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Propagation of the Electric Impulse along the Organs of the Electric Eel, *Electrophorus electricus* (Linnaeus).

C. W. COATES,
New York Aquarium,

R. T. COX, W. A. ROSENBLITH,
Department of Physics, New York University

&

M. VERTNER BROWN,
Department of Physics, College of the City of New York.

(Plate I; Text-figures 1-3).

Observations already reported[1] have shown that in the discharge of the electric organs of the electric eel a pulse of potential gradient runs along the organ from anterior to posterior. The speed of the pulse was roughly estimated by several methods and was found much higher than the highest recorded speeds of impulses along nerves. The cathode-ray oscillograph used in these observations did not, however, make possible anything better than rough determinations of the speed. A more suitable cathode-ray oscillograph[2] having lately become available, it seemed worth while to attempt more accurate measurements.

The method employed is almost the same as one of those used before. The fish is taken out of water and laid in an insulating trough. The trough is grooved across one side every 10 cm. and aluminum strips inserted in any of these grooves make good electrical connection through the skin to the large electric organs and serve as electrodes for connecting the organ to the oscillograph. Text-fig. 1 shows the positions of these electrodes on the fish in one of the observations. Electrode 1 was at the anterior end of the large organ and electrode 2 was 10 cm. behind it. With these positions a conveniently measurable voltage was developed in the segment of the organ included between the two electrodes. The first two electrodes were consequently kept in these positions during all the observations. Electrode 3 was placed at a distance behind electrode 2 differently chosen in the various observations. Electrode 4 was placed far enough behind electrode 3 that the peak voltage between 3 and 4 was comparable to that between 1 and 2.

Oscillographic traces were photographed with three different connections of the electrodes to the oscillograph. First electrodes 1 and 2 were connected to the vertically deflecting plates of the oscillograph tube. When the discharge of the eel developes a voltage between these two electrodes,

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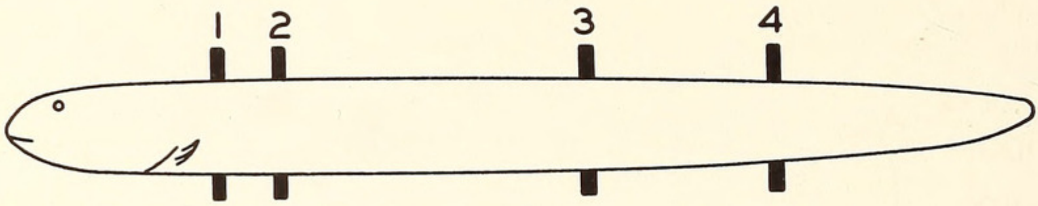
[1] Coates, C. W., Cox, R. T., and Granath, L. P. The Electric Discharge of the Electric Eel, *Electrophorus electricus* (Linnaeus). *Zoologica*, New York, 1937. Vol. 22, Part 1, pp. 1-32.

[2] Allen B. Dumont. Type 175A Oscillograph.

this voltage applied to the plates deflects the beam of electrons in the oscillograph tube. The luminous spot which the beam makes where it strikes the fluorescent screen at the end of the tube rises and falls with the voltage developed in this segment of the organ, the displacement of the luminous spot at any instant being proportional to the voltage existing at the same instant between the electrodes. While the discharge of the fish is causing this vertical motion, voltage from a "sweep circuit," applied to the horizontally deflecting plates of the oscillograph tube, carries the luminous spot horizontally across the fluorescent screen at a constant rate. The luminous spot thus traces a graph, which can be photographed, in which the voltage between the electrodes is plotted vertically against the time plotted horizontally.



Text-figure 1.

