The physical nature of life

Ad. J. Kalmijn*, Ivan Fernando Gonzalez, Michael C. McClune

The Faraday Laboratory, Physical Oceanography Research Division, Scripps Institution of Oceanography, La Jolla, University of California, San Diego, CA 92093-0220, USA

Abstract

Life evolved from the primeval world of physics. Sensory systems inform animals of the natural environment, enabling them to conduct responsively. The discovery of weak, DC bioelectric fields in the vicinity of aquatic organisms and the role they play in guiding sharks and rays to their prey has led to the recognition of fundamental, hitherto less well known, physical aspects of sensory biology. The inferred cybernetical algorithm of electric-field orientation in sharks and rays is highly effective and extremely robust. In orienting to the weak DC electric fields of ocean currents and to the earth’s magnetic field, sharks and rays unwittingly practice the motional-electric principles that Einstein had in mind when he introduced the special theory of relativity. At the sense-organ, receptor-membrane, and ion-channel levels, the elasmobranch ampullae of Lorenzini operate on the basis of graded positive feedback driven by negative conductance, supposedly employing voltage-sensitive ion channels as the active, excitable elements. The electric sense of sharks and rays presents an exquisite implementation of the very biophysical principles that also govern the graded, much richer than all-or-none, integrative brain processes of animal and man.

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1. Introduction

1.1. Natural philosophy

In the beginning, there was no life on earth. Our planet was pure physics, governed by the laws of Nature, in strict conformity to the rules of mathematics. This primeval world, though, had a fascinating feature, that of an inherent tendency to self-organization. Hence, the system of the world was destined locally to give rise to progressively higher levels of structural and functional organization, at the cost of an overall increase in entropy. Over geological time, these centers of self-organization evolved into entities that we call living creatures: unicellular organism, plants, and animals, among which we pride ourselves on having attained the highest level of intellectual sophistication.

Thus, life evolved from a world of pure physics, to become the highest, most wonderful part of it. Although free-living organisms have materially liberated themselves from the inanimate world they originated from, they maintain intimate physical connections with their natural habitat. In higher animals, we find elaborate sensory systems and powerful processing mechanisms providing them with perceptual renderings of the world in which they live. Familiar with the laws of Nature, animal and man have acquired the intellectual ability to project the recent past into the near future and to plan their actions accordingly. The scientific endeavor thus takes part in the process of evolution. Where will it lead?

1.2. Science comes to age

Aristotle (384–322 BC) taught us to observe and contemplate Nature. Galilei [6,7] and Faraday [3–5] pioneered the experimental approach, whereas Newton [17] and Maxwell [18] established the mathematical-physics method. When classical science was just on the verge of reaching its pinnacle, relativity and quantum mechanics emerged, first merely to remove some, seemingly minor inconsistencies, but subsequently requiring a complete overhaul of the foundation of all natural sciences, including sensory biology. In fact, Einstein [1,2] started with amending our imprecise sense of time. The study of the elasmobranchs’ electric sense vividly illustrates this historical development.

The notion of an electric sense in sharks and rays originated from keen observation and a sheer inkling.
Convincing evidence for such a novel sensory modality required, however, physically rigorous behavioral experiments, conducted under biologically valid conditions (Part 1). Research on the orientation of sharks and rays to the weak-electric fields of ocean streams and of their own swimming in the earth’s magnetic field raised the question of how we and the cruising animals view the world in our respective frames of reference (Part 2). Electrophysiological recordings from the ampullary sense organs have revealed a form of graded positive feedback also playing an important role in higher brain processes (Part 3).

2. Part 1. Physical rigor and biological significance

2.1. Animal electricity

In biological organisms, the forces between atoms and molecules are largely electrical, just as in the inanimate world. The violent discharges of the electric ray, *Torpedo*, and of lightning storms are merely large-scale versions of the ubiquitous smaller electric fields in nature. Animals *internally* use electricity to monitor and control their own physiological processes. Aquatic animals also inadvertently produce electric fields in their vicinity, as a result of being ionically different from the water and having electrogenic processes in the gills, mucous membranes, and skin. Surprisingly, only few groups of animals are known to use their inherent electrical sensitivity to detect the *external* fields of other organisms.

