

Detection and processing of electromagnetic and near-field acoustic signals in elasmobranch fishes

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The acoustic near field of quietly moving underwater objects and the bio-electric field of aquatic animals exhibit great similarity, as both are predominantly governed by Laplace's equation. The acoustic and electrical sensory modalities thus may, in directing fishes to their prey, employ analogous processing algorithms, suggesting a common evolutionary design, founded on the salient physical features shared by the respective stimulus fields.

Sharks and rays are capable of orientating to the earth's magnetic field and, hence, have a magnetic sense. The electromagnetic theory of orientation offers strong arguments for the animals using the electric fields induced by ocean currents and by their own motions in the earth's magnetic field. In the animal's frame of reference, in which the sense organs are at rest, the classical concept of motional electricity must be interpreted in relativistic terms.

In the ampullae of Lorenzini, weak electric fields cause the ciliated apical receptor-cell membranes to produce graded, negative receptor currents opposite in direction to the fields applied. The observed currents form part of a positive-feedback mechanism, supporting the generation of receptor potentials much larger than the input signal. Acting across the basal cell membranes, the receptor potentials control the process of synaptic transmission.

Keywords: ampullae of Lorenzini; inner ear; approach algorithm; motional-electric fields; magnetic compass headings; positive feedback

1. INTRODUCTION

Sensory systems inform biological organisms of the physical world in which they live. Thus, the question arises: What are the physical features in the natural habitat that animals have adapted to in the course of evolution? Behavioural observations reveal the sensory modalities implemented and, combined with studies on the structure and function of the sense organs, indicate the animals' detection capabilities.

An early form of vertebrate hearing is the detection of moving underwater objects, where the water perturbations created are (i) governed by the acoustic wave equation, and (ii) received by the fishes' inertial sense organs of the inner ear (Kalmijn 1989). Recently, the problem of directional hearing in the acoustic near field has found a new solution by analogy with the electrically guided approach of sharks and rays, as the characteristic features of the bio-acoustic and bio-electric fields of prey are very similar.

Since its first publication, the electromagnetic theory of orientation (Kalmijn 1974) has received vital theoretical and behavioural support. Important issues under investigation are (i) a relativistic description of the fields that sharks and rays receive in their own frame of reference, and (ii) proof that, in detecting their magnetic compass headings, the animals use the electric sense. The

two issues are related in that the theory of relativity has suggested a natural behavioural method of testing the motional-electric principle.

The biological validity of electrophysiological studies on excised ampullae of Lorenzini is uncertain: therefore, refined, less invasive techniques using whole animals were applied (Kalmijn 1988*b*). Inspired by the graded response of the sensory epithelium, a transduction model featuring high gain due to positive feedback, based on the biophysical properties of electrically excitable ion channels, has been developed and tested experimentally.

2. ELECTRORECEPTION AND DIRECTIONAL HEARING

Although electrical excitability is an inherent property of animal life and electric fields abound in natural waters, few aquatic species have acquired the ability to access the wealth of electrical information. The electric sense of sharks and rays was first established when the weak bio-electric fields measured in the vicinity of aquatic animals were noticed to elicit well-orientated feeding responses (Kalmijn 1966, 1971). This observation raised the difficult question as to how the animals locate the source of a prey's electric field. The same issue arises in directional hearing, where a predator orientates in the non-radial acoustic near field of a moving object, relying on the inertial sense organs of the inner ear (Kalmijn 1989).

(a) Source localization in the electric and acoustic near field

New insight into the detection of underwater objects has been gained by analysing the relevant physical features, first of the bio-electric field of animals, then of the acoustic near field of moving objects in general. Although highly variable, the electric and acoustic fields are bound by the laws of physics, which give them a certain degree of regularity—certain steady salient features, which one expects predatory fishes to rely on in locating prey. The preferred mathematical method of exposing the appropriate physical features is multipole expansion, in which the fields of arbitrary prey are expressed in series of multipole terms. At sufficient distance from the source, either the first term, the monopole, or the second, the dipole, tends to prevail. Hence, the initial studies have focused on the monopolar versus dipolar nature of the fields and the significance of the lower terms in predation.

