

ELECTRIC TISSUE

RELATIONS BETWEEN THE STRUCTURE, ELECTRICAL CHARACTERISTICS, AND CHEMICAL PROCESSES OF ELECTRIC TISSUE

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INTRODUCTION

Several recent papers have shown comparisons between the results of electrical measurements made on the discharge of the electric eel, *Electrophorus electricus* (Linnaeus) and those of chemical measurements on the electric tissue (1-4). The present paper is concerned with the same research but will deal mainly with an analysis of the electrical measurements themselves and the relation between the electrical characteristics and the structure of the organs.

The electric eel offers several advantages in such an inquiry over the other electric species. In contrast to most of them, it can be kept in captivity. Its electrical characteristics are rather constant and do not change materially even when it is kept for some minutes out of water. Also its electric organs, being long and lying just under the skin, allow electric connections to be made at any points along their length, whereas the electric organs of the rays, *Torpedo* and *Narcine*, are conveniently accessible only at their poles. Thus, in the organs of the electric eel, it is possible to compare the electrical activity of their different parts. The observed electrical variations may then be studied in relation to the variations found in the dimensions of the organs and the arrangement of the electroplaxes.

Organs of the Electric Eel

The electric eel has three pairs of electric organs, the main organs, which extend along the posterior four-fifths of the length of the fish, the much smaller organs of Hunter, which lie under the main organs along their entire length, and the organs or "bundles" of Sachs, which lie above the main organs in the posterior half of the fish. The discharges of the main organs and of the organs of Sachs can be clearly distinguished from each other. Hunter's organs, on the other hand, seem to discharge with the main organs, which they closely resemble in the arrangement of the electroplaxes and from which they are only separated by a thin layer of muscle. In the present paper, wherever

the dimensions of the organs are involved, the organs of Hunter will be considered as a part of the main organs, and where the main organs are mentioned it is to be understood that Hunter's organs are included. The point is of no great importance, however, for the cross-section of Hunter's organs is so small that their exclusion would hardly change any of the significant results by more than the probable error.

DIMENSIONS OF THE SINGLE ELECTROPLAX LAYER

The variation in the dimensions of the organs is illustrated in Fig. 1, in which, for one specimen, their cross-sectional area is plotted as ordinate against the distance along the organs from anterior to posterior.

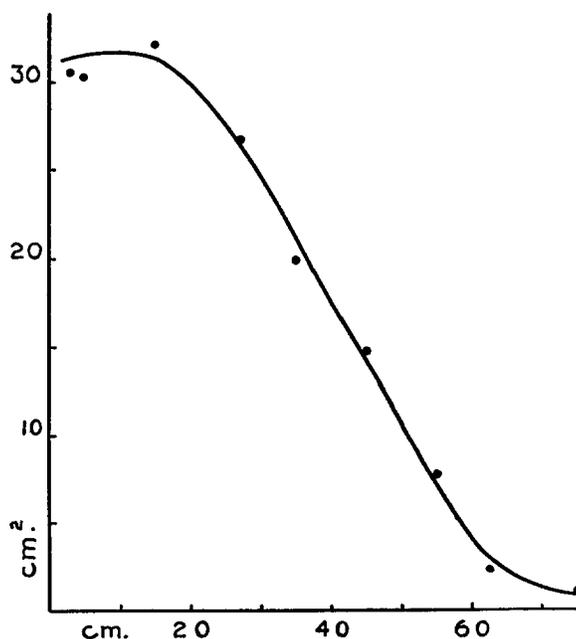


FIG. 1. Variation in cross-section of main organs. Area of cross-section (cm.²) vs. distance from anterior end (cm).

The electroplaxes are arranged in a regular structure which has often been described. Plates showing sections of the organs at several places were included in one of the papers already cited (2). At any one cross-section the electroplaxes have a uniform thickness in the direction of the length of the fish, which is also the direction of the electric current in the discharge. But along the organs this thickness varies, the electroplaxes at the anterior end being very much thinner than those at the posterior end. In Fig. 2a the number of electroplaxes per unit length along the organs is plotted, as the

cross-sectional area was plotted in Fig. 1, against the distance from the anterior end. The likeness of the two figures is apparent. This likeness reflects a structural characteristic which is most simply described by considering a

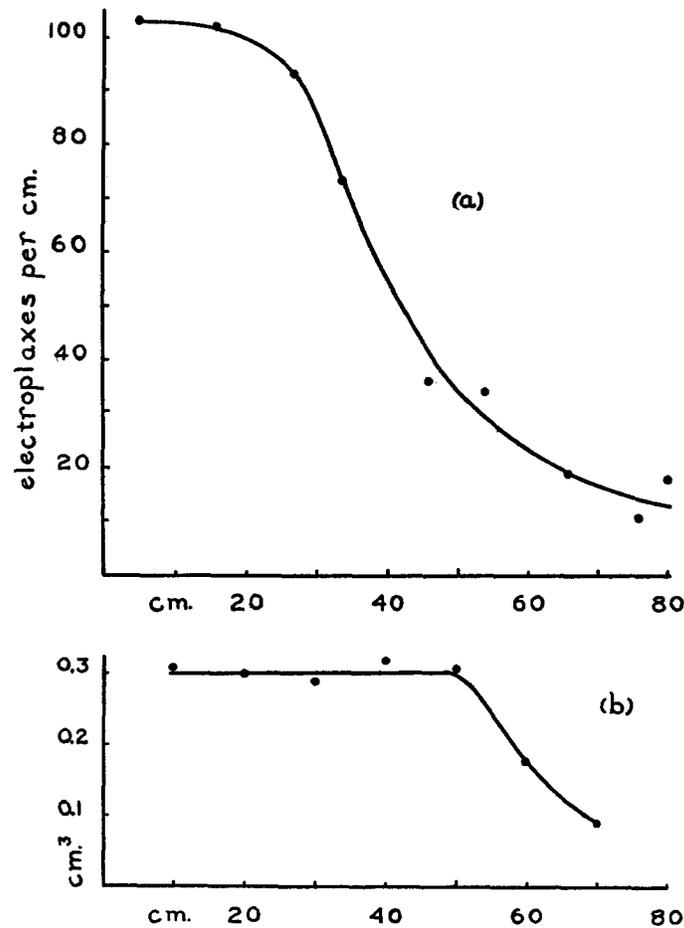


FIG. 2. Variation in packing of electroplaxes in main organs. (a) Number of electroplax layers per cm. (b) Volume of single electroplax layer (cm.³), vs. distance from anterior end (cm.).

slice across the organs one electroplax thick. From Fig. 1 such a slice will have an area decreasing from anterior to posterior, and from Fig. 2 it will have a thickness increasing in the same sense. The similarity of the two figures shows that the volume of the slice is roughly uniform along the organs, the decrease in area toward the tail being offset by the increase in thickness.

This volume, at any point along the organs, is found by dividing the cross-sectional area by the number of electroplaxes per unit length. The plotted points of Fig. 2*b* show volumes found in this way from readings on the smooth curves of Figs. 1 and 2*a*. Over most of the length of the organs the deviations from a uniform volume are no greater than the errors of the measurements. The break in the curve appears at a place on the organs at which their cross-section has diminished from the anterior end until it is comparable with that of the organs of Sachs at the same place. At points a little anterior to this place, the organs of Sachs are of much smaller cross-section than the main organs.

The uniformity in the volume of the single electroplax layer has been observed before (5). The purpose in presenting it again is to introduce a discussion of its relation to the electrical characteristics of the tissue somewhat more detailed and based on the observation of more specimens than that given before.

