ELECTRIC FISHES

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250

CONTENTS

I. INTRODUCTION

There are seven families of marine and fresh-water fish capable of delivering appreciable voltages outside their bodies. For example, the giant electric ray (Torpedo nobiliana) can electrocute a large fish with its pulses of 50 amperes at 50 to 60 volts. Though much smaller, the African catfish (Malapterurus) produces as much as 350 volts, and the electric eel (Electrophorous) of the Amazon and other South American rivers puts out more than 500 volts. In contrast, there are weakly electric fishes which generate from a few tenths to several volts, but even these species exceed the highest output of other animals which produce minute electrical currents in their nervous, muscular, and glandular tissue.

"There now seems to be no doubt about the survival value of the peculiar capability of the electric fishes. For the powerfully electric species it serves obvious offensive and defensive functions, and recent work has shown that in the weakly electric ones it serves as part of a sensory guidance system for navigation in murkey waters and for the detection of predators and prey. The advantages, in fact, are such that natural selection brought about the development of electric organs quite independently in almost every one of the families" (Grundfest, 1960a, pp. 115-116). In several cases, different physiological solutions were developed for the generation of electrical energy and the shaping and timing of the electric pulses.

"Animal electricity" was first studied in electric fishes, and throughout the 19th century these animals were the center of research on electrophysiology. As far back as 1791 Galvani suggested that there was a kinship between the electricity of "torpedo and cognate animals" and the "animal electricity" that he believed he had observed in muscles and nerves. A dispute arose between Galvani and Volta wherein the latter thought that Galvani had demonstrated "metallic" electricity by the contact of two dissimilar metallic surfaces rather than animal electricity. This was correct in that Galvani's frog nerve-muscle preparations were merely more sensitive detectors of electricity than any instruments available at that time. But "Volta was wrong in denying the existance of animal electricity. In trying to prove his contention that the electric fish contained some sort of generator Volta discovered the electrochemical battery, or 'galvanic' cell. The 'voltaic pile' of cells in series he called 'an artificial electric organ' which he thought 'victoriously demonstrated' his argument" (Grundfest, 1960a, p. 117).

At the present time, work on electric fish offers some potentially very useful leads to the solution of the problems of synaptic transmission such as the induction by the nerve impulse of the chemical mechanism that underlies the relay of the impulse from one nerve to the next and from the nerve cell to muscle or gland tissue.

II. ELECTRIC ORGANS

Morphology

Electric organs are derived from muscle and consist of an array of cells called electroplaques. These component cells may be stacked in columns like a roll of coins along each side of the body, running longitudinally and parallel with the spinal column. The eel is an example of this type and has some 6,000 to 7,000 electroplaques in each column, with 70 columns in the organs on each side of its body. In the adult eel they make up about 40 percent of the bulk of the body. In contrast, the columns in the electric ray are arranged vertically, i.e. at right angles to the spine, forming a large compact electric organ in each of the animal's wings. A third pattern is found in the African catfish, in which the organ is in the form of a mantle of tissue just below the skin, surrounding the entire body from gills to the tail. The bilateral electric organs of several species are shown in Figure 1.

Each electroplaque is a thin wafer-like cell whose two surfaces differ markedly. In most species, one surface is innervated directly by a dense network of nerve terminals or indirectly through one or several stalks which emerge from one of the electroplaque surfaces (Figures 2 and 3). But in almost all cases only one surface of the cells is innervated. The opposite side has a number of deep folds and convolutions to increase its total area. All of the electroplaques in one species are oriented in the same way. In addition to the main organ, an accessory electric organ is present in the electric ray. The electroplaques of this organ have a different orientation, i.e., they are innervated on their dorsal rather than their ventral surfaces. The surface of the electroplaques innervated and other aspects of their structure in a number of electric fish are summarized in Table 1.