Outside the source region, the common bio-electric fields of animals are essentially free of divergence and vorticity and thus ruled by Laplace's equation, which renders the multipole expansion extremely simple. Also, for the field to be steady, the electric current leaving the source must re-enter it again, precluding the existence of a monopole term. Therefore, in its original form, the theory of object detection was based on what I referred to as the dipole approach algorithm (Kalmijn 1989). In brief, when a shark senses an unexpected change in the direction or strength of the ambient electric field, it assumes a local source and corrects its course of swimming in such a fashion as to null any apparent rotation of the prey field with respect to the body axes. As a result, a shark will be guided to its target in nearly all cases, without having to determine the precise position of the prey from a distance (figure 1).

In regard to directional hearing, a few years ago it became evident that the acoustic near field of moving objects is not usually predominantly monopolar, as had been tacitly assumed in most older theories, but—to a first approximation—dipolar, like an animal's bio-electric field (Kalmijn 1988*b*). This is certainly true for the low-frequency accelerations that the lateral line and inner ear of sharks detect. Since, in the vicinity of the source, the acoustic near field largely behaves as if the medium were incompressible, that is, free of divergence, it also is governed by Laplace's equation in regions free of vorticity, outside the boundary layer and the wake. Hence, by the same token, the approach algorithm may be applicable to directional hearing, where the inner ear gives a predator the direction of the acceleration it must keep constant with respect to its body axes to reach its prey.

The acceleration-based algorithm has led to due appreciation of the most primitive, yet commonly practised form of hearing, called thus because (i) the prey's acceleration field is detected by the sense organs of the inner ear, and (ii) Laplace's equation is the form that the acoustic wave equation reduces to near the source. The acceleration considered so far is the local derivative of the fluid velocity with respect to time, 'local' meaning at a certain place with respect to the source. In addition, in transecting a prey's field, the predator is, over time, exposed to a sequence of spatially varying fluid velocities

subjecting the inner ear to yet another form of acceleration, the vectorial derivative of the velocity, 'vective' meaning due to the predator's motion with respect to the source. Applied to either the local or vective acceleration, the algorithm guides the predator to its target (Kalmijn 1997; figure 1).

(b) Strength of approach algorithm and conclusions

The approach algorithm proposed for the electric and acoustic senses of aquatic animals seems, thus far, biologically and mathematically quite feasible. The computer implementation of the algorithm is not limited to dipole fields, but deals equally well with monopole and quadrupole moments, added to give the prey simulation greater detail (figure 1). The algorithm is also extremely robust, as it readily accommodates temporal and spatial changes in the stimulus field. Thus, when a prey moves away during the attack, the algorithm changes a predator's approach path accordingly. It is of interest that, before fishes gained access to the acoustic far field using pressure-to-motion converters, hearing was so similar to the elasmobranch's electric sense. Actually, in most if not all modern fishes, inertial hearing may still be as important as it was in ancient times.

3. THEORY OF ELECTROMAGNETIC ORIENTATION

What led me to the theory of electromagnetic orientation, was Faraday's (1832) remark 'where water is flowing... or a ship is passing... electric currents should occur'. Maxwell (1873) extended Faraday's seminal ideas, but the true nature of motional electricity was not elucidated until Einstein (1905) critically analysed 'the electrodynamics of moving bodies'. Although it is perfectly legitimate to examine a shark's motional-electric field in the ocean frame of reference, it is the animal who has to do the orientating. In its frame, neither the animal, nor its sense organs are moving in a magnetic field. Hence, the real challenge is to perceive the situation from the shark's point of view, a revealing but not a trivial task.

(a) Orientation to the ocean's electric and magnetic fields

The electric field of ocean streams indicates to sharks and rays their drift relative to the bottom sediments or deeper water layers. The strength of the field depends, aside from the velocity, on the resistances of the stream and the return path. Moreover, the information available to the animals in the stream is different from that in adjacent waters. Thus, where the electric current of an ocean stream invades a quiet bay, it may provide the local shark and ray population with directional cues in familiar territory. The animals may also explore the situation by periodically diving to deeper water or to the bottom, as many do (Kalmijn 1988*b*). Their ability to orientate in uniform DC electric fields has been proven behaviourally in our marine facility and in a shallow bay near the Gulf Stream (Kalmijn 1982).