ELECTRICAL CHARACTERISTICS AT THE PEAK OF THE DISCHARGE

Measurements with Open External Circuit

The simplest of the electrical measurements is that of the peak voltage developed during the discharge between electrodes placed against the skin which covers the organs. A cathode ray oscillograph is used for the measurement. All measurements are made with the fish out of water. As might be expected, the peak voltage depends on the circuit external to the fish and has its greatest value when this circuit is open so that there is no external current. When the "maximum voltage" is mentioned in this paper, the peak voltage with the external circuit open will always be meant. If having the external circuit open prevented any current in the electric organs, then the maximum voltage would be the true open circuit voltage and would therefore be equal to the E.M.F. of the segment of the organs between the electrodes. But, whether the external circuit is open or not, closed circuits must exist during the discharge in the body of the fish. It is certainly to be expected that such circuits will be formed by the electric organs and the adjacent non-electric tissue together. Possibly also there may be closed circuits lying wholly within the electric organs. The current flowing in such circuits will be called the "leakage" current. Its effect is to cause a voltage drop in the organs, so that the maximum voltage will be somewhat less than the E.M.F. Although the leakage current is not directly measurable, there will be described in a later part of this paper a method of making allowance for its effect.

In the discharge of a long segment of the organs, the voltage will begin to decline at the anterior end before it reaches its peak at the posterior end. Thus the maximum voltage developed in such a segment is a little less than the sum of the maximum voltages developed in its parts. But the time lag

in a length of 5 or 10 cm. is too small to have an appreciable effect on the maximum voltage. For the voltage stays near its maximum for a time of the order of 1 msec., and the speed at which the impulse runs along the organs is of the order of 1 m. per msec., being somewhat greater at the anterior end and less at the posterior end (6). The voltage is thus near its peak simultaneously over a length of the order of 1 m. in a fish with organs of that length or more. Therefore, in a segment 5 or 10 cm. long, the maximum voltage developed between its ends may be divided by its length to give the maximum voltage per unit length.

In the observations next to be described, the length of the segment was taken as the distance between the nearer edges of the electrodes, 9 cm. with the larger fish and 5 cm. with the smaller. Fig. 3*a* shows the maximum voltage per unit length plotted against the distance from the anterior end of the organs, with the same fish as the one on which the measurements of Figs. 1 and 2*a* were made. The likeness of the graph of Fig. 3*a* to those of the other two figures is evident.

The maximum voltage per electroplax layer is found by dividing the maximum voltage per centimeter by the number of electroplax layers per centimeter. The values shown by the plotted points of Fig. 3*b* were found in this way from readings made on the curves of Figs. 2*a* and 3*a*. The maximum voltage per electroplax layer decreases from anterior to posterior but has everywhere the order of magnitude of 0.1 volt, a value familiar from studies of biological boundary potentials.

The fish thus far described was 103 cm. in length. Lately, in the course of a comparison of maximum voltage per unit length with concentration of choline esterase, we have made similar measurements on other electric eels (2). With three of these (Nos. 1, 2, and 4 of the paper just cited) the lengths of which were 51, 57, and 114 cm. respectively, both the cross-sectional area and the maximum voltage per unit length were determined at a number of points along the organs. The results of these measurements are shown in Fig. 4, those from fish 1 at the upper right, No. 2 at the upper left, and No. 4 below. Although these fish were so different in size, the proportionality between the cross-sectional area and the maximum voltage per unit length was found with all of them.

The number of electroplax layers per unit length was not determined in these three fish at enough points to provide graphs similar to those of Figs. 2 and 3*b*. For the points at which this measurement was made, the volume of the transverse layer one electroplax thick and the maximum voltage per electroplax layer were computed. The volumes of the single electroplax layer, in cubic centimeters, are shown in parentheses above the points on the graphs to which they correspond. The maximum voltages per electroplax layer are shown in brackets below. The volumes are naturally different for

the different fish but do not vary widely in any one. The maximum voltages per electroplax layer lie within extreme values 0.16 and 0.11 volt for all three fish.

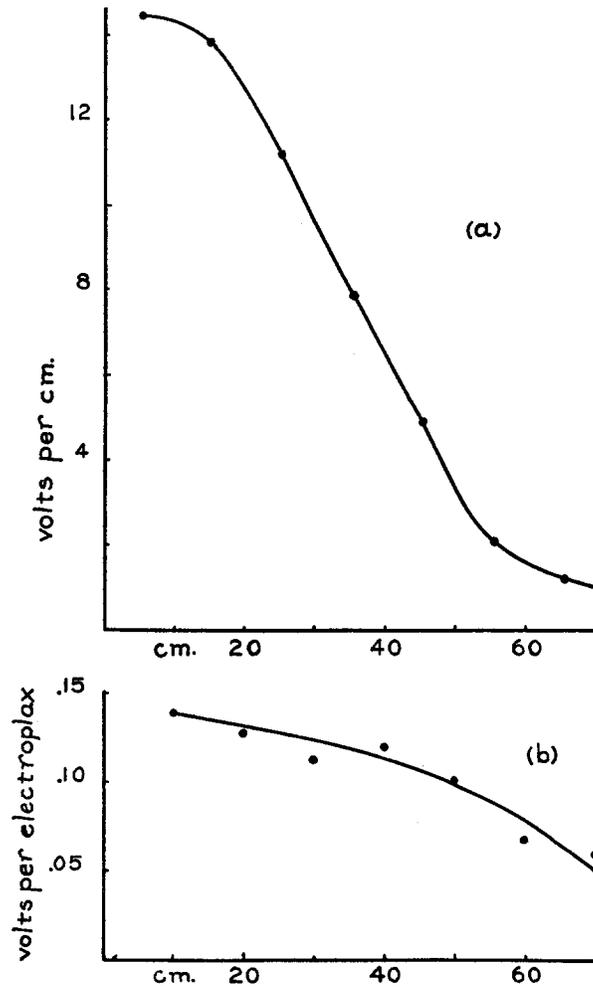


FIG. 3. Maximum voltages in main organs. Maximum voltage (a) per cm., (b) per electroplax layer vs. distance from anterior end (cm.).

Measurement with Closed External Circuit

Current may be drawn from the fish by joining a resistance between the electrodes. The peak voltage may be measured with the oscillograph as before. The resistance being known, the peak current may be calculated by Ohm's law, $V = IR$. When different values of the external resistance R are

used, so that the peak voltage V and the peak current I are both varied, it is found that the graph of V against I , as they are measured when care is taken not to tire the fish, approximates a straight line with both the electric eel

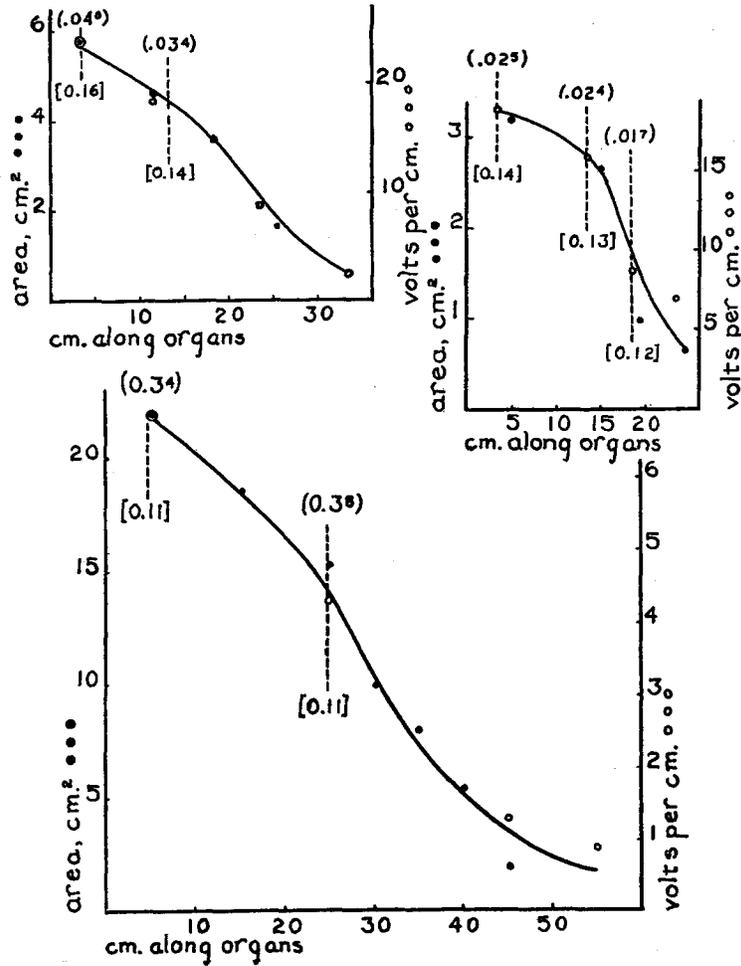


FIG. 4. Dimensions and maximum voltages in three specimens. See text for explanation.