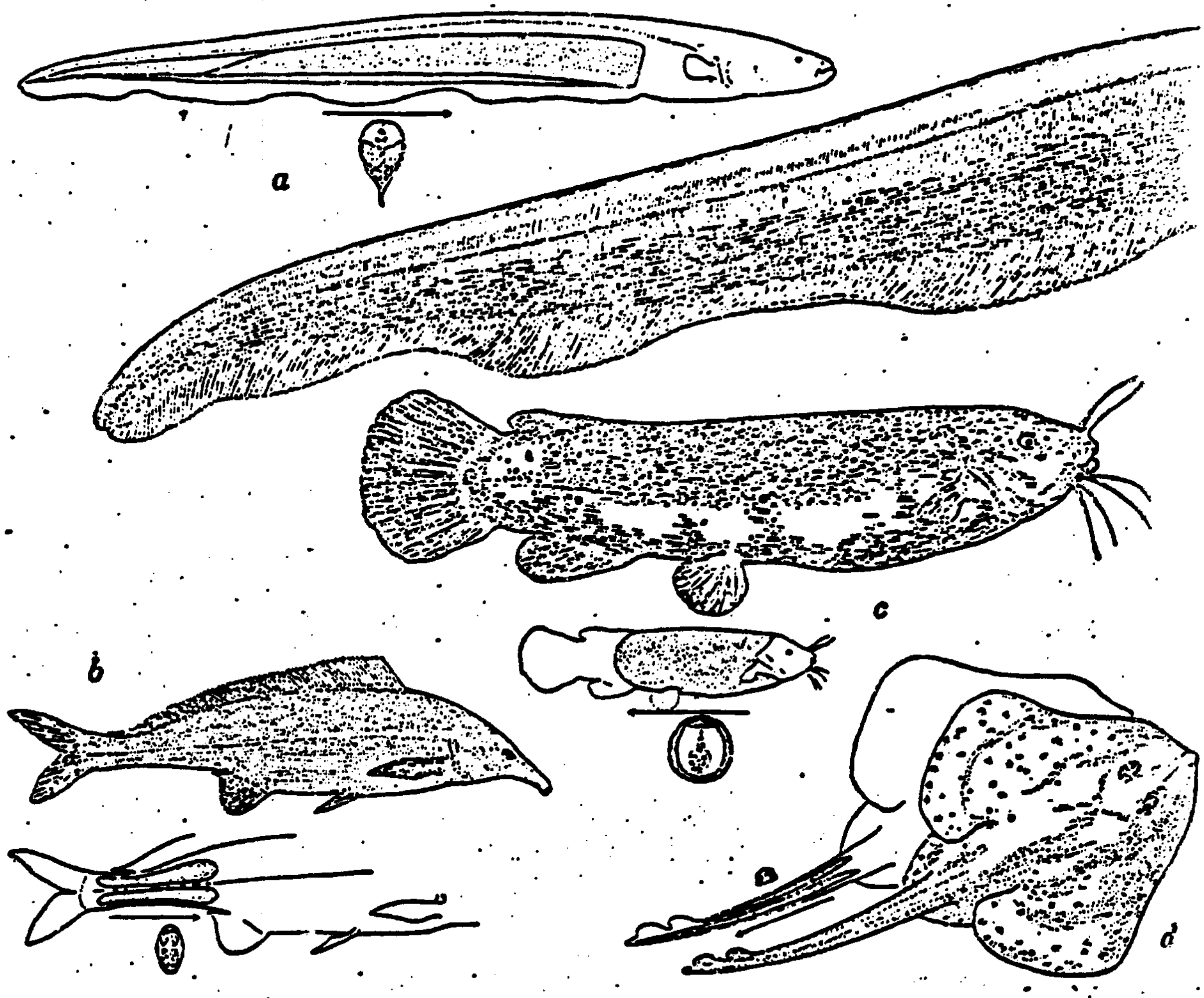

Figure 1. The electric organ arrangement in various electric fishes. The electric eel (a) has three organs (stippled area at top left): large main organ, smaller organ of Sachs behind it and organ of Hunter immediately underneath. Main organ and organ of Hunter appear in cross section below. Arrow indicates direction of current flow in body of fish during electric discharge. In Mormyrus (b) organ is situated near tail. Organ of Malapterurus (c) forms a mantle just under skin of fish. Electric skate (d) has organ in tail. Electric ray (e) has a kidney-shaped organ in each wing. Cross-sectional view shows columns of electroplaques in organs. The direction of the discharge (arrow) is perpendicular to the broad surface of ray. (After Grundfest, 1960a) Figure 1 continued on next page.