Whereas in orientating to ocean currents sharks and rays detect the fields induced by the flow of water, in establishing their magnetic compass headings they rely—from an outside observer's point of view—on the fields they themselves induce by moving with respect to the

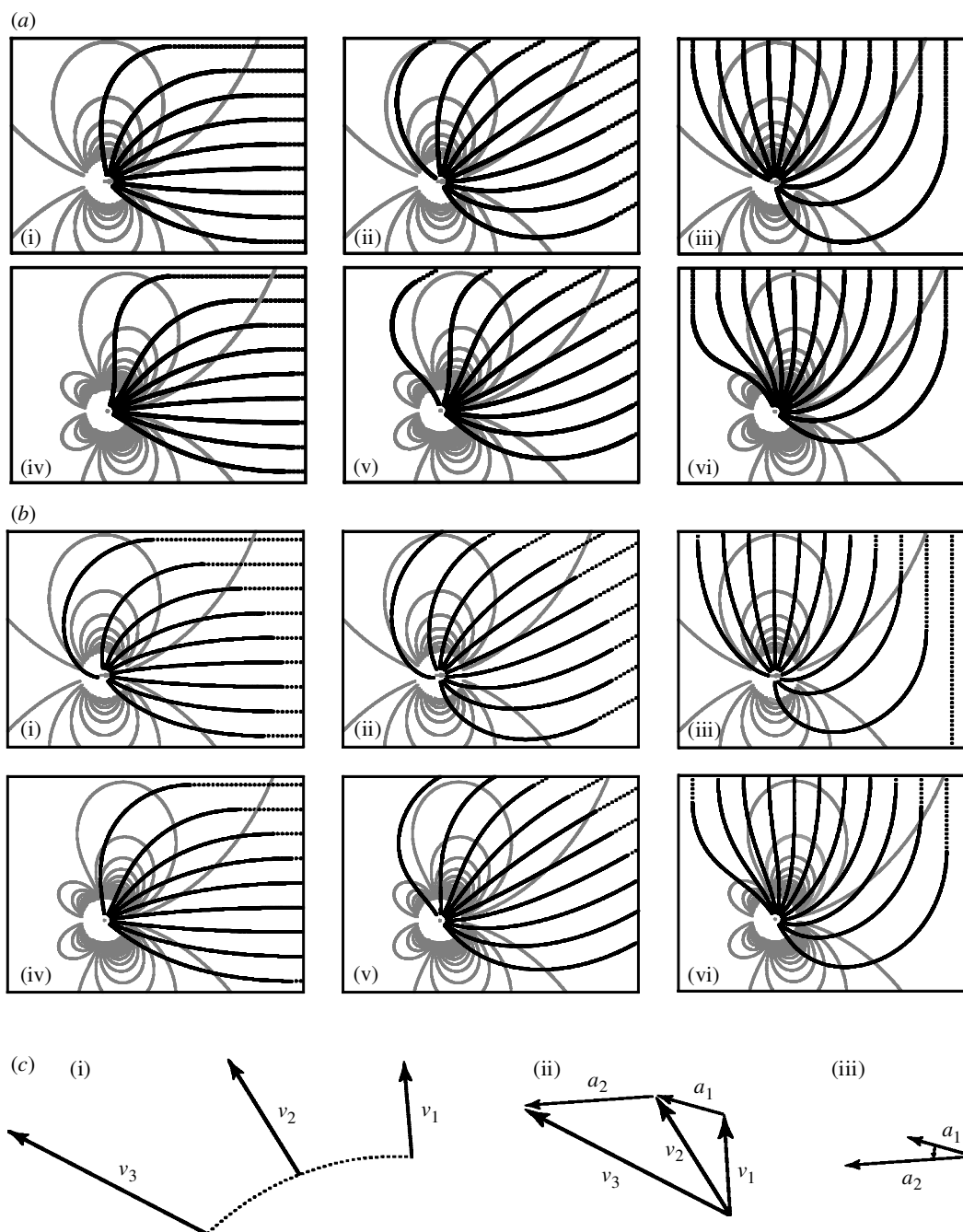


Figure 1. Electric and near-field acoustic implementation of approach algorithm. (a) Guided approach in the electric or acceleration field. The grey dipole (i–iii) and multipole (iv–vi) field lines represent the bio-electric fields of stationary prey, in the electrical case; or the acceleration fields of moving prey, in the acoustic case. The predator enters the fields from three different directions along the paths indicated by the dotted lines, viewed in the frame of the prey. When the electrical stimuli received by the electroreceptors, or the local acceleration stimuli received by the inertial sense organs of the inner ear are sufficiently strong, the predator begins its guided approach. The solid lines indicate the approach paths along which the predator maintains a constant angle between the electric field or the local accelerations it receives and its body axes, respectively. After Kalmijn (1997). (b) Guided approach in the velocity field. The grey dipole (i–iii) and multipole (iv–vi) field lines represent the velocity fields of quietly moving prey. The predator enters the fields from three different directions along the paths indicated by the dotted lines, viewed in the frame of the prey. When the vective acceleration stimuli received by the inertial sense organs of the inner ear are sufficiently strong, the predator begins its guided approach. The solid black lines indicate the approach paths along which the predator maintains a constant angle between the vective accelerations it receives and its body axes. After Kalmijn (1997). (c) Diagram illustrating the vective derivative of the prey's velocity field. The fluid velocities and vective accelerations to which the predator is subjected are depicted for three consecutive positions along the approach path. (i) Three velocity vectors (' \mathbf{v} ') sampled one unit of time apart. (ii) Velocity vectors (\mathbf{v}) and associated time-rate of change vectors (' \mathbf{a} '), i.e. the vective accelerations experienced by the predator. (iii) Angular velocity, i.e. change in direction of vective acceleration (\mathbf{a}) per unit of time, indicated by curved arrow.