and electric rays (2, 7, 8). This was to be expected if the organs can be described electrically in terms of E.M.F. and ohmic internal resistance. For let E be the E.M.F. and r the internal resistance of the segment of the organs between the electrodes. For the present we neglect the leakage current and assume that the current in the organs is equal to the current I in the external

resistance. On this assumption, the potential difference between the electrodes will be given by $V = E - Ir$, a linear relation between V and I if E and r are constants of the equation.

If, instead of neglecting the leakage current, we should assume only that the aggregate of electric and non-electric tissue can be described electrically as some network of E.M.F.'s and ohmic resistances, a linear relationship between V and I would still be expected. For by Thévenin's theorem of electric networks, any ohmic network will supply current to a resistance joining any two of its points as if it were a single E.M.F. and internal resistance. The equivalent E.M.F. will be equal to the voltage existing between the two points when no current is drawn from the network, and the equivalent resistance will be equal to the resistance of the network between the two points.

The fact that the measured values of peak voltage and peak current show a linear relationship may then be taken as evidence that the organs can be described electrically, at least at the peak of the discharge, as some arrangement of E.M.F.'s and ohmic resistances. It should not be assumed, however, that all the characteristics of the tissue will be shown by a study of its discharge. That the resistance is not ohmic under all conditions is shown by the fact that it acts as a rectifier to an external voltage opposed to and greater than its own (9). The boundary of nerve axon is also rectifying, as was shown by Cole and Baker (10). It is reasonable to expect, as has been generally assumed, that most characteristics of electric and nervous tissue will be similar. Thus, for example, it is likely that under the action of an alternating voltage of high enough frequency electric tissue will show an effective reactance as well as a resistance. For the present we are concerned with finding the electrical characteristics needed to describe the discharge, and for this purpose E.M.F. and ohmic resistance appear to suffice. But the additional assumption that the leakage current is negligible can be taken only as a provisional and crude approximation.

Making this assumption and using the equation $V = E - Ir$, we may use the measured values of V and I to find the value of r , the internal resistance of the segment of the organs between the electrodes. If V is plotted against I as in Fig. 5, r will be the downward slope of the graph. By changing the positions of the electrodes, the resistance of different segments of the organs can be determined. The method of making electric connection with the organs does not seem to be critical in the determination of the internal resistance, as the area of the electrodes in contact with the skin can be varied considerably without materially changing the measured peak voltage. This indicates also that the resistance of the skin is not an important part of the resistance r , for the resistance of the skin would vary inversely with its area in contact with the electrodes.

The resistance of a conductor of length L and cross-sectional area A is

given by $r = \rho L/A$, where ρ is the resistivity of the material of which the conductor is made. In the usual units it is the resistance in ohms between opposite faces of a cube 1 cm. on a side. The resistivity of the electric tissue may be estimated from the values of r obtained from the $V - I$ graph by taking L as the distance between the electrodes and measuring the cross-sectional area of the organs. If the resistivity of the electric tissue were uniform, the values of r for segments of equal length would be expected to increase from anterior to posterior as the cross-section of the organs decreases. Actually, however, the resistance does not show any variation comparable with that of the cross-sectional area. The resistivity must therefore decrease in about

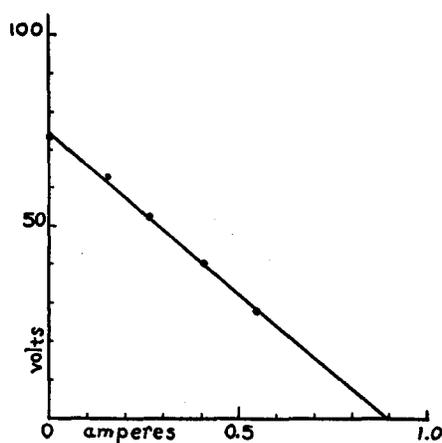


FIG. 5. Evidence of ohmic characteristics of tissue. External peak voltage vs. external peak current with various external resistances joining electrodes on main organs.

the same proportion as the area. It has been mentioned before that the number of electroplaxes per centimeter decreases in about this proportion. Fig. 6 shows the resistivity of the electric tissue of the fish of Figs. 1, 2, and 3, plotted against the number of electroplax layers per centimeter.

It will be seen that the plotted points lie near a straight line through the origin, so that the resistance of unit cube of electric tissue is proportional to the number of electroplax layers of unit area which it contains. The resistance of 1 cm.² of a single electroplax layer has thus a uniform value (about 5 ohms for this fish) whatever the thickness of the electroplax. This is an interesting result since much the most probable explanation for it is that the resistance of the electric tissue, at least at the peak of the discharge, is mainly in the boundaries of the electroplax. In Table I are given values of the resistance of 1 cm.² of single electroplax layer for the other electric eels already mentioned, together with an estimate for the electric ray, *Narcine brasiliensis*,

made from data of Cox and Breder and the lowest value reached during activity by the boundary of the squid giant axon, as given by Cole and Curtis (8, 11). However, only the order of magnitude of the measurements on the electric tissue is significant. The uncertainty resulting from the neglect of the leakage current has already been mentioned. In addition to this, there is the fact that the electroplax boundaries are highly convoluted and may have an area of much more than 1 cm.^2 in 1 cm.^2 of single electroplax layer. For

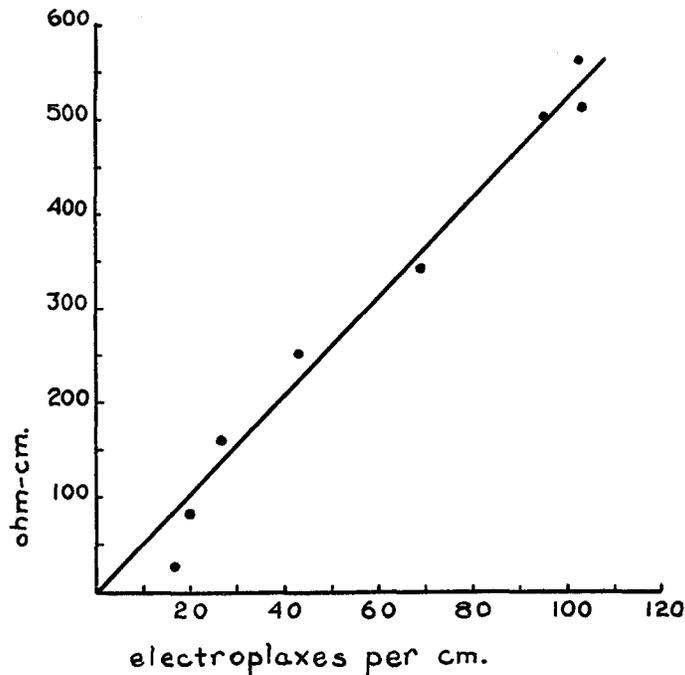


FIG. 6. Uniformity in resistance of unit area of electroplax layer. Resistivity of electric tissue (ohm-cm.) *vs.* number of electroplax layers per cm.

both of these reasons, the true value of the resistance of 1 cm.^2 of electroplax boundary may well be several times greater than the values given above.