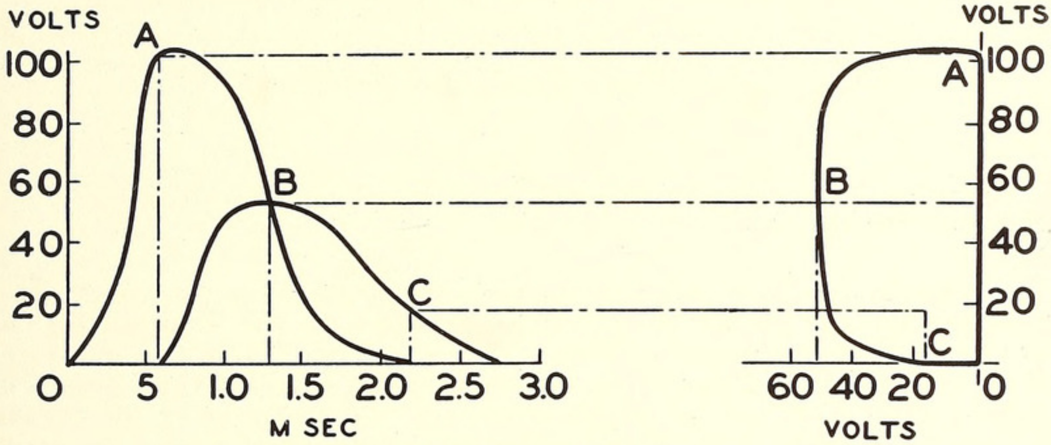
Position of electrodes for determining voltage at anterior and posterior ends of electric organs.

Next the vertically deflecting plates were connected to electrodes 3 and 4 on the fish and the graph of voltage against time was obtained for the discharge in this posterior segment. Plate I, Figs. 1 and 2, show traces obtained for the discharge of the two segments in an eel 108 cm. long. The sweep circuit could not be synchronized with the discharge of the organs. Consequently traces of a number of discharges occurring during successive horizontal sweeps of the electron beam are shown overlapping in each figure.

These two figures show the voltage-time relation for each segment, but they give no indication of the time-lag between the pulses in the two segments. To determine the time-lag the fish was connected to the oscillograph in a third way. The sweep circuit was disconnected from the oscillograph tube, the anterior segment 1-2 was connected to cause a vertical deflection of the electron beam, and the posterior segment 3-4 was connected to cause a horizontal deflection. The trace obtained with this connection is shown in Plate I, Fig. 3. Because the voltage rises in the anterior segment before it begins to rise in the posterior segment, the initial deflection is vertical. This shows as the vertical side at the right of the loop. The right-angled bend of the trace at its upper left corner indicates that the voltage in the anterior segment has ceased to rise but has not started to fall at the instant at which the voltage begins to rise in the posterior segment. After this, the voltage starts to fall in the anterior segment while remaining near its peak in the posterior segment. Finally it falls in both together and the loop is closed.

If the time-lag between the discharges in the two segments were known, it would be possible to construct the trace shown in Fig. 3 from measurements on the two traces shown in Figs. 1 and 2. For if the time-lag were known, corresponding instants on the time-axes of the two traces could be paired, and voltages simultaneously existing in the two segments could be determined. A graph showing the voltage in the anterior segment plotted vertically against the simultaneous voltage in the posterior segment plotted horizontally would be similar to the loop of Fig. 3, which was obtained with the oscillograph when the two segments were connected respectively to the vertically and horizontally deflecting plates. Conversely, by assuming various values for the time-lag and plotting the corresponding values of the two voltages one against the other, there will be obtained a number of graphs of which the one most like the recorded loop will have its assumed time-lag nearest the actual time-lag.

This procedure is illustrated by Text-fig. 2. The oscillographic traces copied in this figure were obtained with an eel 124 cm. long. The traces of the discharge in the anterior and posterior segments are superimposed with an assumed time-lag of 0.6 millisec. so as to give a loop analogous to the one which was recorded. Points A, B, and C, corresponding to three instants during the discharge, serve to illustrate the construction. A shows the voltage in the anterior segment (plotted vertically) at the start of the discharge in the posterior segment. B shows the voltage in the anterior segment at the instant at which it is equal to that in the posterior segment (plotted horizontally). C shows the voltage in the posterior segment at the end of the discharge in the anterior segment.