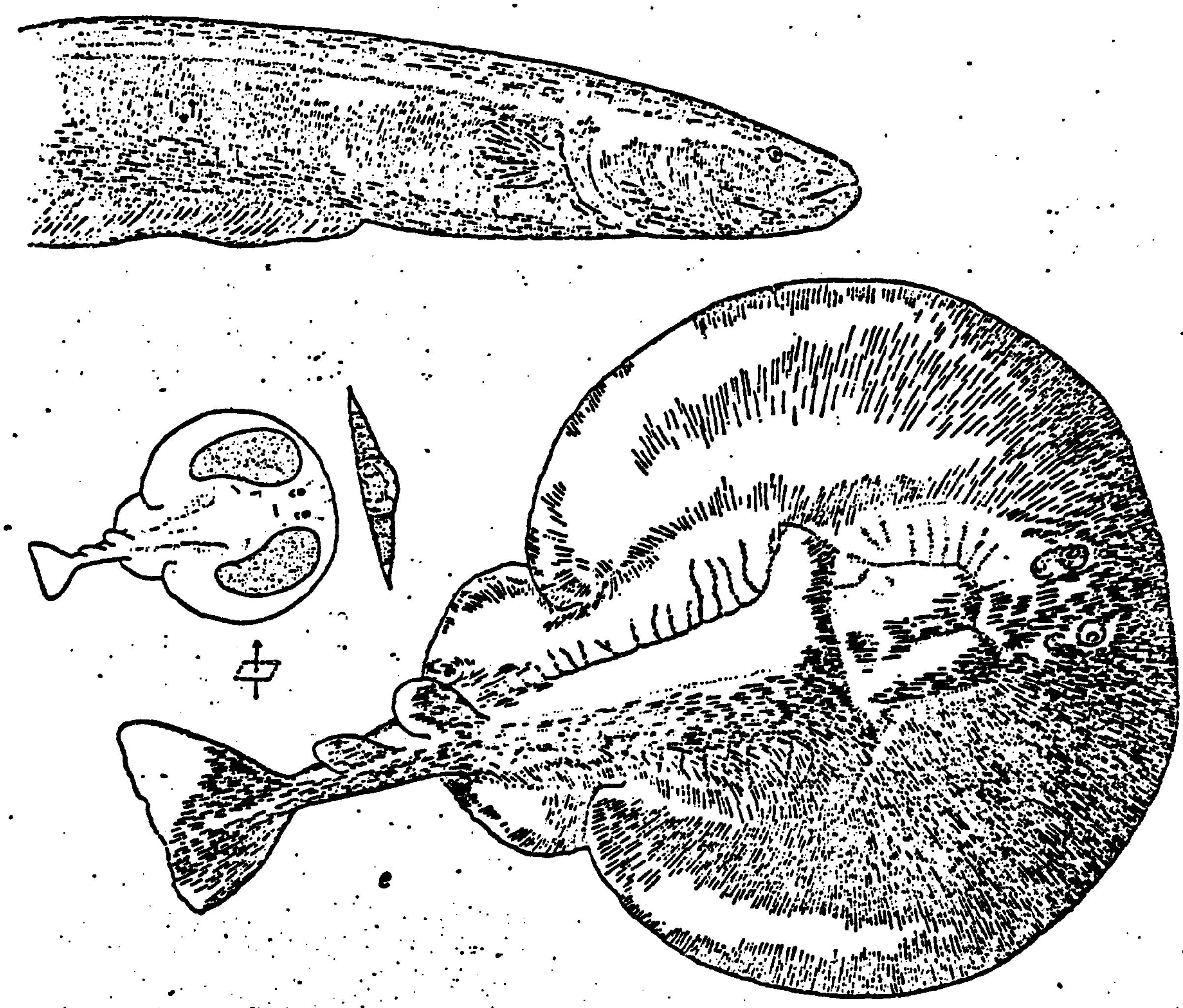

Figure 1 continued.