On the $V-I$ graph of Fig. 5, the maximum current is given by the point at which the graph meets the horizontal axis. This is the current produced at the peak of the discharge when the segment of the organs is completely short-circuited by a negligible resistance joined between the electrodes. This current may be divided by the cross-sectional area of the organs in the segment between the electrodes to give the maximum current per unit area of cross-section. It is found that the maximum current per unit area is roughly uniform along the organs of any one fish. This follows from the rough uni-

formity, already mentioned, of the maximum voltage per electroplax and the resistance of unit area of the single electroplax layer. In the fish of Fig. 5 the maximum current per unit area had the average value 0.05 amp. per cm.², and for fish 1, 2, and 4 the average values were respectively 0.04, 0.06, and 0.02 amp. per cm.² Values of 0.08 and 0.10 amp. per cm.² were found for two specimens of *Narcine*. An estimate of 0.24 amp. per cm.² has been made for a single specimen of *Torpedo occidentalis* (7). (In the papers from which the figures for *Narcine* and *Torpedo* were obtained, the values of current per unit area given were those for maximum external power. Since maximum external power is attained at half the maximum current, the values given above are twice those given in the papers.)

In the preceding calculations it has been supposed that the right and left organs discharge simultaneously. In *Narcine* and *Torpedo*, where the organs are far apart in the body of the fish, this has been shown to be true. In the

TABLE I
Values of the Resistance of a Layer 1 Cm.² in Area

| Species..... | <i>Electrophorus electricus</i> | | | | | | | <i>Narcine</i> b. average adult | Squid, giant axon |
|---|---------------------------------|------|------|-----|------|-----|-----|--|-------------------------|
| Specimen No..... | 1 | | | 2 | | 4 | | | |
| Distance along organs, cm..... | 3.5 | 13.5 | 18.5 | 3.5 | 13.5 | 5 | 25 | | |
| Resistance of 1 cm. ² , ohms..... | 3.2 | 3.6 | 2.3 | 3.4 | 2.2 | 4.7 | 4.5 | 1.1 | 25 |

eel, the right and left organs are too near together for the use of the test made on the rays. Nevertheless it seems to us probable that the right and left organs of the eel discharge together, because, with the electrodes adjacent to the organs on one side, the oscillographic traces of successive discharges show no difference of a kind to suggest that some of them occur in the nearer and some in the more remote organ. If, contrary to what we suppose, it should be the fact that the right and left organs of the eel discharge separately, then the values given for the resistivity of the tissue and the resistance of unit area of the single electroplax layer should each be halved, and those given for the maximum current per unit area should each be doubled.

ELECTRICAL CHANGES DURING DISCHARGE

Schematic Representation of Electric Tissue

The electrical characteristics thus far discussed are only those at the peak of the discharge. It has been pointed out that these characteristics are related in more than one respect to the dimensions of the electroplax layer. This fact makes it seem reasonable to expect that the electrical changes taking

place during the discharge in each electroplax layer may be at least partly inferred from external electrical measurements on a segment of the intact organ. But before considering how the electrical characteristics of the tissue change during the discharge, it will be desirable to develop a method of allowing in the calculations for the effects of the leakage current.

The actual paths of this current must form an extremely complex network. Every part of the organs, during the discharge, is electrically positive with respect to every posterior part and electrically negative with respect to every anterior part. Also the organs are in electric connection along their whole length with the adjacent non-electric tissue. Hence we should expect, even

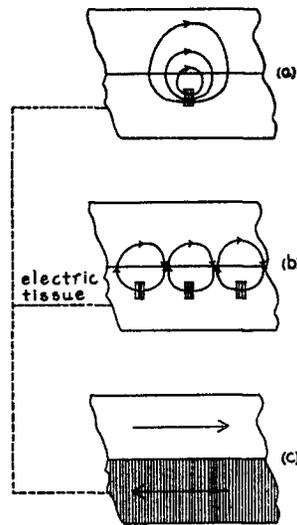


FIG. 7. Schematic representation of the internal currents.

without considering the possibility of closed circuits wholly inside the electric organs, that each small part of the organs, considered apart from the rest, would produce a current not confined to any single path or to any few paths. This is shown schematically in Fig. 7a, in which the shaded area represents the part of the electric tissue producing the currents shown.

Considering a number of such small regions in the organs, we should expect a condition shown schematically in Fig. 7b, where for simplicity only one path of the current has been shown through each small region considered. It is evident here that the currents into and out of the organs will partially cancel one another. If then we consider a continuous segment of the organs, not too near either end and short enough that the electrical characteristics of the tissue can be considered uniform along the length of the segment, it will be a fair assumption to consider the currents laterally into and out of the segment as cancelling one another, leaving only longitudinal currents, one way inside

the electric tissue and the other way outside, in the non-electric tissue, as shown in Fig. 7c.

Each of these currents will be uniform along the segment, and it will therefore be permissible to represent each as following a single path, without transverse connections except at the ends of the segment. It does not appear that there would be any necessary difference in this conclusion if circuits closed wholly within the electric tissue were considered also.

An external resistance connected between the electrodes will provide another path for the current. The presence of this connection may be expected to produce some distortion of the leakage current near the ends of the segment and thus impair the validity of the assumption just made that this current is uniform. But if the external resistance is high, this distortion will probably be slight, and if it is low the external current will be so large in comparison

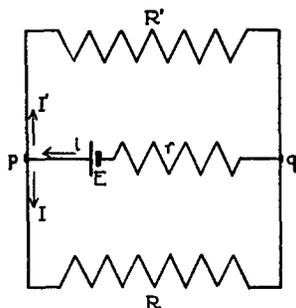


FIG. 8. Proposed equivalent circuit of electric tissue, leakage path, and external resistance. For meaning of symbols see text.

with the leakage current that a moderate error in the assumption made concerning the leakage current will probably not be serious. Consequently in either case we may hope to represent the actual conditions fairly well by the circuit shown in Fig. 8, in which E denotes the e.m.f. of the electroplaxcs in series between electrodes at p and q , r denotes the internal resistance of the electric tissue, R' the resistance of the leakage path, and R the external resistance. Since the discharge is intermittent, it is clear that at least one, if not both, of the quantities E and r , which characterize the electric tissue, must be variable.

At any one instant during the discharge, let the currents in the resistances r , R' , and R be denoted by i , I' , and I respectively. Of these three currents only I , the current in the external resistance, is found directly from the measurements. It is known from the relation $V = IR$, where V is the voltage between the electrodes, as measured with the oscillograph. The voltage is related to the currents in the other two branches by the two equations

$$V = I'R' \quad V = E - ir$$

Since $i = I + I'$, the second of these equations may be written $V = E - Ir - I'r$. If I' is replaced by V/R' , its value according to the first equation, we obtain $V = E - Ir - Vr/R'$, which may be written $V(1 + r/R') = E - Ir$ or, dividing by r , $V(1/r + 1/R') = E/r - I$. It is convenient now to let $1/r + 1/R' = 1/r'$. The new resistance r' is simply the resistance of r and R' in parallel. Making this substitution and multiplying by r' , we obtain

$$V = Er'/r - I'r'$$

This is a linear relation between V and I , provided the resistances are ohmic. To test it, the voltage and current at a given instant in one discharge must be compared with those at the corresponding instants in other discharges through different external resistances. The comparison is made by measurements on oscillographic traces like those shown in Fig. 9.

