

TRANSVERSE IMPEDANCE OF THE SQUID GIANT AXON DURING CURRENT FLOW

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(Received for publication, November 1, 1940)

INTRODUCTION

During the passage of an impulse in Young's squid giant axon preparation (Young, 1936), a considerable increase in the membrane conductance was found but relatively little if any change in the membrane capacity (Cole and Curtis, 1939). The conductance increase was interpreted as a measure of the increase of ion permeability which is commonly assumed to be a part of the nerve impulse.

It is generally believed that when a current flows through a nerve membrane, the ion permeability is increased at the cathode and decreased at the anode. If this is true and the interpretation of the impedance change obtained during activity is correct, there should be an increase in the membrane conductance at the cathode and a decrease at the anode without a change in the membrane capacity during current flow. With these assumptions, an apparent contradiction is then found in the observations during the propagation of an impulse. During the foot of the action potential (before the point of inflection in the rising phase) the simple cable theory requires that the direction of positive current flow be outward across the membrane, or cathodic. This would require an increase of membrane conductance, which was not found. At the point of inflection, where the current flow reverses from outward to inward, there should be a decrease of the membrane conductance to a value less than that at rest. But it was at about this point that the large and rapid increase of the membrane conductance was observed. The first step in resolving these contradictions is to investigate the validity of the assumptions. For this it is necessary to determine the dependence of the membrane conductance upon the direction and magnitude of the membrane current flow in the resting axon.

The polarizing current could be applied suddenly for sub-rheobase cathode

and all anode polarizations, but the results of this procedure might be misleading when excitation and propagation take place at the cathode. Although the nature of the "depolarization" which occurs at the onset of activity is not known, it is often thought of as a breakdown or "relaxation" process. It would not be at all unreasonable, from analogy with non-living systems, to expect that a polarizing current might be able to maintain a depolarization originally set up by excitation. Consequently, to avoid ambiguity, excitation should be avoided by increasing the polarizing current to its maximum value slowly. Then the terminal impedance change could be compared with that obtained after an excitation took place at the sudden make of the current to determine whether or not a depolarization could be maintained and whether or not the precaution of a slow rise was necessary. This question can also be answered, by gradually polarizing the nerve without excitation, and then allowing an impulse initiated at a distance to pass through the polarized region.

After the investigation of these steady effects of polarization, before and after activity, the next step is to trace the time course of the sub-threshold changes at the start of polarization. If we assume that before excitation the membrane has reproducible and reversible electrical characteristics, it should be possible to determine them and so explain the sub-threshold observations. The impedance changes at the site of excitation and during the passage of an impulse through a polarized region are of obvious importance in the quantitative description of the processes of excitation and propagation in nerve. It may be expected, however, that an explanation of these impedance data will itself be a rather complete theory of nerve activity.

Material and Apparatus

A description of the material and apparatus was given in the previous paper (Cole and Curtis, 1939) and only the modifications and extensions required in the present experiments will be given in detail.

Axon, Measuring Cell, and Bridge.—The giant axon in the hindmost stellar nerve of the squid, *Loligo pealii*, was dissected out and placed in the measuring cell. This cell was a strip of insulating material with a groove, *AA* (Fig. 1) 550 μ square, just large enough to accommodate the axon, cut in the top and covered with a glass cover slip. Sea water was circulated past the axon and the whole was usually kept at a temperature of about 4°C. Two platinized platinum impedance electrodes 550 μ square were mounted flush with the sides of the groove and facing each other. The transverse alternating current impedance of the axon was measured between these electrodes over a frequency range from 1 kc. to 500 kc. in a Wheatstone bridge (Cole and Curtis, 1937) with heterodyne, amplifier, and cathode ray oscillograph for detector. The measuring current through the cell was kept as low as possible without undue sacrifice of overall sensitivity, and in all cases the bridge balance was independent of this current.