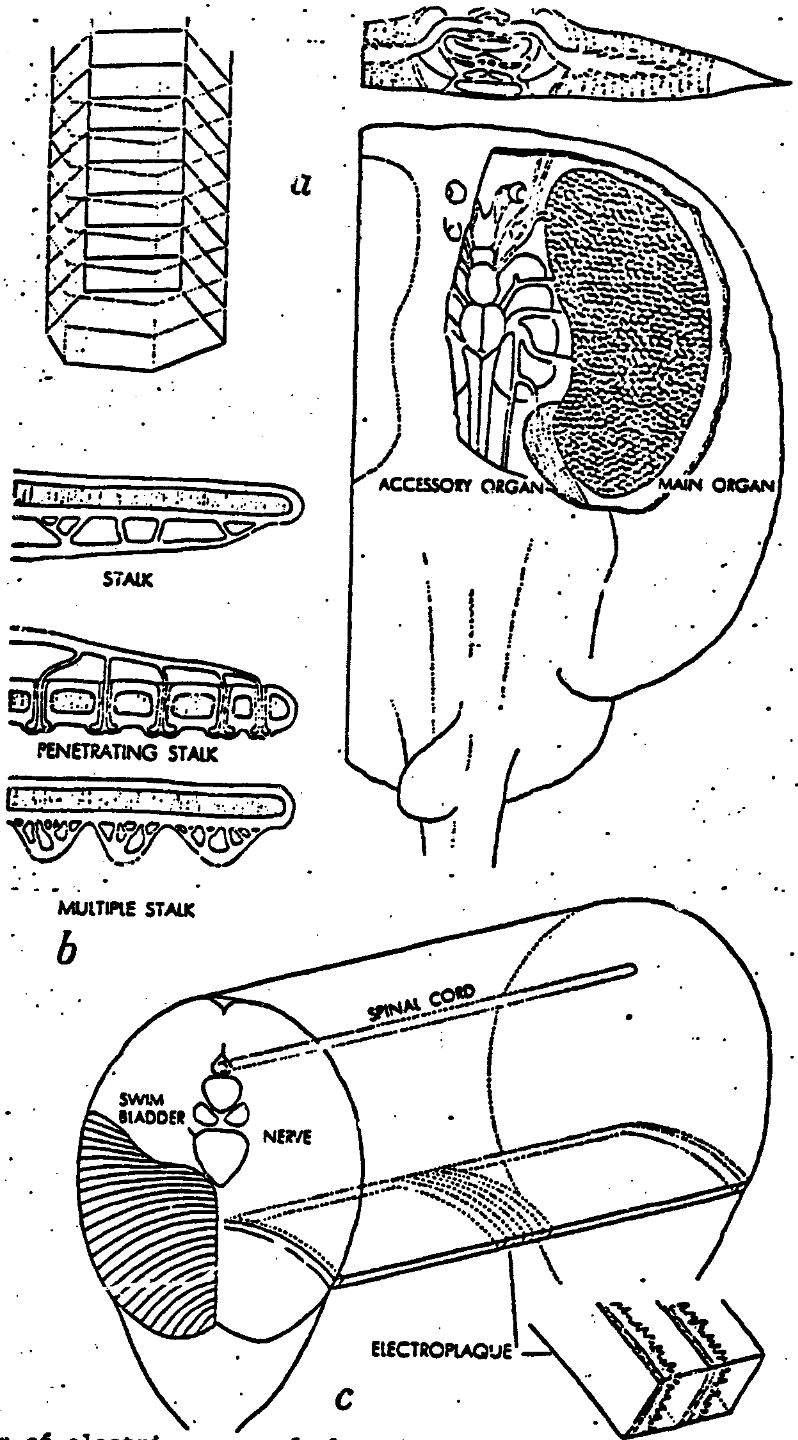

Figure 2 Details of electric organ of electric rays (a), mormyrids (b) and electric eel (c) are shown. Electroplaque columns are vertical in body of the ray (top right). Nerve terminals (colored branching at top left) directly innervate column. Cranial nerves (heavy colored lines at right) connect organs with electric lobes (solid colored area) of brain. Recently discovered accessory organ is found only in ray genus Narcine. Among different mormyrid species electroplaques are indirectly innervated via three types of stalk. As in some other fishes, uninnervated membranes of electroplaques in main organ of eel are convoluted. (After Grundfest, 1960a).