True, the stray fields of aquatic animals are usually so weak as to require an interest in physics to study them. The task is particularly difficult, as the prevailing bioelectric fields are of a DC nature but the electrodes needed to measure them are notoriously noisy in the DC to low-frequency range. Hence, to sense the oceanic electric fields, animals had to make large morphological and physiological investments. Sharks and rays who met the challenge, though, are inherently more sensitive than our instruments to DC and low-frequency fields, since the animals operate ionically throughout, whereas we suffer from the adverse effects of the exchange between ionic and electronic charge carriers at the metal–water interfaces.

The finding of bioelectric fields in the vicinity of aquatic animals led Kalmijn [8] to conjecture that sharks and rays use the high electrical sensitivity he had just discovered to zero in on their prey. Since his inferences met with disbelief among his fellow scientists, including his teacher, Dr. S. Dijkgraaf, he conducted the behavioral tests [9] needed to satisfy even the stoutest skeptic—though not himself, since he did not understand how the predators could possibly establish the position of their prey as the source of the field. After proving this indeed to be physically impossible, he concluded that sharks and rays are guided to their prey, not knowing where it is until they arrive at their target.

2.2. Multipole fields

We will need a little mathematical physics to understand how Kalmijn [13] imagines that the animals have solved the problem. We can mathematically expand the bioelectric fields of arbitrary prey in terms of multipole series. This compelled him to search for the physical features (i) that arbitrary multipole fields have in common and (ii) that present the sensory cues required for the predators to arrive at their target. In pursuance of Faraday’s conceptual method, he wanted to plot the multipole fields in order to inspect them visually. To his surprise, he found no texts or programs instructing how to do so fast yet accurately and, therefore, developed a method of his own based on three-dimensional Taylor series.

Field lines may be traced by concatenating small steps in the direction of the field. This method, though, has the disadvantage that it systematically makes plots of curved field lines swing wide, requiring very small steps to obtain a faithful rendering. The problem may be alleviated by taking at the beginning of each step the slope of the field with respect to the $x$, $y$, $z$ axes, the change of the slope, and the change of the change of the slope, and to calculate the $dx$, $dy$, $dz$ of the steps by truncated Taylor series. The direction of the steps thus takes into account the extent to which the field lines deviate from straight. For the sake of speed, the step size may be made inversely proportional to the curvature of the field lines.

From the field plots of Fig. 1A, the task of sharks and rays seemed quite hopeless. In desperation, Kalmijn reasoned that it had to be extremely simple for the animals to execute the attacks so fast and proficiently, despite the weakness, complexity, and variability of the prey fields. The more of the sense organs the animals use and the less information they ask for, the more sensitive they can be, he argued. Hence, it would be best for them solely to determine the direction of the electric field averaged over the entire electroreceptive skin surface, that is, of a single vector representing the field in the head region. But what could the direction of this vector tell the shark about the position of his prey?

2.3. Approach algorithm

At a single moment in time, the direction of the field averaged over the surface of the head gives a shark no clue whatever as to the position of the prey. Yet, by moving through the field, sharks nevertheless receive all the information they need to correct their course of swimming in order to arrive at the target. They merely
have to sense the change in the direction of the field they detect with respect to their body axes and adjust their direction of travel accordingly, that is, turn in such a fashion as to null the apparent changes in the direction of the field, thus executing their task cybernetically. By all criteria, the proposed algorithm meets the requirement that it has to be very simple and highly efficient.