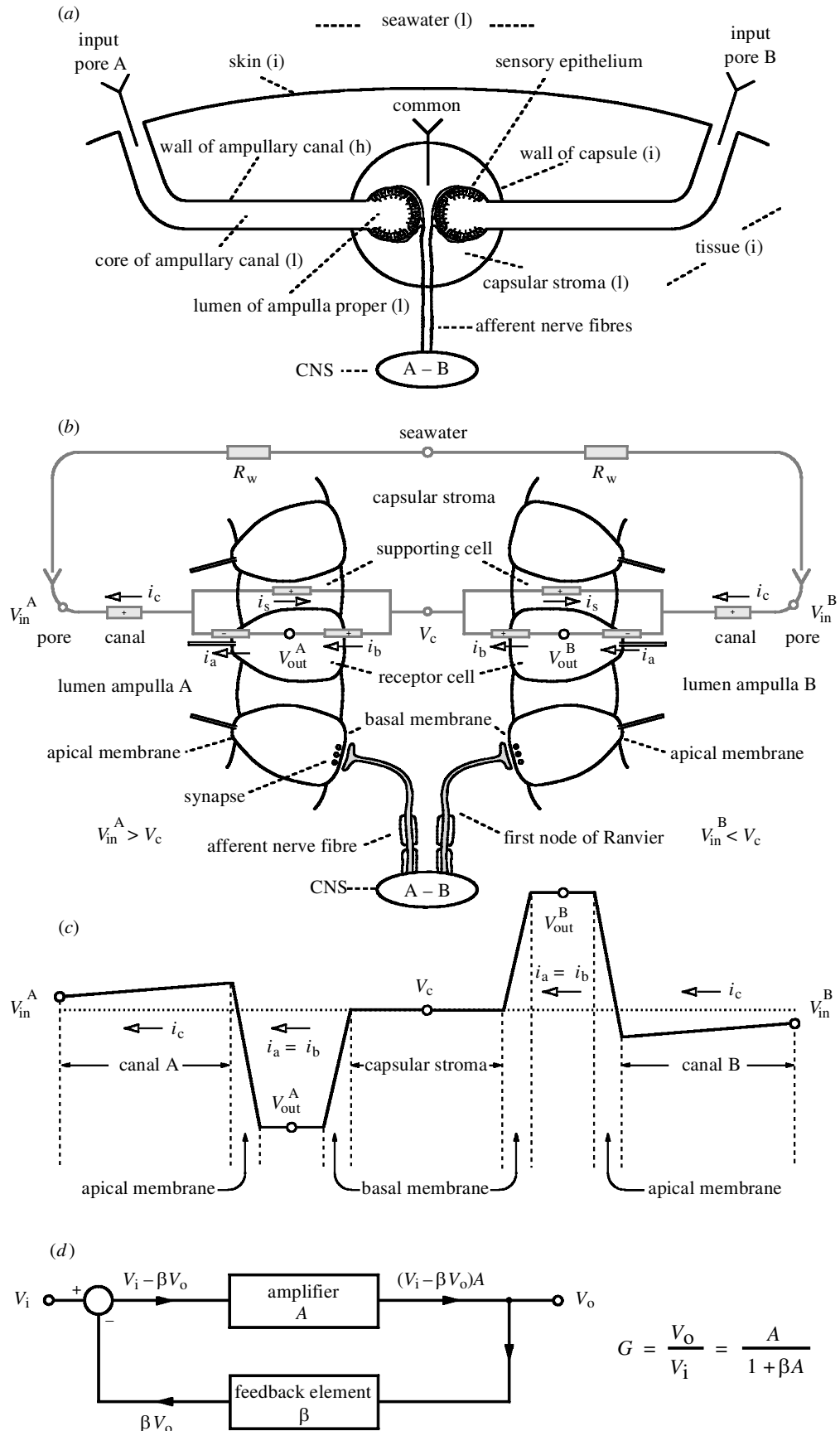


Figure 2. Structure and functioning of elasmobranch ampullae of Lorenzini. (a) Pair of oppositely orientated ampullae, representing about 200 sense organs of hyoid capsule in the stingray *Urolophus halleri*, in a uniform electric field of $0.5 \mu V m^{-1}$. Canal length 0.05 m. The canal wall and sensory epithelia offer high resistance, the core of the canal low resistance, concentrating the signal on the sensory epithelia of ampullae proper. Ciliated receptor cells connect synaptically to four to six afferent nerve fibres, passing the signal to the central nervous system (CNS). (l) Means low, (i) intermediate, and (h) high (Cont.)

water in the presence of the earth's magnetic field. In detecting their drift with the flow of water, the electric sense operates in a passive mode, whereas in detecting the earth's magnetic field, it operates in an active mode, where active means that the fields the animals detect stem from their own motor activity. The difference between active and passive renders it feasible for the animals to sense, simultaneously, their drift with ocean streams and their magnetic compass headings.

To find out how the motion of sharks and rays allows them to distinguish between the two kinds of fields, we must first formulate realistic hypotheses, founded on existing knowledge and, above all, open to behavioural tests. I have thought of, but discarded several ideas for lack of simplicity. As in predation, I expect the animals to rely on the most salient field features in a cybernetic fashion, by nulling any deviations from a set course. Since the sense organs are not DC, but very low-frequency AC receptors, operating from less than 0.125 Hz to 8 Hz, a shark may, in alternation, explore the direction of the ambient electric field by transiently turning without changing speed and probe its magnetic headings by transiently accelerating without turning. The electric sense is exquisitely suited for this task. Moreover, the animal may monitor its movements with the linear and angular inertial detectors of the inner ear.

The classical theory does not suffice to explain the situation correctly (cf. d'Abro 1952). To arrive at a consistent theory, we must pursue a fresh approach starting from the new concepts of space and time. What we tried to 'explain' by Faraday's empirical law then becomes a logical consequence of the relative motion between a shark and the charges that constitute the electric currents causing, as we call it, the earth's magnetic field (Kalmijn 1988a). Actually, the electromagnetic principle is based on the fact that, to an observer moving with respect to the charges creating an electrostatic field, the circulation does not vanish even at low velocity, due to the relativity of simultaneity in the respective frames of reference. Thus, a long time ago, sharks evolved a system that

scientists had difficulty understanding until Einstein resolved the issue relatively recently.