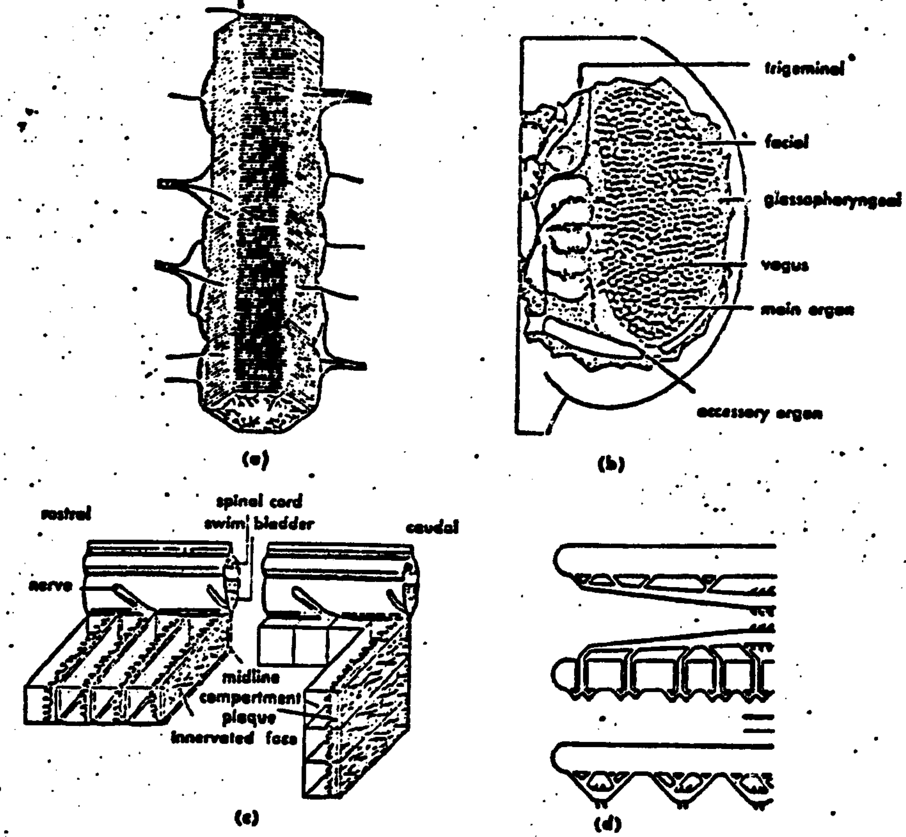

Figure 3. Samples of organ and electroplaque structure. (a) Column of electroplaques in series array, representing essentially the arrangement in the torpedine electric fishes and in Astroscopus. (b) Dorsal view of innervation which applies to Torpedo and main organ of Narcine; innervation is by individual nerve fibers to ventral surface of each electroplaque entering four different points of the periphery and supplying a limited area of the surface. In Astroscopus and the accessory organ of Narcine innervation is on the rostral surface, and nerve supply is more complicated. Figure also applies to Torpedo, except that accessory organ is absent. (c) Diagrammatic view of series and parallel arrays of electroplaques in the electric eel. A somewhat similar series-parallel arrangement occurs in other electric fish in which one surface is innervated. In Raia innervation is on rostral surfaces. (d) The mormyrid electroplaques are innervated on one or several stalk processes which form from branches that arise in the caudal surface of each electroplaque. In some, branches penetrate through the electroplaque body and innervation is then ahead of the electroplaque. In Malapterurus there is only a single stalk which arises from the center of the caudal face of the electroplaque. (After Grundfest, 1960b).

Table 1. Anatomy of electroplaque in several electric fish. (After Grundfest, 196(

Species	Origin (muscle)	Inner-vation*	Orientation	Dimensions R-C	Dimensions D-V	Dimensions M-L†	No. in columns	No. of columns per side
Torpedo nobiliana	Branchial	V	D-V	8 mm	10 μ	8 mm	1000	1000
Narcine brasiliensis								
Main organ	Branchial	V	D-V	4 mm	10 μ	4 mm	500	400
Accessory organ	Branchial	D	Oblique	4 mm	20 μ	4 mm	200	10
Raia clavata	Skeletal	R	R-C				200	12
Astroscopus y-graecum	Ocular	D	D-V	10 mm	50 μ	10 mm	200	20
Electrophorus electricus	Skeletal	C	R-C	200 μ	1 mm	15 mm	6000	75
Eigenmannia virescens	Skeletal	C	R-C	2 mm	200 μ	200 μ		5
Sternopygus elegans	Skeletal	C	R-C	1 mm	60 μ	60 μ		15
Gymnotus carapo	Skeletal	R and C	R-C	200 μ	500 μ	500 μ	80	4
Sternarchus albifrons	?	?	R-C					
Gnathonemus compressirostris	Skeletal	C	R-C	50 μ	10 mm	5 mm	100	2
Mormyrus rume	Skeletal	C	R-C	50 μ	10 mm	5 mm	100	2
Gymnarchus niloticus	Skeletal	C	R-C	100 μ	100 μ	100 μ	140	4
Malapterurus electricus	?	C	R-C	40 μ	1 mm	1 mm	3000	1500

* Abbreviations are R, rostral; C, caudal; D, dorsal; and V, ventral. † Medial-lateral.

Electrophysiology

The electroplaques in each column of an electric organ form a series array, so that the hook-up in series adds the outputs of the cells and builds up the voltage, while the arrangement of columns of electroplaques in parallel functions to build up the amperage. "The large area of the organ of the strongly electric fishes is analogous to the large number of plates in a storage battery cell of high current output" (Grundfest, 1967, p. 405). The discharge characteristics of electroplaques in several fishes are outlined in Table 2.

In the electroplaques of marine electric fish, only the innervated surface of the cell is reactive. Electrogenic activity cannot be evoked by direct electrical stimulation, but only by stimulating the nerve or with chemical agents, i.e., the cell is electrically inexcitable. The electroplaque's cell membrane, like that of the nerve or muscle cell, is selectively permeable to potassium ions but not to sodium ions, so that the higher concentration of the former inside the cell membrane and the latter outside the cell creates a resting potential across the membrane , with the inside negative and the outside positive. After a stimulus is applied, the permeability of the membrane changes, permitting the movement of both types of ions (and, therefore, an electric current) to flow across the membrane. Generally, only the innervated membrane of the electroplaque

Table 2. Electroplaque discharge and response characteristics in several electric fish. (After Grundfest, 1960 b.)