Though compelling, does the proposed approach algorithm really lead the predator to its target? The graphical representations and the mathematical expressions of the prey field made it possible to envision and calculate the paths of approach that sharks would take, as Fig. 1A shows. The algorithm appeared to work perfectly well, but mathematically it was not at all obvious how to prove its validity for arbitrary multipole fields. However, by executing the algorithm on a graphics computer, Kalmijn verified that, except for a few interesting, well-understood singularities, it indeed always guides the animals to the source of the field along paths indistinguishable from those observed in the laboratory and at sea.

The computer implementation of the algorithm is as simple as it realistically should be. It merely corrects the animal’s course of travel so as cybernetically to null any deviation from the norm, that is, from the initial angle between the electric field and the body axes. The predator need not be precise. Even when it takes the curves wide it will, by adhering to the algorithm, reach the target, as the method accommodates any changes in the strength and polarity of the field, and in the position of the source. Moreover, the algorithm does not require any sophisticated brain processing on the part of the animal, as its strength derives from the intrinsic mathematical-physics properties of multipole fields.

2.4. Physical validity

Recently, conclusive evidence that the algorithm guides sharks and rays to the source of an arbitrary multipole field presented itself when Kalmijn (unpublished) woke in the night and restated the instruction “turning so as to keep the angle with respect to the field lines constant” into “turning so as to keep the angle with the equipotential surfaces constant”. The two instructions are equivalent, because all field lines are normal to the equipotential surfaces. As a matter of
fact, each positive pole and negative pole of a multipole source is enclosed by an infinite set of equipotential surfaces of decreasing or increasing potential—so to speak, sets of closed surfaces inside closed surfaces without end, as in Fig. 1B.

The direction of the field is outward for closed equipotential surfaces of positive poles and inward for closed surfaces of negative poles. The validity of these statements rests on Gauss’s law, which says that the integral of the field strength over a closed surface equals the integral of the source strength over the volume enclosed. In terms of equipotentials, the algorithm is self-evident. When a shark or ray crosses a closed equipotential surface from the outside to the inside under an arbitrary angle and maintains the angle upon crossing all subsequent closed equipotential surfaces it successively encounters, it will invariably arrive at the pole of the field source associated with the set of equipotential surfaces.

2.5. Biological relevance

But how do sharks and rays notice the presence of prey? They may smell the prey; see the prey; or hear it by the water perturbations it produces. However, in experiments at sea conducted during night, sharks attracted by an odor plume invariably attacked the source of an electric field simulating prey when the field was sufficiently strong to be sensed at the position of the odor source. When a shark, swimming in an ocean stream at a set angle with respect to the ambient electric field, senses a sudden change in the direction or strength of the field, it may conclude to the presence of prey. It then needs only continue running the algorithm until it comes close enough to determine the position of the source.

Interestingly, the low-frequency water commotions created by quietly swimming prey produce fluid-acceleration fields that are mathematically similar to the prey’s bioelectric fields. That means, fishes of all kinds may use the acceleration-sensitive sense organs of the lateral line and inner ear to approach their prey, guided by the same algorithm as proposed for the electrical sensory modality. In fact, not only the fluid-acceleration field, but also the fluid-velocity field of moving prey may guide a predator to its target [14,15] as illustrated in Figs. 1C and D. In view of this mathematical similarity, the common, inertial function of hearing exhibits a close kinship with the electric sense.

3. Part 2. Learning physics from sensory biology

3.1. Magnetic sense of sharks and rays

Since sharks and rays are capable of orienting with respect to, what we call, the earth’s magnetic field, they have—by definition—a magnetic sense. In nearly all animals believed to have a magnetic sense, the physical principles of the detection mechanisms are unknown. Sharks and rays, however, have the sensory apparatus required to explain their magnetic orientation, namely their keen electric sense. Moreover, behavioral tests designed to verify that sharks and rays are able to interpret the electric fields they receive when swimming in the Earth’s magnetic field in terms of their compass headings are in progress. Here, we will only briefly discuss how Einstein paved the way to solving the shark problem.