(b) *The physical nature of the elasmobranch's magnetic sense*

Before any further consideration as to how sharks and rays process the electromagnetic information, one crucial issue remains to be addressed: Do sharks and rays really use their electric sense in orientating to the earth's magnetic field? However compelling the physical and biological evidence may be, the truth can only be learned from the animals in suitably designed behavioural experiments. A hint as to how to conduct the tests was given by Einstein in his 1905 article, where he states in non-biological terms that the electromotive force of a shark moving in the observer's frame of reference is but an electric field in the frame of the shark, that is, the proper frame in which the sense organs are at rest. Hence, in behavioural experiments now in progress, we apply vertically directed, electric fields to simulate the sensory cues that the animals receive in an equatorial magnetic field.

4. PRINCIPLES OF WEAK ELECTRIC FIELD DETECTION

Although it is well documented that sharks and rays orientate to uniform DC electric fields of $0.5 \mu\text{V m}^{-1}$ and detect DC dipole fields at $0.01\text{--}0.02 \mu\text{V m}^{-1}$ (Kalmijn 1982), this astounding sensitivity is biophysically hard to conceive. Yet, the behavioural figures leave no doubt that the ampullae of Lorenzini respond to signals of 25 nV (figure 2a). Even a single nerve fibre may respond significantly to electric fields merely eight times stronger than needed for the animal to orientate behaviourally. My observation of graded, negative receptor currents in the sensory canals of intact, live rays, reported here, has lately led to the intriguing idea of electrically excitable ion channels amplifying the input signal in a stable positive-feedback loop.

Figure 2. (Cont.) resistance. Drawing not to scale. (b) Sensory epithelia and input circuit of differentially arranged pair of ampullary organs. In response to input voltages V_{in}^A and V_{in}^B , electrically excitable ion channels of apical receptor-cell membranes generate a negative receptor current, that is, opposite in direction to the electric field applied. The receptor current (i_a), driven by apical receptor-cell membranes, flows through the ampullary canal, skin pore 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 the original input signal, by electrically excitable ion channels of apical cell membranes, thus leading to stable positive feedback, causing large amplification of the original signal. Receptor potentials V_{out}^A and V_{out}^B thus developing across basal receptor-cell membranes control synaptic transmission, modulating activity of nerve fibres conveying the electric signal to the CNS. Equivalent circuit superimposed in half-tone. Negative circuit elements (−) represent active electrical devices, simulating electrically excitable ion channels causing negative receptor currents. Positive elements (+) are regular resistances. (c) Signal distribution in response to voltages V_{in}^A and V_{in}^B at skin pores, with respect to the potential of ampullary capsule V_c . Negative receptor currents, produced by excitable ion channels of apical receptor-cell membranes, cause signals along the length of the ampullary canals to increase, rather than decrease, signals across apical receptor-cell membranes to change in polarity, and receptor potentials V_{out}^A and V_{out}^B , offering amplified replicas of the input signal, to develop across basal cell membranes. The input voltage on the right is opposite in polarity to the input voltage on the left, leading to inverted mirror images of signal distributions. (d) System gain G as a function of feedback factor βA , with A denoting amplification and β the fraction of output signal V_o that is subtracted from input signal V_i . When $\beta A > 0$, the system exhibits stable, non-regenerative, negative feedback, and $G < A$. When $\beta = 0$, $G = A$. When $-1 < \beta A < 0$, the system exhibits stable, regenerative, positive feedback, and $A < G < \infty$. As βA approaches -1 , the gain increases progressively steeply. When $\beta A = -1$, G is undefined and the system exhibits unstable, regenerative, positive feedback, and output increases in rampant fashion. Elasmobranch electroreceptors and nerve cells in general operate in a graded fashion when $-1 < \beta A < 0$; nerve cells generate impulsive action potentials when βA reaches -1 . V_i corresponds to the potential V_{in} at the skin pores of the Lorenzian ampullae, V_o to the intracellular potentials V_{out} of the receptor cells, all with respect to the capsular stroma.

