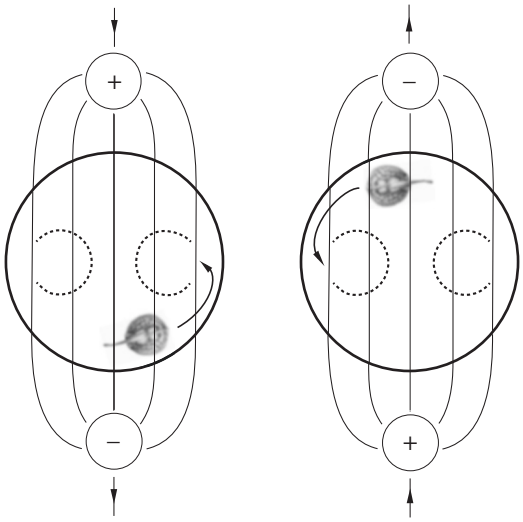
Shark electrically sensing drift in ocean stream

$$\nabla\varphi = \mathbf{v}\times\mathbf{B} - \rho\mathbf{J}$$

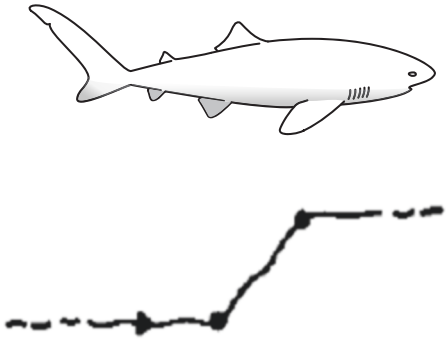
Equation governing motional electric orientation



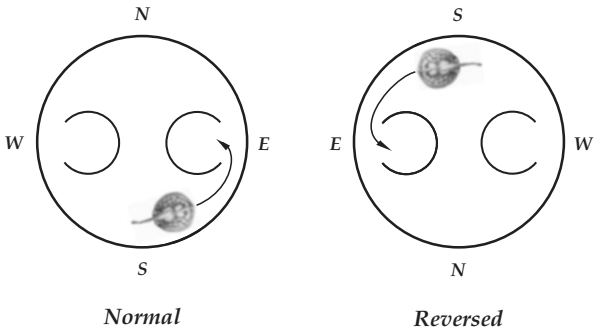
Shark electrically sensing magnetic compass heading



Stingray *Urolophus halleri* seeks food in enclosure to the left of ambient electric field

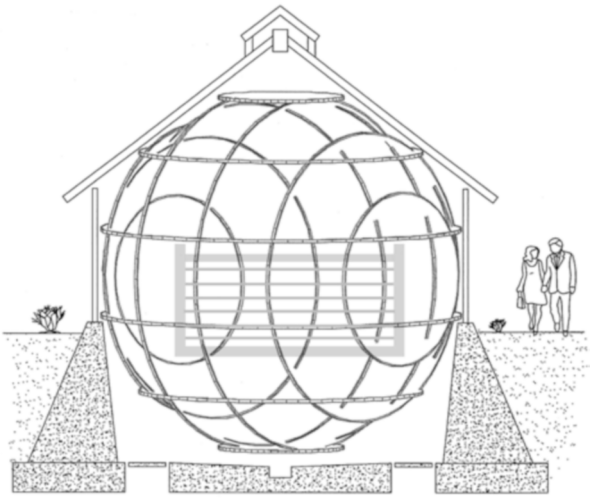


At sea, shark follows 60-degree rotation of ambient electric field



Stingray *Urolophus halleri* seeks food in enclosure in the East of earth's magnetic field

EMRF and RV Boston Whaler



Electromagnetic Research Facility. 3-axis, 18-coil ambient *magnetic* field control system surrounding cylindrical, 12 ft in diameter, 7 ft deep seawater tank with ambient *electric* field control system. Modular building and EM control systems designed by the Principal Investigator, Dr. Ad. J. Kalmijn.

Project's Research Vessel RV Boston Whaler on Bimini Bay for Orientation Experiments

The founding fathers

Michael Faraday James Clerk Maxwell Oliver Heaviside Hendrik A Lorentz Albert Einstein