3.2. If Einstein had known...
Hence, the vexing question arises: can we, or can we not, explain the electromagnetic orientation of sharks and rays without Einstein’s special relativity? The answer is yes and no. Yes, if you are an engineer, shackled to the Earth frame of reference, who wishes to check the numbers or, perhaps, design an electromagnetic robot. No, if you are a scientist demanding a consistent explanation from the shark’s point of view. Even Faraday’s and Maxwell’s revered equations do not suffice unless interpreted relativistically, though they come deceptively close. Classically, the orientation of sharks and rays is based on ad hoc inferences. The special theory of relativity has made the induced electric fields sharks and rays receive logical consequences of the relative motions taking place.

Although this is not the place to expound our statements, we will take the opportunity to emphasize that Einstein’s special theory is not only relevant to high-speed phenomena. This misconception is due to the historical fact that the low-speed relativistic effects were known already before in the guise of Maxwell’s equations, which did not seem in need of further explanation. Maxwell’s equations, though, were introduced on empirical grounds and, with time, appeared to be intrinsically inconsistent until Einstein gave them new meaning when he postulated the speed of electromagnetic waves to be the same in all inertial frames. Thus he arrived at the correct electrodynamics of moving bodies, sharks and rays included.

4. Part 3. Ampullae of Lorenzini shed light on brain processes

4.1. Negative conductance

The ampullae of Lorenzini, the electoreceptors of sharks and rays, have given us a hint as to their operation in that they produce a negative receptor current, −ΔI, in response to a DC-to-8-Hz positive voltage stimulus, +ΔV. When a submerged thornback ray is subjected to a uniform electric field rendering the skin pore of an ampulla positive, the sense organ responds with an electric current exiting the pore. The same pore-positive stimulus causes a decrease in the action-potential rate in the afferent nerve fibers. Since the receptor current is proportional to the small-signal input voltage, each ampulla acts as negative conductance or, equivalently, as a linear, two-port, voltage-to-current converter of negative sign.

The equivalent circuit for each individual ampullary organ consists of (i) the resistance of the gelatinous ampullary canal core, (ii) the serially arranged conductances of the apical and basal membranes of the receptor cells in the sensory epithelia separating the ampullary lumen from the capsular stroma, (iii) the shunt resistance of the supporting cells in parallel with the receptor cells, as illustrated in Fig. 2. The stimulus received by a differentially arranged pair of ampullary

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**Fig. 2.** Ampulla of Lorenzini, morphology and equivalent circuit. Sensory epithelia and input circuit of differentially arranged pair of ampullary organs. In response to input voltages $V_A^{in}$ and $V_B^{in}$, voltage-sensitive ion channels of apical receptor-cell membranes generate negative receptor currents, opposite in direction to electric field applied. Receptor currents ($i_a$), driven by apical receptor-cell membranes, flow through ampullary canals, skin pores, and seawater medium ($i_c$), supporting cells ($i_s$), and, most importantly, through basal receptor-cell membranes ($i_b$). The resulting graded potential differences across basal receptor-cell membranes are again sensed, together with original input signal, by electrically excitable ion channels of apical cell membranes, thus leading to stable positive feedback, causing large amplification of original signal. Receptor potentials $V_{out}^A$ and $V_{out}^B$ thus developing across basal receptor-cell membranes synaptically control activity of afferent nerve fibers conveying electric information to central nervous system. Equivalent circuit superimposed in half-tone. Negative circuit elements (−) denote active electrical devices, simulating electrically excitable ion channels causing negative receptor currents. Positive elements (+) denote passive conductance elements (after Kalmijn [15]).
sense organs is the voltage gradient in the seawater medium integrated along an arbitrary path connecting the two skin pores. The source resistance of the stimulus is the effective volume resistance of the seawater between the two skin pores.