Method of Measurement

The comparison requires first of all that corresponding instants on the different traces be identified. If the instant at which the discharge starts could be clearly distinguished on the oscillographic traces, corresponding instants would be those at equal intervals after the start. It is evident from the traces shown that the instant at which the discharge starts cannot be precisely determined. But it will also be noticed that a very short while after the beginning there is an interval during which the voltage rises at a nearly uniform rate, as shown by the nearly straight rising branch of the oscillographic trace. Extending this straight portion back until it meets the base line determines a point which may be taken as marking the zero time from which intervals are to be measured.

This procedure is illustrated in Fig. 10, in which one trace from each row of Fig. 9 has been copied. The zero times of the three traces have been found in the manner just described, and the traces have been shifted until the three zeros coincide on the time scale. The ordinates of the traces at 1 msec. give three values of the voltage V , and the quotients of the voltages by the resistances give the corresponding values of the current I . Thus three points are determined on a graph of V against I , for a comparison with the linear equation $V = Er'/r - I'r'$.

Actually in obtaining the results now to be described, measurements made on a number of traces were averaged to determine each point. The traces were obtained in the following way. The fish was removed from the water and placed in contact with two electrodes 10 cm. apart, which were connected to the cathode ray oscillograph. While the fish was made to discharge by light prodding, different resistances were connected between the electrodes, and the screen of the oscillograph was photographed. Five or six exposures were made with the external circuit open and as many with each of the resistances 400, 200, and 100 ohms, and with the oscillograph at a higher gain five or six were made with each of the resistances 100 and 50 ohms. In order to avoid any effect of fatigue on the discharge, the number of discharges was kept within a limit which had been found safe in other observations, and the whole procedure was carried through in the shortest time possible, 2 or 3 minutes.

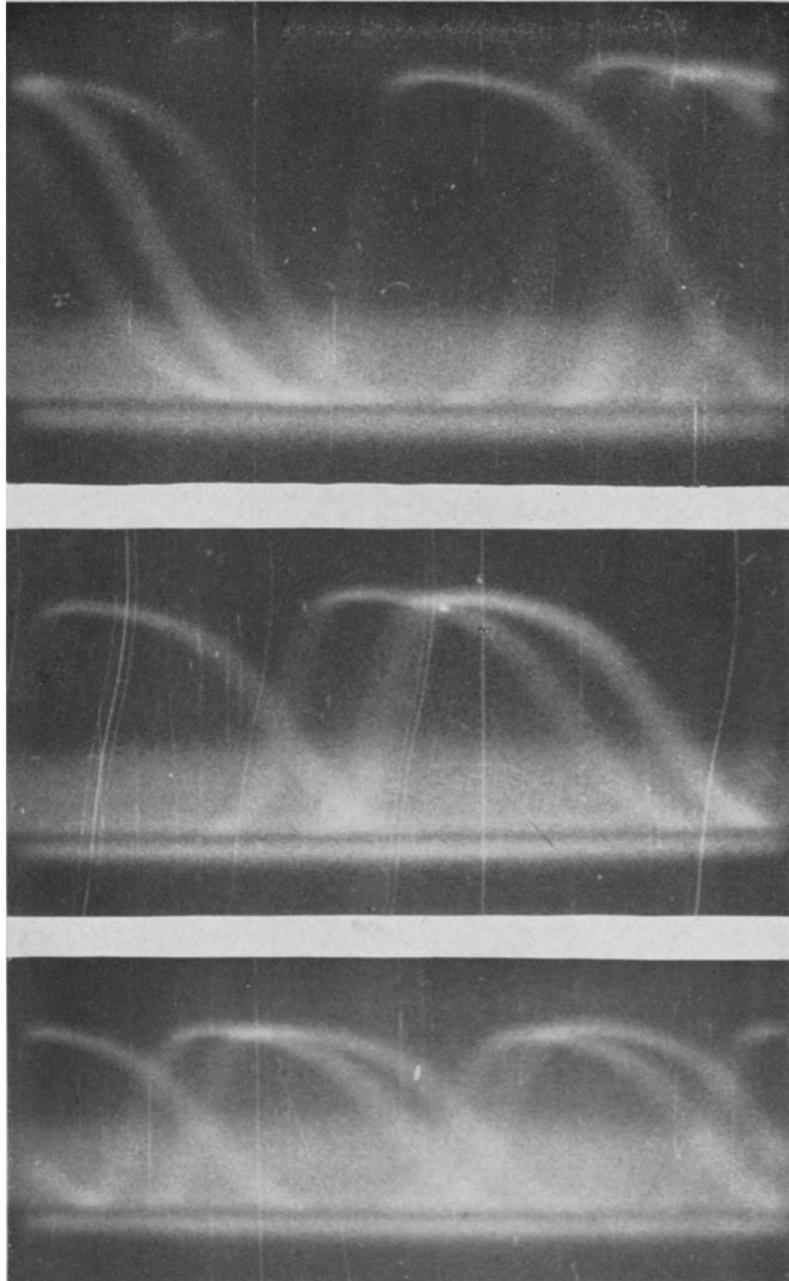


FIG. 9. Oscillograph records of discharge of segment of main organs. External circuit open (top), closed through 200 ohms (middle), through 100 ohms (bottom). For scales of voltage and time see Fig. 10.

To insure that any fatigue, if it did occur, would have no systematic effect on the results of the experiment, the order in which the different resistances were connected to the fish was reversed in alternate series of exposures.

Some of the traces were obscure because of overexposure or excessive overlapping and others were incomplete because the discharge occurred at the beginning or end of the timing sweep of the oscillograph. Of those that were complete and legible on the film a certain number, greater in some series of observations and less in others but about one in six on the average, were very different from the rest either in height or pulse form or more often in both. Most of the traces are quite uniform and the anomalous ones are usually distinguished without any trouble. Their difference is so marked that it once appeared reasonable to suppose that they showed the dis-

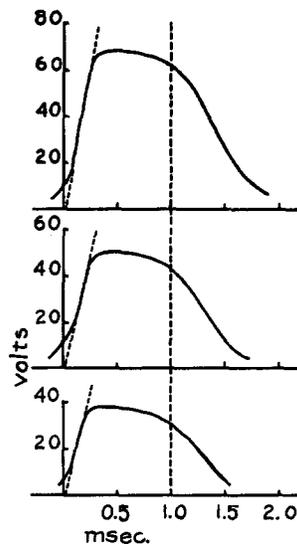


FIG. 10. Tracings from Fig. 9, showing correlation of voltage and time measurements

charges of Hunter's organs, while the regular ones showed the discharges of the main organs alone. But the energy of the anomalous discharges seems to be disproportionate to the size of Hunter's organs, and it appears more likely that they are produced by the same organs as the regular discharges but are modified in some way, perhaps by a lack of synchronization between the discharge in different portions of the organs (5, 9). The traces which were clearly anomalous were not used for the measurement of voltage.

There were 184 usable traces altogether in the six series of observations that were made. Measurements from all but four of these were used in computation. These four were all obtained with one fish, using the oscillograph at high gain and an external resistance of 100 ohms. The peak voltages measured on these traces were much lower than those measured with the same fish and the same external resistance but with the oscillograph at low gain. It seemed probable that the four traces in

question were made with too high a gain for the calibration to be linear and the measurements of voltage were therefore unreliable.

Voltages were measured on each trace at intervals of 0.2 msec., starting at 0.4 msec. from the zero time determined in the manner already described. Measurements were started at 0.4 rather than 0.2 msec. because at the earlier instant they could not be made with any accuracy. This instant falls on the steeply rising part of the trace, where a small shift in the estimated zero time makes a very large change in the measured voltage. At times after 1.4 msec. (after 1.2 with one fish), the voltage was too small for reliable measurement. Thus there were measured generally six values of the voltage during 1 msec. of the discharge. Altogether something more than 1000 measurements were made.

Results

Figs. 11, 12, and 13 show some of the results of three series of observations. The plotted points along each line show, for one value of the time, the values of voltage and current obtained with different values of the external resistance. Each line was fitted to its set of points by the method of least squares. The lines marked (0.4) show measurements at 0.4 msec.; the others show measurements at 1.0 and 1.2 msec.