Species	Discharge			Response			
						Duration, msec	
	Amplitude, volts	Form	Frequency	Amplitude, mv	Type*	Postsynaptic potential	Spike
Torpedo nobiliana	60	Monophasic	Repetitive on excitation	Max. 80	1	5	None
Narcine brasiliensis							
Main organ	30	Monophasic	Repetitive on excitation	Max. 80	1	5	None
Accessory organ	0.5	Monophasic	Repetitive on excitation	Max. 80	1	5	None
Raia clavala	4	Monophasic	Repetitive on excitation	Max. 80	1	25	None
Astroscopus y-graecum	7	Monophasic	Repetitive on excitation	Max. 80	1	5	None
Electrophorus electricus	700	Monophasic	Repetitive on excitation	Min. 100	2	2+	2+
Eigenmannia virescens	1	Monophasic positive direct current	250/sec	Min. 100	2	1	2
Sternopygus elegans	1	Monophasic positive direct current	50/sec	Min. 100	2	2	10
Gymnotus carapo	1	Triphasic	50/sec	Min. 100	3	1.5	1
Sternarchus albifrons	1	Diphasic	750/sec	Min. 100	3		
Gnathonemus compressirostris	10	Diphasic	Variable	Min. 100	4		0.2
Mormyrus rume	12	Diphasic	Variable	Min. 100	4		5
Gymnarchus niloticus	Low	Monophasic	300/sec	?	?		
Malapterurus electricus	300	Monophasic	Repetitive on excitation	Min. 100	4		2

* Response types: 1, electrically inexcitable electroplaques which produce only a postsynaptic potential and only on the innervated surface; 2, responses are both postsynaptic potentials and spikes, produced only at innervated surface; 3, opposite, uninnervated surface also is electrically excitable, producing a spike, whereas the innervated surface develops both a postsynaptic potential and a spike; 4, the synaptic junction is at a distance from the major surfaces of the electroplaque on one or several stalks produced by the caudal surface, and both major surfaces produce spikes.

is affected. The opposite membrane usually remains inactive, maintaining a negative potential and offering little resistance to the flow of electric current. Inasmuch as current flows from positive to negative, the orientation of the electroplaque determines the current's direction in the fish. For example, the innervated surfaces of the eel's electroplaques all face the tail, so that current flows from tail to head inside the fish and from head to tail in the water to complete the circuit. "The great number of electroplaques in series enables the eel to produce the voltage necessary to overcome the high resistance of its freshwater environment. The columns in parallel enable it to generate a current, in brief pulses, of about one ampere, so that even in fresh water the organ generates considerable power. The electric rays, living in salt water, show a corresponding adaptation to the lower resistance of this medium. The giant ray <u>Torpedo nobiliana</u> has up to 1,000 electroplaques in series, much fewer than the eel, and so generates a lower voltage. But it has some 2,000 columns in parallel in each organ, giving it its extraordinary amperage " (Grundfest, 1960a, p. 119). The generation of electricity in electroplaque membranes considered as batteries is shown in Figure 4.