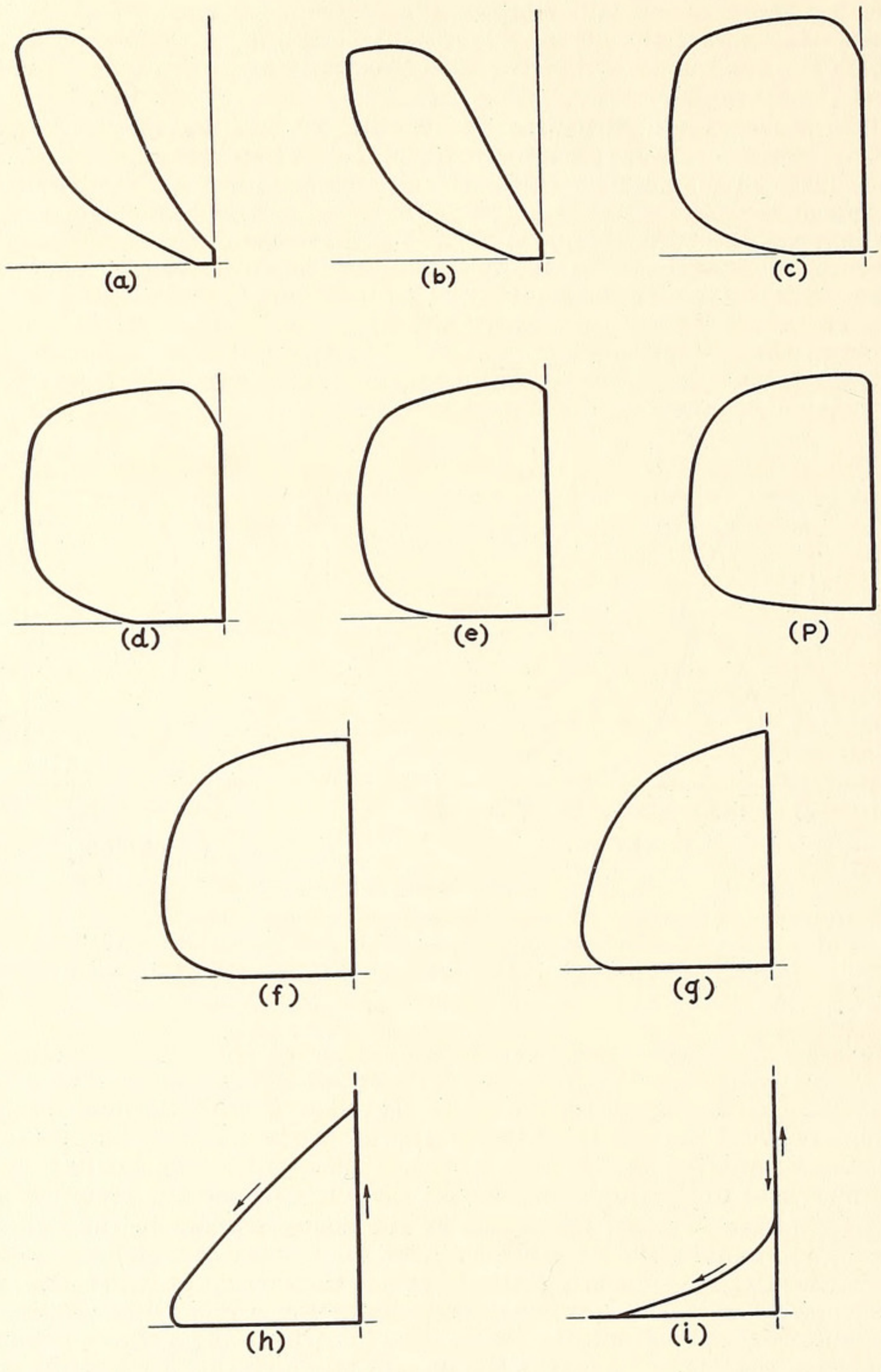
Text-figure 2.