That the points fit the lines within the uncertainty of the measurement justifies, to this degree of accuracy, the assumption that the electrical behavior of the tissue may be described in terms of E.M.F. and ohmic resistance, not only at the peak of the discharge but at other times as well.

The differences in the slopes of the lines indicate that the resistance of the tissue increases after the peak of the discharge is passed. This agrees with observations made before by another method (9).

It will be noticed that if the three lines are extended to the left of the axis of voltage they come very near to meeting in a point. This is simply explained if it be supposed that the E.M.F. of the tissue and the leakage resistance are constant during the time of the measurements. For it will be recalled that, according to the diagram of Fig. 8, each line is described by the equation, $V(1 + r/R') = E - Ir$. In this equation let $V = E$. Then $I = -E/R'$. Hence if E and R' are constant during the discharge and thus the same for all the lines, the point having coordinates $V = E, I = -E/R'$ will lie on all the lines, which must therefore intersect at this point. It does not seem likely that the near intersection of the lines is an accident resulting from errors of measurement, and the assumption that the E.M.F. and the leakage resistance are at least nearly constant appears to be much the most probable explanation.

The complete results of all six series of measurements appear in Figs. 14, 15, 16, and 17 in a more concise graphical representation obtained as follows. In the equation $V(1 + r/R') = E - Ir$, let $I = 0$ and denote the corresponding value of V by V_0 . We have then $V_0(1 + r/R') = E$. Now use with this

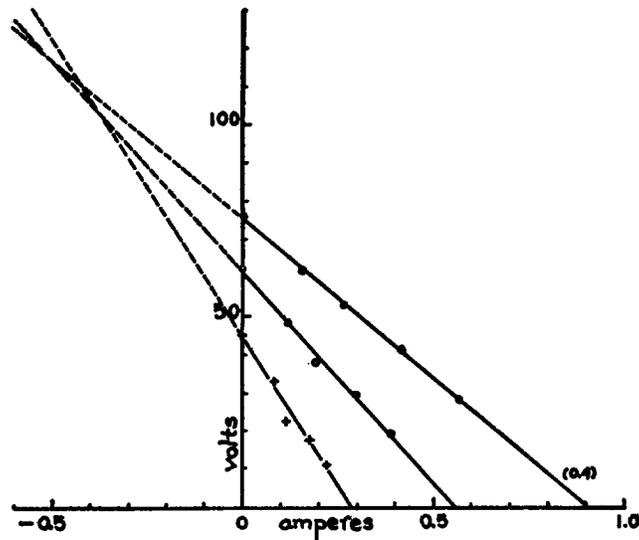


FIG. 11. Evidence of change in resistance of electric tissue and approximate constancy of e.m.f. and leakage resistance during discharge. For explanation see text.

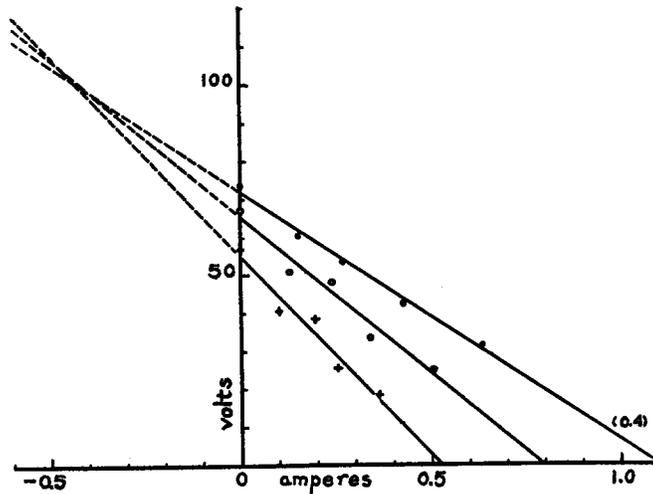


FIG. 12. Resistance and e.m.f. during discharge. Similar to Fig. 11 but another series of observations.

the equation $1/R' = 1/r + 1/R'$ to eliminate r , and we find $V_0 = E - (E/R')r'$. This is a linear relation between V_0 and r' if E and R' are constants.

In reference to a line on the V - I graph of Figs. 11, 12, and 13, V_0 is the

intercept of the line with the axis of voltage and r' is the downward slope of the line. The line is thus completely determined by the values of these two quantities. Therefore if we now employ a new graphical representation with V_0 and r' as coordinates, a single point of the new representation will correspond to a line on the former one. The three black dots along each line in Figs. 14, 15, 16, and 17 represent measurements at 0.4, 1.0, and 1.2 msec., such as are represented by the three lines in each of Figs. 11, 12, and 13. The lines of Figs. 14 to 17 were fitted to these points by the method of least squares. The white dots in Figs. 14 to 17 represent measurements at 0.6, 0.8, and 1.4

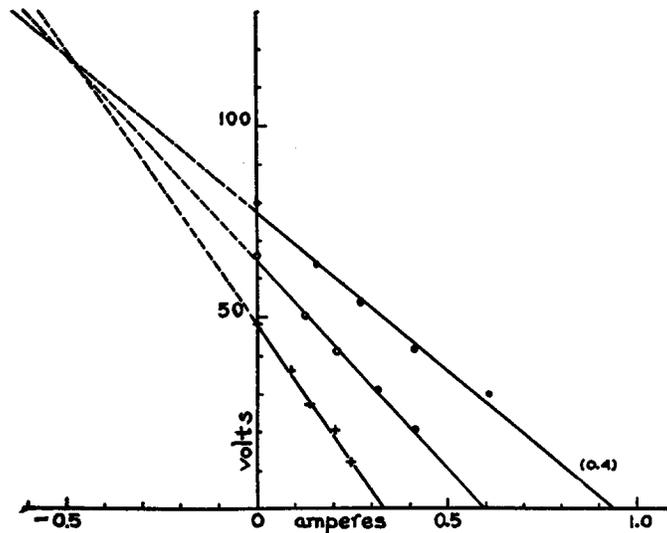


FIG. 13. Resistance and E.M.F. during discharge. Similar to Figs. 11 and 12, but another series of observations.

msec., which were omitted from Figs. 11, 12, and 13 to avoid confusing the figure with too many lines.

In so far as the plotted points of each series fall on a straight line, the measurements support the hypothesis of a constant E.M.F. and leakage resistance. Taking the equation of the line as $V_0 = E - (E/R')r'$ and letting $r' = 0$, we obtain $V_0 = E$. Thus the intercept of the line on the axis of V_0 gives the E.M.F. In the same equation, letting $V_0 = 0$, we obtain $r' = R'$, so that the intercept on the axis of r' gives the leakage resistance.