Polarizing Circuit.—The current, or polarizing, electrodes were spaced as far apart as possible along the length of the axon, to separate the anode and cathode regions of membrane current flow and allow individual investigation of each region. The maximum membrane current density is to be found directly under an electrode and since it is approximately uniform only under a short electrode, the impedance should be measured through one of the polarizing electrodes. The other impedance electrode could then be placed in the extrapolar region for a longitudinal measurement but this involves a second membrane or an inactive end, and, in addition, a rather clumsy theoretical analysis. It is simpler to use a transverse impedance measurement where one-half of the polarizing current enters at each impedance electrode, *E*, through a resistance, *R*, and the total current leaves the measuring cell at the third, distant, electrode as indicated in Fig. 1. The two resistances, *R*, were 10,000 ohms each and this value

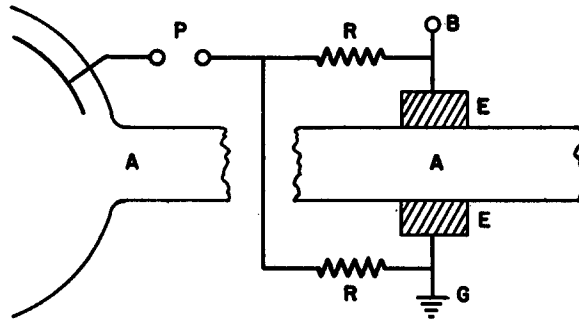


FIG. 1. Circuit for impedance measurements during current flow. Axon was placed in trough *A A* and transverse impedance measurements made between electrodes *E E* by the alternating current bridge connected at *B* and ground, *G*. The polarizing current from source *P* divided and flowed into this trough and axon through the two resistances *R R* and the electrodes *E E*. The current returned through the distant electrode at the left hand end of the trough.

was sufficiently large practically to eliminate differences of current flow in the two paths caused by asymmetries of the impedance electrodes, axon position, and membrane potential. Since a part of the bridge current flows through these two resistances in series, the sensitivity of the measurement of the axon impedance was decreased but this loss was not excessive. An approximately uniform current density under the electrodes was expected because the length of the electrodes, 0.55 mm., was considerably less than the "characteristic length" of about 3 mm. found for this axon (Cole and Hodgkin, 1939). It was found experimentally that a current flow from the impedance electrodes to two remote electrodes, one at each end of the cell, produced the same impedance change as was produced when this same current flowed to a single electrode at one end of the cell. Since this procedure was equivalent to a 50 per cent reduction of the effective electrode length, the polarizing current density in the membrane was essentially uniform in the region where the impedance measurements were made.

The magnitude of the polarizing current was made practically independent of the characteristics of the electrodes and of the nerve, by applying a sufficiently high potential

through a series resistance of 150,000 ohms to the terminals, P . The currents were varied up to a maximum of about 1 milliamper and were measured directly with a meter and also calculated from the resistances and potential.

The current was controlled by the opening of three contacts operated from motor driven cams, and the oscillograph sweep circuit was controlled by a fourth contact. The complete cycle of this contactor was usually repeated at intervals of about 1 second. Sudden on and off currents were easily obtained, and use of a variable shunt condenser gave "exponentially blunted"¹ currents with a range of time constants up to 100 msec. With well platinized impedance electrodes, the effect of the maximum polarizing current on the measured impedance of the cell filled with sea water was less than 0.1 per cent.

EXPERIMENTAL

The first experiments were made with an exponentially blunted polarizing current, followed by an equal and opposite current of the same duration and form, as shown in Fig. 2, to minimize the injury to the axon. For this

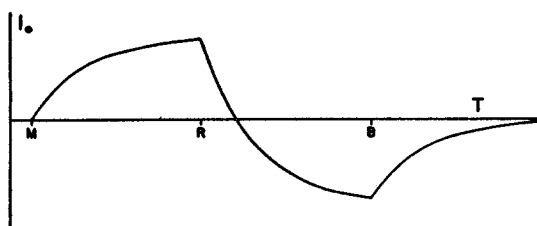


FIG. 2. Schematic drawing of the exponentially blunted current flow, I_0 , applied in the sequence: make, M , reverse, R , break, B , vs. time, T .