Construction of graph of anterior voltage vs. posterior voltage by superposition of graphs of anterior voltage vs. time and posterior voltage vs. time. Assumed time-lag, 0.6 millisecs. (The scale of voltage is only roughly approximate).

Text-fig. 3 shows a more extended example of the same construction. The traces copied here were obtained with an eel 167 cm. long. The graphs (a)—(i) have been constructed as in Text-fig. 2 with various assumed time-lags between the starts of the discharge in the anterior and posterior segments. Graph (e) in the second row is seen to be very similar to the loop drawn next to it, which is a copy of the photographically recorded loop.

The time-lag between the starts of the rising voltage in the two segments is thus found to be 0.6 millisec. Now the instant at which the voltage between the electrodes 1 and 2 starts to rise is the instant at which the front of the pulse of potential gradient starts down the organ from electrode 1 at the anterior end. Similarly the instant at which the voltage starts to rise between electrodes 3 and 4 is the instant at which the front of the pulse reaches electrode 3, for as soon as the front of the pulse passes a given point that point will be at a different potential from points farther along the organ. Hence the time-lag found, 0.6 millisec., is the time required for the front of the pulse to traverse the distance from electrode 1 to electrode 3. This distance was 60 cm. Dividing the distance by the time-lag, we find the average speed of the pulse along the anterior 60 cm. of the large organ to be 100 cm. per millisec. or 1,000 meters per sec.

With the same fish oscillographic traces were photographed with elec-



Text-figure 3.

Construction of graph of anterior voltage vs. posterior voltage with various assumed time-lags.

Graph	a	b	c	d	e	f	g	h	i
Assumed time-lag, (milliseconds.)	.06	0.1	0.3	0.5	0.6	0.7	0.9	1.2	1.8
Computed speed of pulse, (meters per second.)	10,000	6,000	2,000	1,200	1,000	860	670	500	330

The photographically-recorded trace (P) is shown for comparison at (e).

trodes 1 and 2 in the same positions as in Text-fig. 1 but with electrodes 3 and 4 at 40 cm. and 60 cm. respectively from the anterior end. The time-lag between the starts of the rising voltage in the anterior and posterior segments was again determined by the procedure just described and was found to be only 0.15 millisec., approximately. From this result the average speed of the pulse along the anterior 40 cm. of the organ is found to be about 2,500 meters per sec.

The pulse takes 0.6 millisec. to travel along the organ 60 cm. from the anterior end and 0.15 millisec. to travel 40 cm. from the anterior end. The difference of these two time-lags, 0.45 millisec., is the time required for the pulse to traverse the segment of the organ between 40 cm. and 60 cm. from the anterior end. The average speed of the pulse along this 20 cm. stretch is thus only 450 meters per sec.

None of these determinations can be taken as at all precise. Nevertheless it is clear that the speed of propagation of the pulse along the organ diminishes from anterior to posterior. The speed at the anterior end of the organ must then be greater than the average speed along the anterior 40 cm., which was reckoned as 2,500 meters per sec. Even with allowance made for the inaccuracy of this measurement, it seems safe to take 2,500 meters per sec. as a minimum estimate for the speed at the anterior end. The large electric organ of this fish was at least 120 cm. long, and the average speed of the pulse over the segment between 40 cm. and 60 cm. from the anterior end was found to be 450 meters per sec. Considering the fall in speed toward the posterior end it seems safe, after allowing for the inaccuracy of the measurement, to take 450 meters per sec. as a maximum estimate of the speed at the posterior end. The ratio of the speed at the anterior end to that at the posterior end must then be greater than 5 to 1.

Measurements were made in all on three fish of different lengths. The results are summarized in the following table.

TABLE 1.

Propagation of pulse along large organs of three eels of different sizes.

Eel	Length (cm.)	Circumference at anterior end of large organ (cm.)	Distance from anterior end to electrode 3* (cm.)	Time-lag (millisec)	Speed (meters per sec.)
I	108	20.5	40	Between 0.25 and 0.3	About 1500
II	167	34	40	0.15	2500+
			60	0.6	1000
III	124	25	20	0.1—	2000+
			40	0.45	900

* Electrode 1 was always at the anterior end of the large organ. Hence this distance is the distance traversed by the pulse during the measured time-lag. The speed is computed from the distance and the time-lag.