The plotted points of Figs. 14 to 17 fall, with three exceptions, quite near the lines. The greatest deviation is 6 per cent and the root-mean-square deviation is 1.8 per cent, the three exceptional points being excluded. The exceptional points all represent measurements at 1.4 msec. and all fall far above the line. On the other hand, two of the graphs have points representing

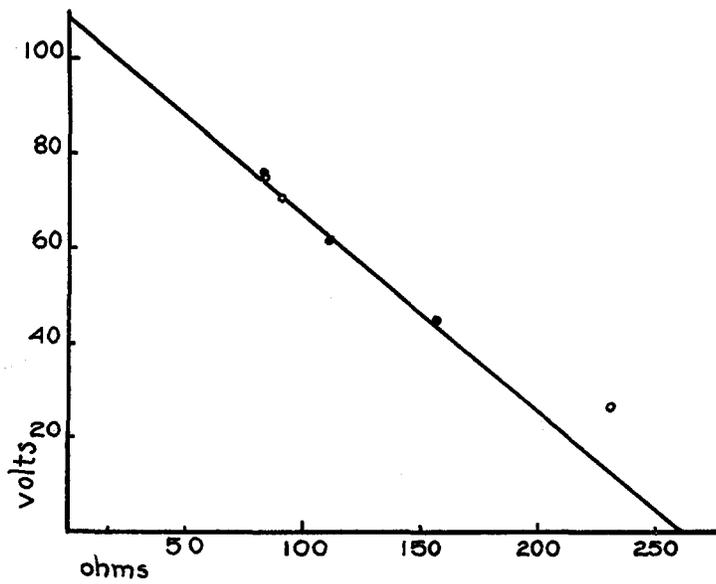
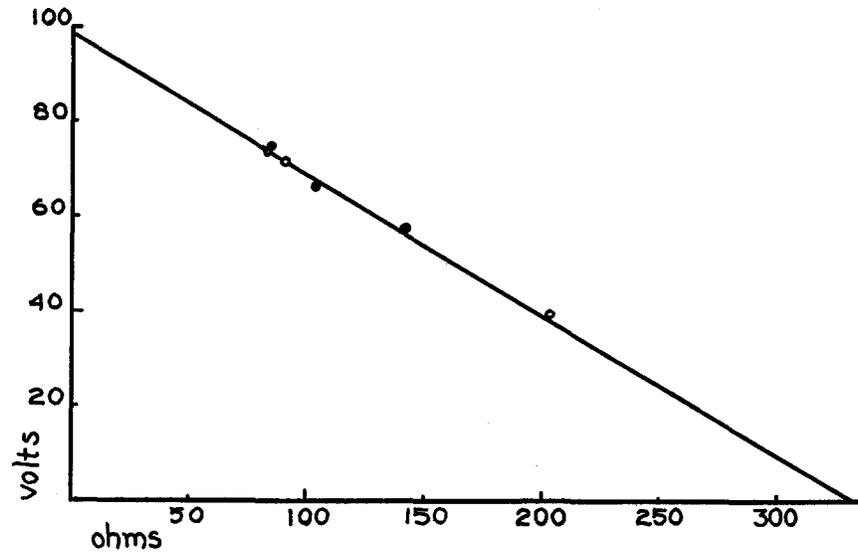


FIG. 14. Resistance and E.M.F. during discharge. Voltage with external circuit open vs. parallel resistance of electric tissue and leakage path. Two series of observations. For explanation see text.

measurements at 1.4 msec. which fall quite near the line, one above and one below. The measurements made on different oscillographic traces at 1.4

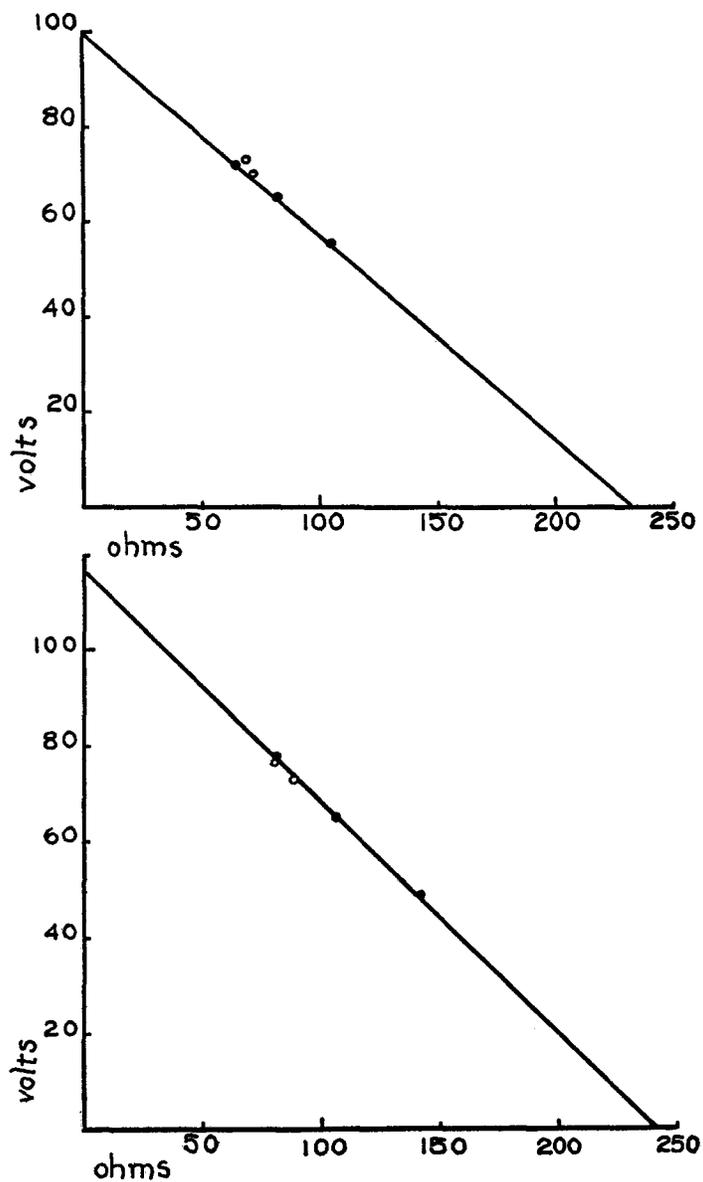


FIG. 15. Resistance and E.M.F. Similar to Fig. 14. Two more series of observations.

msec. show wide variations, and it is possible that the deviations of the exceptional measurements are all accidental. On the other hand, they may be

caused by some electrical characteristic of the tissue of which the diagram of Fig. 8 takes no account and the effect of which becomes important toward the end of the discharge. Our measurements are insufficient to give any safe ground for conjecture on this point.

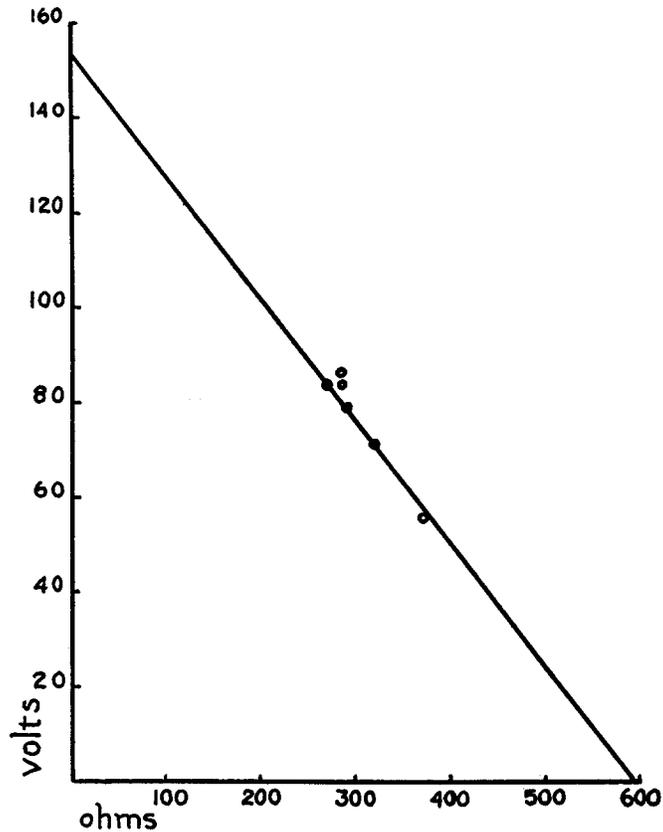


FIG. 16. Resistance and E.M.F. Similar to Figs. 14 and 15. Another series of observations.

In any case it seems clear that the internal resistance of the electric tissue, r in the equations, varies during the discharge. From the values of r' and R' it is easy to calculate, by means of the equation $1/r' = 1/r + 1/R'$, the value of r for each instant of time at which measurements were made. Fig. 18 shows the variation of r with the time, reckoned from the measurements shown in the upper half of Fig. 14.