the contactor applied the potential to the resistance and capacity polarizing circuit for about 200 msec. in the sequence on-reverse-off. The Wheatstone bridge was first balanced at each frequency without the polarizing current and then a change of the axon impedance caused by current flow gave an output voltage from the bridge and a band on the oscillograph. Typical records are shown in Fig. 3 for 20 kc. and 125μ amp. maximum current. Soon after the cathode make, m in Fig. 3 *a*, there was a short impedance decrease associated with the excitation. Then a slow decrease of the impedance followed, in both *a* and *b* of Fig. 3, as the current increased towards its maximum value. After r , where the reversal was started, the impedance first increased to return to the resting value and then increased still farther to again unbalance the bridge, but in the opposite direction, during the anode current flow. After b the anode current decreased towards zero and the impedance decreased correspondingly to leave the

¹ This term is used in preference to "exponentially rising" to describe the time course given by $1 - e^{-t/T}$ and shown in the initial rise of Fig. 2.

bridge balanced finally. The bridge unbalances were found in the reverse order when the anode was applied first, as is seen in Fig. 3 *c*, and a double excitation took place at the reversal. The final magnitudes of the impedance changes at the cathode and anode are the same, whether the cathode (Fig. 3 *a* and *b*) or anode (Fig. 3 *c*) was applied first. Within the limit of sensitivity, for all frequencies and currents, the change of impedance at the cathode was a decrease from the resting value and that at the anode, an increase. For this axon, 125 μ amp. with a time constant of 50 msec. gave excitation as shown in Fig. 3 *a*, and with an increase of the time constant to 80 msec. the same current was subthreshold (Fig. 3 *b*). It is apparent that the final impedance change was not appreciably altered by activity. As might then be expected, it was found that near rheobase, with suddenly applied polarizing current, the steady value of impedance change was independent of excitation, as seen in Fig. 4. In general, whether the current reached its maximum value very abruptly, or very slowly, the final change of impedance was the same. Also when a distantly initiated impulse was sent through the polarized region after the impedance change during current flow had become constant, the impedance would decrease during the passage of the impulse and then return to the previous level. We thus have evidence that the steady state effect of the polarizing currents employed is not altered by excitation. Consequently the use of exponential blunting to avoid excitation was unnecessary and sudden makes and breaks were subsequently used.

After the direct-reverse polarizations described, the impedance required several seconds to return completely to the resting value, irrespective of whether cathode or anode was applied first. This effect was entirely a result of the anode polarization and was not reduced by an equal cathode polarization either before or after. Since reversal technique apparently did not materially improve the survival of the axons, it too was an unnecessary complication and was abandoned in favor of the simple on and off polarizations, as shown in Fig. 4.

Having found a change in the transverse impedance during polarization, the next step was to determine which component of the axon was responsible for it. The procedure was the same as that used for the analysis of the impedance change during activity (Cole and Curtis, 1939) with the advantage that we are here dealing with something more closely approximating a steady state. At each frequency, the bridge was balanced to give the resting parallel resistance, R_p , and capacity, C_p (Cole and Cole, 1936; Cole and Curtis, 1937). The polarizing current was then applied for intervals long enough to allow the impedance change to reach a steady value