In the electric eel the electric organs lie parallel to the spinal cord. From special large cells, the electric nerve cells, lying in the cord, nerves branch out to the adjacent parts of the organs. The discharge in every part of the organ is excited by the nerves running to that part. For if the cord is cut at any point, parts of the organ posterior to the cut do not discharge. On the other hand, if the organ is transsected at any point without injury to the cord, the segment of the organ posterior to the transsection still discharges.

The path traversed by the nervous impulse which initiates the discharge at any point is certainly no shorter than the distance to that point along the body of the eel. It seems necessary then to conclude either that the nervous impulse travels along the cord as fast as we have found the electric pulse traveling along the organ or else that there is some special mechanism which delays the discharge in the anterior part of the organ while the nervous impulse runs down the cord to initiate the discharge in posterior parts.

If we take the first of these hypotheses and assume a speed of the nervous impulse along the fibers in the cord as high as 2,500 meters per sec., and if we apply the rule given by Blair and Erlanger[3] that the speed is proportional to the square of the diameter of the fiber, then we find that the fiber must have a diameter of about 140 microns or .014 cm. We have not found a record of the size of the nerve fibers in the spinal cord of the electric eel, but a diameter of 140 microns is several times greater than that of the largest ordinary nerve fibers. If, instead of following the rule of Erlanger and Gasser, we adopt the conclusion of other investigators that the speed is proportional to a power of the diameter between the first and second, then still larger nerve fibers must be assumed for the electric eel.

The evidence which we have on the second hypothesis, that of a special process delaying the discharge in the anterior part of the organ, is as yet slight and inconclusive.

It is at any rate easy to see how the effective use of the organ requires the pulse to travel along it at a much higher speed than that at which nervous impulses are commonly transmitted. The point is most readily discussed in terms of the description of the organ as a series of galvanic elements effectively insulated from each other except when, during the discharge, a transient drop in the electrical resistance between adjacent elements joins them briefly in series[4]. This series connection persists only for about 1.5 millisec. at any point in the organ. The front of the pulse at any instant is the point on the organ at which the connection is just beginning to be made. If the front travelled down the organ at a speed of 100 meters per second, or 10 cm. per millisec. (which is near the highest speed recorded even in mammalian nerve) the length of the segment connected at any one time would be only 15 cm. As soon as the front had travelled that far along the organ, the connection would be broken behind it as fast at it was made in front. The highest voltage developed would thus be only a fraction of what is developed with the actual speed. The discharge would, it is true, be prolonged by the slower propagation, but this advantage could hardly offset the disadvantage of the lower voltage in repelling the enemies of the fish and stunning its prey, especially since the fish can now repeat its discharge with such rapidity as to have much the same effect as prolonging it, perhaps with a greater effect physiologically.

It thus appears that the evolution of the electric eel has developed a mechanism for the propagation of the pulse along the organ which circumvents whatever factor limits in other animals the speed of the impulse along nerve fibers, and that without this mechanism—whatever it is—the electric power of the eel would be much less effective. It also appears, however, that this mechanism is itself subject to some limitation, for it does not make the discharge exactly simultaneous at every point of the organ. Because of the time lag, the peak voltage between the extremities of the organ is less than the sum of the peak voltages developed in all its segments. Measurements on an electric eel about 170 cm. long showed that the voltage developed in the anterior four-fifths of the large organ is practically as great as that developed between its extremities. This indicates that the posterior fifth of

[3] Blair, E. A., and Erlanger, J., *Am. J. Physiol.*, 106, 524 (1933).