Although these measurements extend over only a part of the duration of the discharge and do not include any of the time during which the voltage

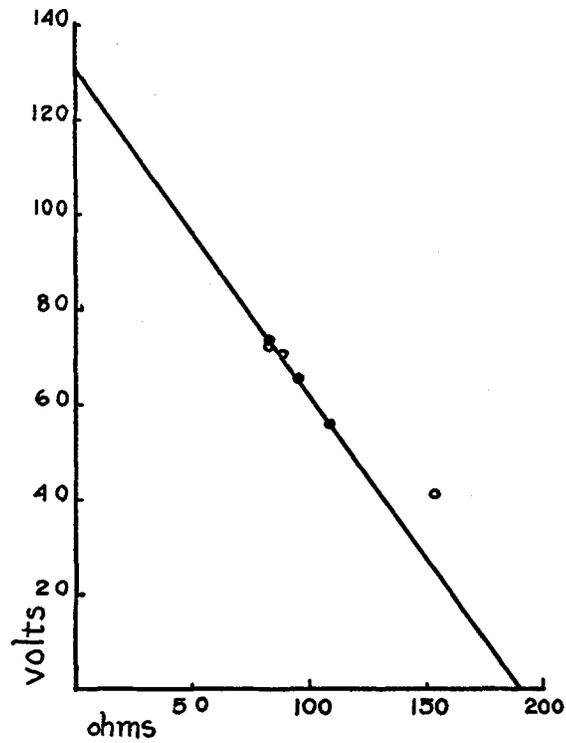


FIG. 17. Resistance and E.M.F. Similar to Figs. 14, 15, and 16. Another series of observations.

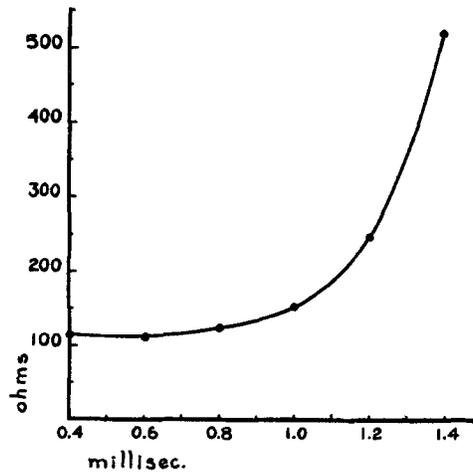


FIG. 18. Variation of internal resistance during discharge. Internal resistance (ohms) vs. time (msec.).

is rising, it seems likely that the variation in resistance is the primary electrical change by which the discharge takes place. According to this view, the E.M.F. is constantly present in the electroplax layer; but, except during the discharge, the resistance of the electroplax boundary is so high that no appreciable current flows and there is thus no appreciable external voltage. The discharge would be started by a very large and rapid drop in the resistance of the electroplax boundary. It would be continued by the resistance remaining briefly at a low value and ended by the resistance increasing to reach again its high initial value.

Electric Energy in Relation to Chemical Change

Since the E.M.F. is apparently constant, at least during the part of the discharge when most of the electric energy is produced, it becomes possible to calculate the total electric energy produced in a single impulse by a given segment of the organs when discharging through a given external resistance. This energy is Eq , where q is the charge passing through the segment of the organs in one impulse. Now $q = \int i dt$, where i is the current in the organs, as before, t is the time and the integration is made over the duration of the impulse. Also $i = I + I' = V(1/R + 1/R')$. Hence it follows that $q = (1/R + 1/R') \int V dt$. Thus the total electric energy is $E(1/R + 1/R') \int V dt$.

The external resistance R is, of course, known. E and R' are the intercepts of the line in the V_0-r' graph, as was pointed out earlier. To evaluate the time integral of V , we have the oscillographic trace, which gives the value of V at each instant of time. The integration can be performed graphically. The part of the total energy which is delivered to the external resistance R is $R \int I^2 dt$ or $(1/R) \int V^2 dt$, the integration being made as before over the duration of the impulse. Values of V^2 are computed from the oscillographic trace, and this integration also may be made graphically. The total energy may thus be compared with the energy released externally.

With an external resistance of 100 ohms, the values found for the ratio of the total electric energy to that released externally are 4, 6, 5, 10, 5, 4: average, 6. In an earlier paper the electric energy delivered to an external resistance of 100 ohms was compared with the energy supplied by the breakdown of phosphocreatine and the formation of lactic acid in the electric tissue during the discharge (4). In one series of fifteen experiments it was found on the average that the energy supplied by the breakdown of phosphocreatine was 4.0 times the external electrical energy. In seven of these experiments, the formation of lactic acid was also determined. In the average of these seven, the energy supplied by the breakdown of phosphocreatine was again 4.0 times the external electric energy, and the energy supplied by this and the formation of lactic acid together was 6.5 times the external electric energy. The

chemical energy of both processes, averaged over the seven experiments, was 44 microcal. per gm. and impulse.

The fish used in the present experiments were some of those used in the former ones, and the electrodes were placed in about the same positions on the electric organs. The average external energy per impulse was about the same in the present experiments as in the former. Therefore the two series of experiments are fairly comparable. The fact that in one series the breakdown of phosphocreatine and the formation of lactic acid supplied 6.5 times the external electric energy, while in the other the total electric energy was estimated to be 6 times the external energy makes it very likely that the chemical changes are sources of the electric energy of the discharge.

If it should turn out that the right and left organs discharge separately and not, as we have supposed, together, the comparison of the chemical and electric energies will not be affected. The values found for both energies per gram and impulse will simply have to be doubled and their ratio will thus be left the same. This follows from the manner in which they were determined. The measured chemical changes were those occurring in known masses of tissue in 1600 discharges, and the changes per gram and impulse were reckoned by dividing the changes per gram by 1600. If only one organ discharges at a time, the number of discharges of the organ from which the tissue was taken would have been only 800, and the true values for the changes per impulse would be twice the computed values.

The measured electric energy, on the other hand, was determined for a single impulse and would not have been affected by a mistake in the number of impulses. But it was determined for the whole mass of discharging tissue included between the electrodes. The energy per gram and impulse was estimated by dividing the energy per impulse by the number of grams of tissue. If only one of the two organs discharges at a time, the number of grams would have been half of that assumed, and the true value of the energy per gram and impulse would be twice the computed value.

SUMMARY

In the main electric organs of the electric eel, the cross-sectional area, the thickness of the electroplaxes, and certain electrical characteristics of the tissue vary widely between the anterior and posterior ends. However, a transverse layer of the organs one electroplax thick has certain characteristics which are roughly uniform along the organs. These are its volume, its maximum voltage, its maximum current per unit area, and the resistance of unit area at the peak of the discharge.

Measurements of the voltage developed by a segment of the organs across different external resistances at different instants during the discharge are all rather well described by representing the segment, with the adjacent non-

electric tissue, as a simple combination of E.M.F. and ohmic resistance. The internal resistance of the tissue varies during the discharge. Its E.M.F. appears to be practically constant, at least during the greater part of the discharge.

Estimates made of the total electric energy show it about equal to the energy supplied by the decrease of phosphocreatine and the formation of lactic acid.

We wish to thank Dr. David Nachmansohn of the College of Physicians and Surgeons, Columbia University, for his helpful discussion. Dr. A. L. Machado of the School of Medicine, University of Brazil, took part in some of the observations and we regret that he could not remain for the completion of the research. We are grateful also to Mr. Sam Dunton, photographer of the New York Aquarium, for his skill and care in the development of the oscillographic traces, and to Mr. Herman F. Beck and Mr. Joseph Puritch for the construction of some of the apparatus, which was made in the Physical Laboratory of New York University at University Heights.

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