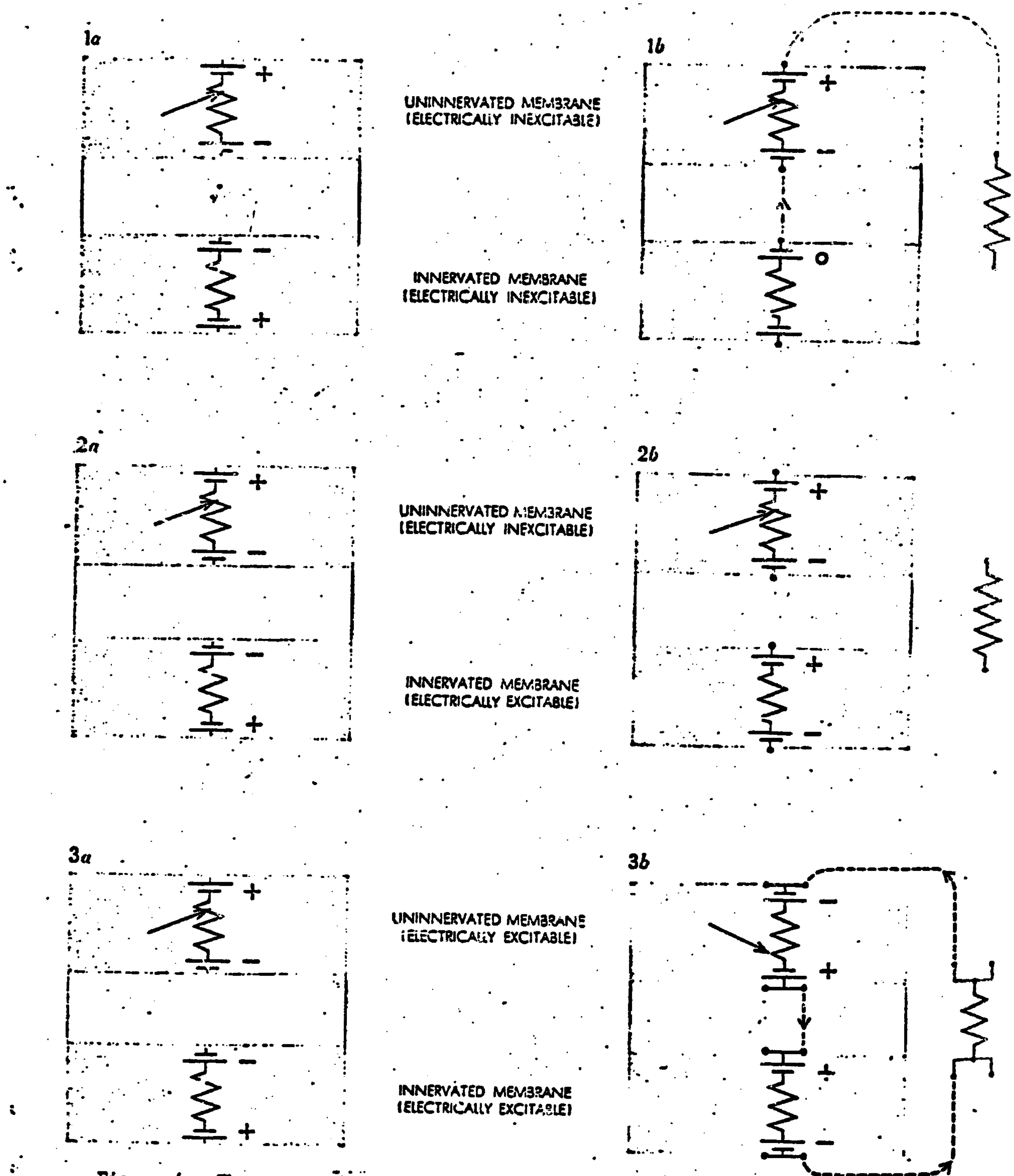

Figure 4. The generation of electricity by electric fishes can be explained by comparing electroplaque membranes (shaded areas) to batteries. Resting potentials of membrane batteries, negatively charged on inner surface and positively charged on outer, are shown at left. In marine fishes nerve stimulus short-circuits battery of innervated membrane (1b). Magnitude of discharge equals resting potential, and current (broken line) flows through electroplaque, then through external medium. In eel, stimulus reverses polarity of battery of electrically

III. NAVIGATION AND DETECTION WITH ELECTRIC FIELDS

The gymnarchus has a weak electric organ which is somewhat like the powerful electric organs of the electric eels and other fishes in that it is derived from muscle tissue. But until recently, no one had found a function for weak electric organs. Now it is known that "gymnarchus lives in a world totally alien to man: its most important sense is an electric one, different from any we possess" (Lissmann, 1963, p. 359). By means of this sense, it is able to swim with equal facility backward or forward, and to avoid obstacles when they are encountered fore or aft. Its movements are made with great precision, and it never bumps into the walls of its tank when darting after small fish.

The small electric organ of gymnarchus consists of four thin spindles containing electroplaques running up each of its sides to a point just beyond the middle of its body. The characteristics of its electric organ discharge vary with the individual and with temperature. For example, specimens may produce voltages of 3 to 7, with a discharge frequency averaging about 300 cycles per second.* "During each discharge the tip of its tail becomes momentarily negative with respect to the head. The electric current may thus be pictured as s spreading out into the surrounding water in the pattern of lines that describes a dipole field (Figure 5). The exact configuration of the electric field depends on the conductivity of the water and on the distortions introduced in the field by objects with electrical conductivity different from that of the water. In a large volume of water containing no objects the field is symmetrical. When objects are present, the lines of current will converge on those that have better conductivity and diverge from the poor conductors (Figure 6). Such objects alter the distribution of electric potential over the surface of the fish" (Lissmann, 1963, 362). If gymnarchus could perceive such changes, it would be able to detect objects in its environment. This it is able to do through skin perforations near its head which lead into tubes filled with a jelly-like substance. Since the jelly is a good conductor, it acts as a lense to focus the lines of electric current which converge from the water into the pores and are led to electric sense organs at the base of the tubes.

All animals are sensitive to strong electric currents, but their response is to currents many thousands of times stronger than those effective in gymnarchus and gymnotus. The latter can readily learn to locate currents whose density is reduced to 2×10^{-5} $\mu A/cm^2$, as calculated from the response distance to the horizontal movement of an electrostatic charge outside the aquarium. Even the electrostatic charge of a plastic comb elicits a response in gymnarchus. The same fish is able to detect the weak current flow from a horshoe-shaped copper wire when it is closed and dipped just below the surface. It is also possible for this fish to distinguish between "geometrically identical objects with differing electrical conductivities. Conversely, it cannot distinguish between dissimilar objects which modify the current distribution in a similar way" (Lissmann and Machin, 1958, p. 454).