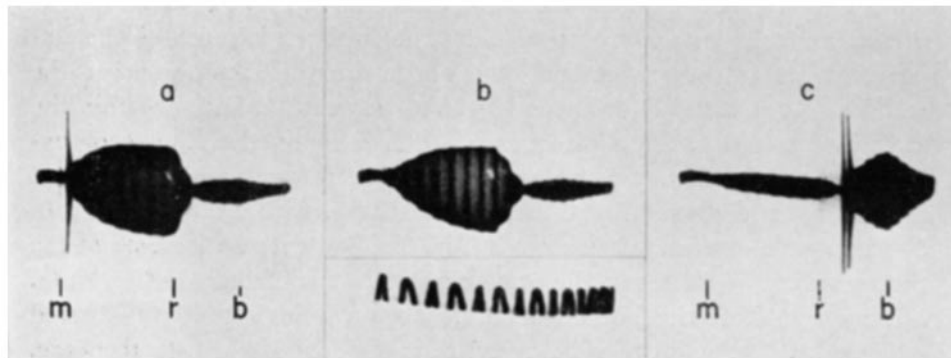


FIG. 3. Oscillograph records of bridge unbalance at 20 kc. caused by make, *m*, reverse, *r*, and break, *b*, sequence in exponentially blunted current flow of $125 \mu\text{amp}$. (a) Cathode first, time constant 50 msec., showing excitation near beginning. (b) Cathode first, time constant 80 msec., sub-threshold. (c) Anode first, time constant 80 msec., showing double excitation at reversal. Exponential time scale indicated by 50 cycle timing wave below. Impedance changes at cathode, -2 per cent; anode, $+0.6$ per cent, determined by calibration.

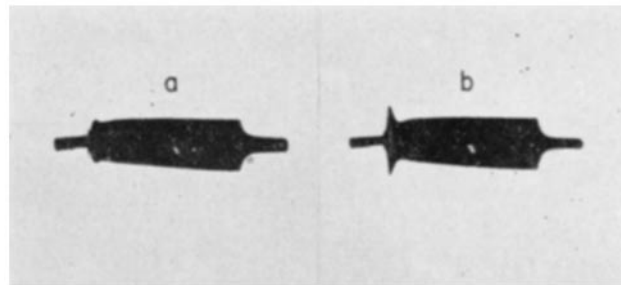


FIG. 4. Oscillograph records of bridge unbalance at 20 kc. caused by sudden make and break of cathode current flow. (a) Sub-threshold response for current just below rheobase. (b) Threshold response for current just above rheobase. Initial maximum is propagated.

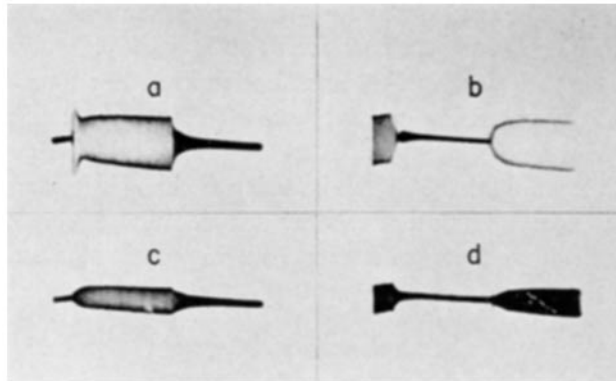


FIG. 5. Oscillograph records of bridge balance and unbalance at 20 kc. during current flow of $63 \mu\text{amp}$. Cathode, (a) with bridge balanced at rest and (b) balanced during current flow. Impedance decrease, 2.0 per cent. Anode, (c) with bridge balanced at rest and (d) balanced during current flow. Impedance increase, 1.05 per cent.