(a) Sensitivity, noise and graded amplification of electric signals

Since in fields of $0.5 \mu\text{V m}^{-1}$ the potential differences across the sensory epithelia are only a few tens of nanovolts, the electric signals in the receptor cells—of which there are about 10 000 per ampulla—must be almost entirely buried in the noise. Nevertheless, they are detected, amplified, synaptically transmitted to the four to six nerve fibres per ampulla and, by them, relayed to the central nervous system (CNS). Together with the signals from the other, *ca.* 1000 ampullae, they are analysed for their salient field features, to give rise to the proper behavioural responses. Therefore, the question is not whether the individual receptor cells are sensitive enough to detect the extremely weak electric fields to which the animals respond behaviourally, but how the animal can distinguish the signal from the noise and how it can profitably maintain such a high electrical sensitivity under real-life conditions.

To suppress noise, the signal is averaged over as many parallel channels and successive stretches of time as possible without compromising spatial and temporal resolution. Thus, in the initial stage of striking at its prey, a shark may employ all its electroreceptors solely to determine the local average direction of the weak bio-electric field. To ascertain that the spatially averaged direction of a field, interpreted to emanate from a prey, actually changes non-randomly with respect to its body axes, the shark may integrate the change in direction over time until the information accumulated is sufficiently credible to initiate the attack. This integration over space and over time gives the approach algorithm its great strength, merely requiring the animal to attend to the most salient feature, the directionality of the field, to which it knows how to respond based on innate or acquired experience.

In the Lorenzian ampullae and the kindred sense organs of the lateral line and inner ear, the receptor cells respond to the respective physically adequate stimuli by generating graded receptor potentials across the basal receptor-cell membranes. In both systems, the receptor potentials present faithful, analogue reproductions of the physical stimuli received. In the hair cells, the transduction process is initiated by a mechanical displacement of the hair bundle; in the electroreceptor cells it starts from voltage differences imposed across the apical cell membrane. Since it seems reasonable that the synaptic processes in the two sensory systems are about equally sensitive to the receptor potentials across the basal cell membranes, the electroreceptor cells must indeed greatly amplify the electrical stimulus and accomplish their task without adding significant noise (figure 2*b,c*).

The currents producing the receptor potentials in the ampullary sense organs not only follow the electrical stimuli in a graded fashion, but also prove to be actively generated, as they flow against the direction of the electric field applied. These results are consistent with the view that the negative receptor currents are generated by the electrically excitable ion channels of the apical receptor-cell membranes and, in crossing the basal membranes, give rise to greatly amplified receptor potentials, driving the synapses. Thus, the ion channels of the apical membranes are, I believe, the active elements in a positive-feedback circuit that gives rise to the required

amplification, remarkably enough, without rendering the system unstable. This is achieved by keeping the feedback factor between 0 and -1 ; the closer to -1 it is, the greater the amplification, but the more severe the threat of instability (figure 2*d*).

(b) Graded and impulsive positive feedback: vital properties of life

The biophysical process of sensory transduction, leading in the ampullae of Lorenzini to greatly enhanced receptor potentials, may conveniently be described by representing the electrically excitable ion channels of the apical receptor-cell membranes by active devices featuring negative conductance. In addition to providing an elegant computational means of analysing the circuitry of the ampullary sense organs, the negative conductance emphasizes the ability of electrically excitable ion channels to respond to electrical stimuli with actively generating ionic currents against the direction of the electric fields applied, a most essential property of life. In a slightly different guise, the positive-feedback model is also applicable to the sense organs of marine and freshwater catfishes and, last but not least, to the graded as well as the impulsive phenomena of the CNS and peripheral nervous system.

5. IN CONCLUSION

The intelligent behaviour of animals and man finds its origin in the processing of sensory data. Seeking regularity and focusing on the most salient features in their environment, in order to endure and thrive, animals have empirically discovered the laws of nature. In this respect, science retraces evolution at a greatly accelerated pace.

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