[4] Cox, R. T., and Coates, C. W. Electrical Characteristics of the Electric Tissue of the Electric Eel, *Electrophorus electricus* (Linnaeus). *Zoologica*, New York, 1938. Vol. 23, Part 2, pp. 203-212.

the organ is not fully joined in series until the connection at the anterior end has begun to be broken. Consequently in this eel the posterior fifth of the organ has little effect other than to prolong the discharge.

Our observations afford only a narrow basis for the comparison of the speeds of the pulse in eels of different lengths. However it seems that there is probably an upper limit to the speed attainable and that there is consequently an increase, as the eel grows, in the time lag between the discharges at the extremities of the organ. It seems therefore a quite reasonable inference that, because of this factor, growth of the eel beyond a certain length would increase the need of prey faster than the additional effectiveness of the discharge would help in its capture. What this length would be we can not say from our observations. The longest electric eel that the New York Aquarium has had was about 2.7 meters long, and this is about the greatest length recorded. It would seem unlikely that growth beyond this point would be helpful to the eel.

EXPLANATION OF THE PLATE.

Plate I.

Oscillographic traces of the discharge of an electric eel 108 cm. long.

Fig. 1. Voltage-time graph of anterior segment. Electrodes at anterior end of Large Organ and 10 cm. behind. Length of horizontal base corresponds to 4 milliseconds. The peak is about 100 volts.

Fig. 2. Voltage-time graph of posterior segment. Electrodes 40 cm. and 70 cm. from anterior end of Large Organ. Scale same as in Fig. 1. (The discharge of lower voltage is of the intermediate type).

Fig. 3. Graph of voltage in anterior segment (vertically) against voltage in posterior segment (horizontally). (The short horizontal trace is made by the discharge of the Bundles of Sachs.)

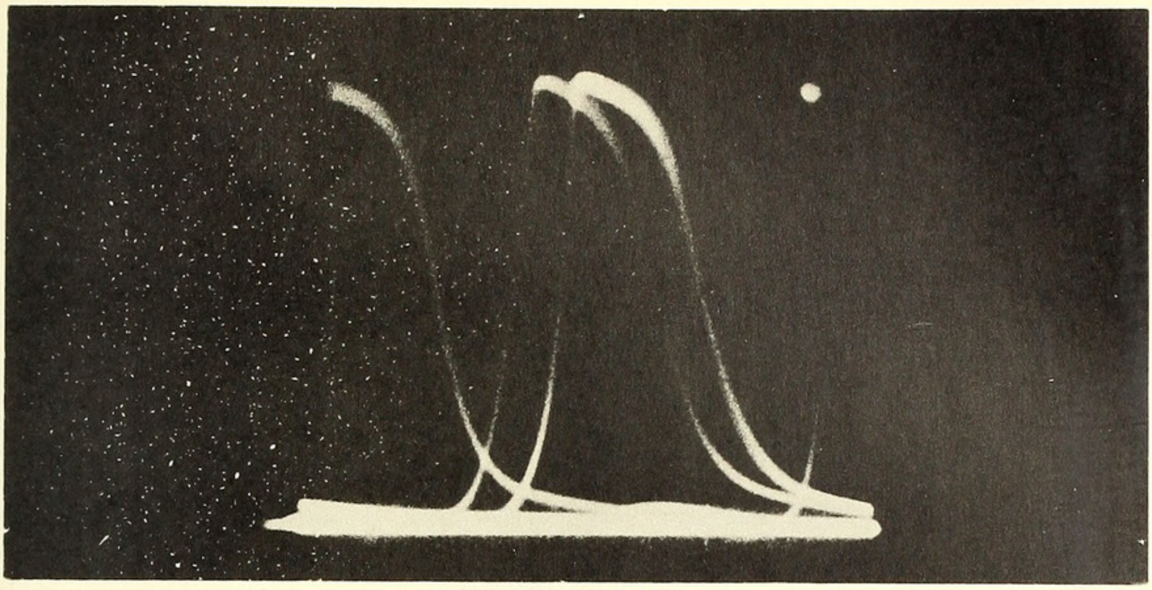


FIG. 1.