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* Discharge frequencies usually increase at higher temperatures.

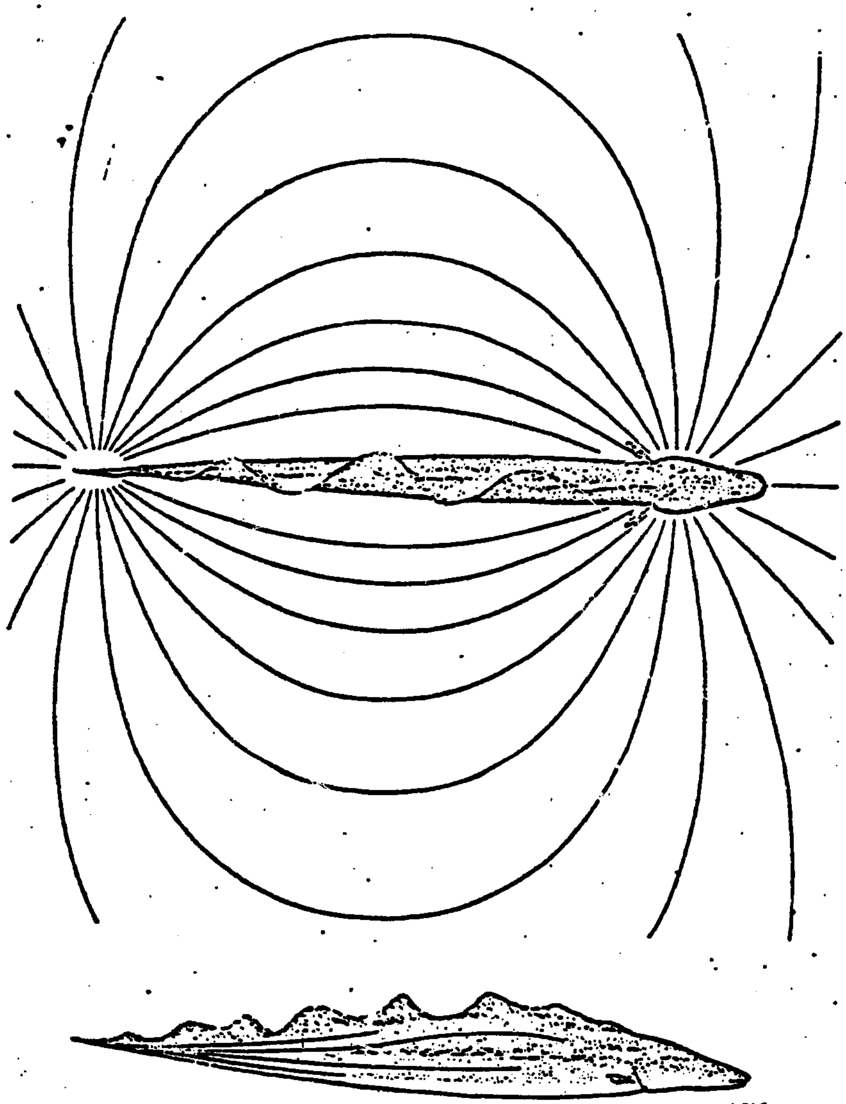

Figure 5. Electric field of Gymnarchus and location of electric generating organs are diagramed. Each electric discharge from organs in rear portion of body makes tail negative with respect to head. Most of the electric sensory pores or organs are in head region. Undistrubed electric field resembles a dipole field, as shown, but is more complex. The fish responds to changes in the distribution of electric potential over the surface of its body. The conductivity of objects affects distribution of potential. (After Lissmann, 1963.)

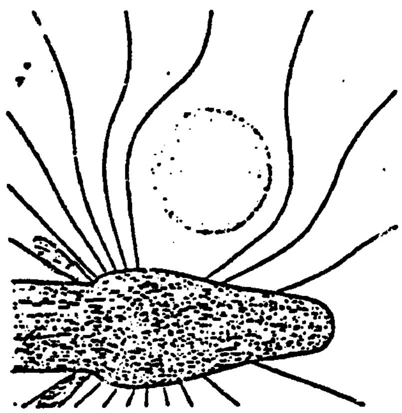

Figure 6. Objects in electric field of Gymnarchus distort the lines of current flow. The lines diverge from a poor conductor (left) and converge toward a good conductor (right). Sensory pores in the head region detect the effect and inform the fish about the object. (After Lissmann, 1963).

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