The negative-conductance formalism applied to the excitable membrane of the receptor cell is perfectly justifiable in terms of voltage-sensitive ion channels. Yet, it is important to understand that the negative conductance we speak of is the ratio between the signal current and signal voltage (slope conductance) measured with respect to the operating point on the $I-V$ curve. Since the ampullary signal is extremely small, in the nano- to microvolt range, the negative conductance is considered constant. This permits one to treat the equivalent circuit by the mathematical rules of linear network analysis. Be aware, though, that we are dealing with an active network, since the negative conductance implies a source of energy.

### 4.2. Positive feedback

The ampullary circuit displays the intriguing feature of graded positive feedback in that the effect of a voltage stimulus across the electroreceptive membranes is such as to increase the voltage across the very same electroreceptive membranes. Though Kalmijn had a hard time convincing his peers that positive feedback need not result in instability, or spiking in neurophysiological jargon, if tamed properly, positive feedback can give rise to any degree of graded amplification, as Fig. 3 exhibits. The stability criterion requires the feedback factor $\beta A$, the fraction of the output signal fed back $\times$ the amplification, to fall between 0 and $-1$. The closer the feedback factor is to $-1$, the larger is the gain $G = A/(1 + \beta A)$.

Depending on whether (i) the apical or basal membrane of the receptor cell offers the negative conductance and (ii) the conductance of the apical or basal membrane is the larger of the two, the equivalent circuit permits four active modes of operation. Since in the rays the input current measured negative and the nerve-impulse rate decreased in response to a pore-positive stimulus, the configuration calls for a negative apical-membrane conductance smaller in absolute value than the positive basal-membrane conductance, thus yielding an inverted signal across the basal membrane larger than the input voltage applied between the skin pore and the ampullary capsule, as in Fig. 4A. The receptor potential across the basal membrane drives the synapse and thus controls the nerve-impulse rate.

### 4.3. In comparison

Teleost ampullary sense organs respond to pore-positive stimuli with an increase in the afferent impulse rate. Hence, if the receptor current appears to be negative, it is the basal membrane that has the negative conductance, as in Fig. 4B, but if the receptor current appears to be positive, it is the apical membrane that has the negative conductance, as in Fig. 4C. In either case, the absolute value of the basal-membrane conductance is smaller than the absolute value of the apical-membrane conductance. Thus, to ascertain whether the apical or the basal membrane has the negative conductance, the sign of the receptor current must be determined. So far, conclusive evidence is available only for elasmobranch fishes. Yet, in order to be stable, a positive receptor current would require the shunt conductance to be negative, hence, excitable as well, for which there is no evidence.

### 4.4. Electric sense and brain function

Can we answer the trite question as to whether the high electrical sensitivity of sharks and rays is extraordinary? It certainly is in so far that we do not know of any other living organisms nearly as sensitive to DC and low-frequency electric fields as sharks and rays. However, from our electrophysiological studies, it is also evident that familiar biophysical principles are capable of explaining the high electrical sensitivity. Actually, now we have recognized the ionic circuitry in the ampullae of Lorenzini, we find the same biophysical principles ubiquitously expressed in sense organs and in the nervous system at large. Where there is graded pro-

![Fig. 3. Graded positive feedback, circuit diagram and formula. System gain $G$ as a function of the feedback factor $\beta A$, with $A$ the amplification and $\beta$ the fraction of the output signal $V_o$ that is subtracted from the input signal $V_i$. When $\beta A = 0$, no feedback takes place, and $G = A$. When $\beta A > 0$, system exhibits stable, nonregenerative, negative feedback, and $G < A$. When $-1 < \beta A < 0$, system exhibits stable, regenerative, positive feedback, and $A + G = \infty$. As $\beta A$ approaches $-1$, the gain increases progressively more steeply. When $\beta A \leq -1$, system exhibits unstable, all-or-none, regenerative, positive feedback. Elasmobranch electroreceptors and excitable nerve cells in general operate in a graded fashion when $-1 < \beta A < 0$. But nerve cells generate impulsive, all-or-none action potentials when $\beta A \leq -1$. $V_i$ corresponds in Fig. 2 to the potential $V_{in}$ at the skin pores of the Lorenzian ampullae, and $V_o$ to the intracellular potentials $V_{out}$ of the receptor cells, both with reference to the capsular stroma (from Kalmijn [15]).](image-url)
cessing, the principles of electroreception are likely to apply.