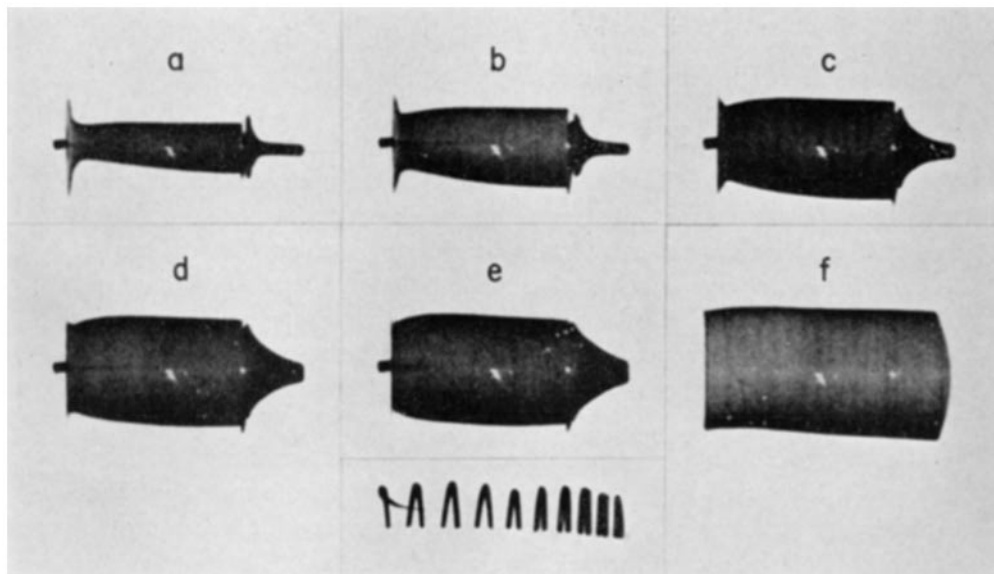


FIG. 6. Oscillograph records of bridge unbalance at 20 kc. caused by cathode current flow. Currents in μamp . are; (a) 105; (b) 210; (c) 315; (d) 420 and (e) 527. Transient impedance changes are caused by excitation under the impedance electrodes at the make, and by excitation propagated from the distant anode at the break. Calibration (f) is a 7.7 per cent impedance decrease. Maximum bridge unbalance during passage of a distantly initiated impulse without current flow (not shown) was -4.3 per cent. Timing wave, 100 cycles.

(Fig. 5 *a* and *c*). The bridge was then rebalanced for this steady value as shown in Fig. 5 *b* and *d*, to give new values of R_p and C_p .

The bridge balance usually could not be found in less than four or five applications of the polarizing current, and with large currents this process might cause irreversible changes. After sufficient bridge data had been taken to establish the nature of the impedance change, its dependence on the polarizing current was more satisfactorily obtained from oscillograph records of the bridge unbalance during a single polarization and a calibration as shown in Fig. 6.

Calculations and Results

The observed values of parallel capacity, C_p , are corrected for the polarization capacity of the electrodes and static capacity of the measuring cell (Cole and Cole, 1936; Cole and Curtis, 1937). The equivalent series resistance, R_s , and reactance, X_s , are then calculated from the parallel resistance, R_p , and capacity, C_p , by the equations

$$R_s = R_p / (1 + R_p^2 C_p^2 \omega^2), \quad X_s = R_p^2 C_p \omega / (1 + R_p^2 C_p^2 \omega^2)$$

where $\omega = 2\pi$ times the frequency.

The values of R_s and X_s are then plotted as abscissae and ordinates to give the complex impedance locus (Cole, 1928, 1932). The loci shown in Fig. 7 are for an unpolarized and a cathodically polarized axon. It will be seen that the membrane phase angle and the infinite frequency resistance are unaltered by current flow. The impedance variation at a single frequency for a range of anode and cathode polarizing currents is shown in Fig. 8. These data indicate that the membrane capacity is practically unaltered and that the impedance change during polarization may be completely explained by a change of membrane conductance (Cole and Curtis, 1938).

The change of membrane conductance, ΔG , for a single value of polarizing current is computed from the extrapolated infinite frequency specific resistance, r_∞ , and the extrapolated zero frequency specific resistances, r_0 , for the unpolarized axon, and \bar{r}_0 for the polarized axon, by (equation 6, Cole and Curtis, 1938)

$$\Delta G = \frac{1}{a} \cdot \frac{\bar{r}_0 - r_\infty}{r_0^2 - r_1^2} \cdot \frac{\bar{r}_0 - r_0}{\bar{r}_0 - r_\infty}$$

where a is the radius of the axon, and r_1 is the specific resistance of the medium.