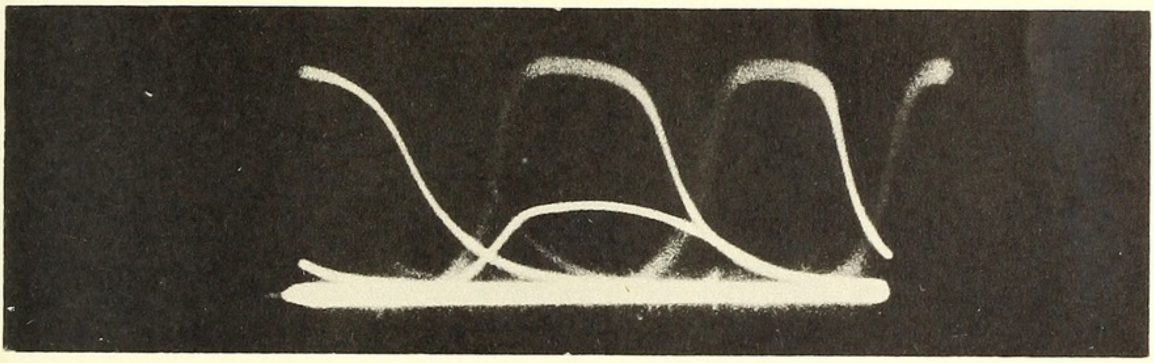


FIG. 2.

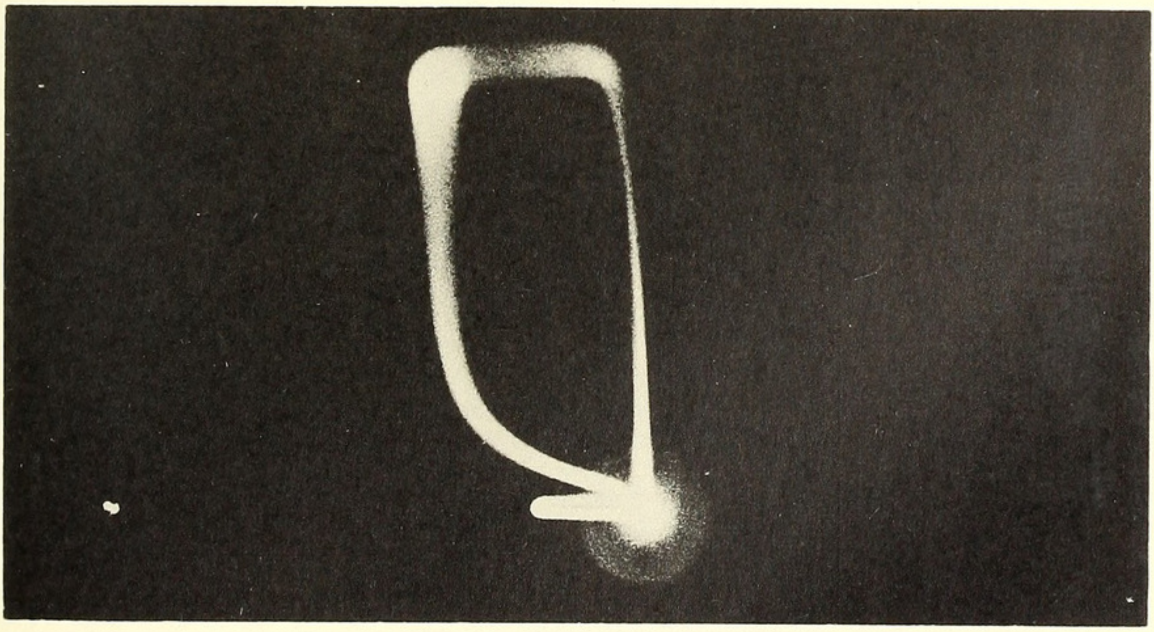


FIG. 3.

PROPAGATION OF THE ELECTRIC IMPULSE ALONG THE ORGANS OF THE ELECTRIC EEL, ELECTROPHORUS ELECTRICUS (LINNAEUS).