Thus, we have learned from our in vivo, in situ electrophysiological recordings in the ampullae of Lorenzini that it is perfectly feasible for the animals to use the negative signal current exits the pore establishes the apical membrane as the excitable one in conformity with the generally accepted notion. B: Apical conductance: positive; basal conductance: negative; apical and basal in series: negative. Increase in nerve-impulse rate and negative outward current in response to pore-positive stimuli. C: Apical: negative, basal: positive, apical and basal in series: positive. Increase in nerve-impulse rate and positive inward current in response to pore-positive stimuli. D: Apical: positive; basal: negative, apical and basal in series: positive. Decrease in nerve-impulse rate and positive inward current for pore-positive stimuli. In the ampullary sense organs of teleost fishes, the increase in nerve-impulse rate in response to pore-positive stimuli suggest either B or C. To determine whether, in teleost fishes, the membrane responsible for excitation is the basal (case B) or apical (case C), the canal signal currents must be measured in vivo and in situ. However, for the canal current to be positive (case C and D) and the circuit to be stable, the epithelial shunt conductance must be negative, for which there is no evidence.

Fig. 4. Signal distribution in ampullary sense organs. Signal-voltage distributions for four permutations of apical and basal receptor membrane conductances, one of which is positive and one negative: A: Ampullae of Lorenzini, apical conductance: negative; basal conductance: positive; apical and basal in series: negative. The in vivo, in situ observation that, in response to pore-positive stimuli, the nerve impulse rate decreases and the negative signal current exits the pore establishes the apical membrane as the excitable one in conformity with the generally accepted notion. B: Apical conductance: positive; basal conductance: negative; apical and basal in series: negative. Increase in nerve-impulse rate and negative outward current in response to pore-positive stimuli. C: Apical: negative, basal: positive, apical and basal in series: positive. Increase in nerve-impulse rate and positive inward current in response to pore-positive stimuli. D: Apical: positive; basal: negative, apical and basal in series: positive. Decrease in nerve-impulse rate and positive inward current for pore-positive stimuli. In the ampullary sense organs of teleost fishes, the increase in nerve-impulse rate in response to pore-positive stimuli suggest either B or C. To determine whether, in teleost fishes, the membrane responsible for excitation is the basal (case B) or apical (case C), the canal signal currents must be measured in vivo and in situ. However, for the canal current to be positive (case C and D) and the circuit to be stable, the epithelial shunt conductance must be negative, for which there is no evidence.

questions goes far beyond their urgency for the explanation of the elasmobranchs’ high electrical sensitivity. The ampullae of Lorenzini offer study objects par excellence, for they have pushed the stability and noise issues to the limits, yet are experimentally readily accessible. The nervous system, though, has the advantage that it can make the signals on which it operates comfortably strong.

5. In Conclusion

We concur with Michael Faraday [4]:

Wonderful as are the laws and phenomena of electricity when made evident to us in inorganic or dead matter, their interest can bear scarcely any comparison with that which attaches to the same force when connected with the nervous system and with life (cf. Series XV, § 23, Par. 1749).

To fulfill Ernst Mach’s prophecies [16], we have endeavored in the present article to prove him correct where he says:

The foundations of sciences as a whole, and of physics in particular, await their next greatest elucidations from the side of biology, and especially from the analysis of the sensations (see “Original Preface”).

Indeed, the life of physics and the physics of life are inseparable parts of Nature, parts of one mighty whole.

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