The data shown in Fig. 7 give $\Delta G = 0.03 \text{ ohm}^{-1} \text{ cm.}^{-2}$ for a cathode

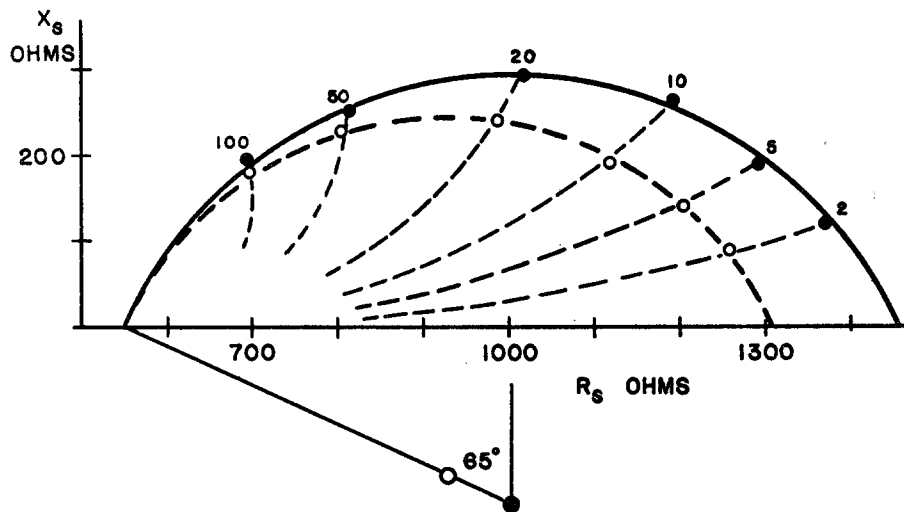


FIG. 7. Transverse impedance locus, series resistance, R_s , vs. series reactance, X_s , for axon at rest (●), and during cathode current flow of $125 \mu\text{amp.}$ (○). Frequencies are indicated in kilocycles. The light dotted lines represent the theoretical paths of the impedance at each frequency for a change of membrane conductance.

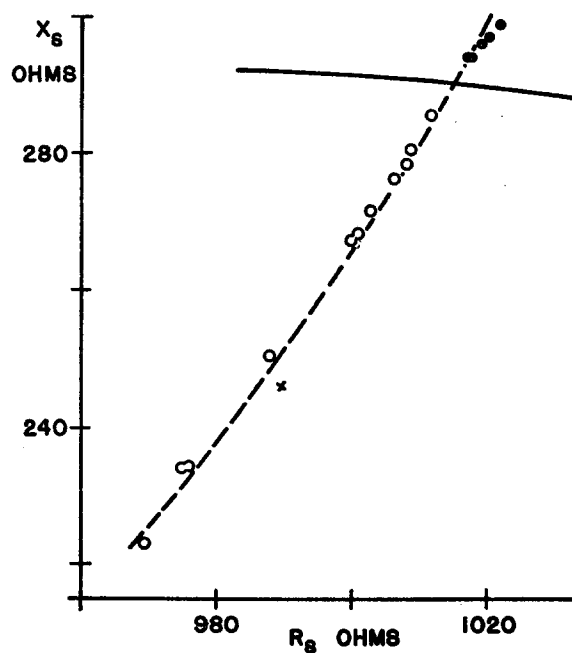


FIG. 8. Transverse impedance locus, series resistance, R_s , vs. series reactance, X_s , at 20 kc. during current flow. (○), Cathode currents up to $250 \mu\text{amp.}$, (●), anode currents up to $63 \mu\text{amp.}$ The solid line is portion of the locus for frequency variation and resting axon. The dotted line is a portion of the theoretical locus for constant frequency and a variation of the membrane conductance. (x), maximum impedance change during passage of a distantly initiated impulse.

polarizing current of 125 $\mu\text{amp.}$ and three other axons give values for ΔG of 0.017, 0.026, and 0.033 $\text{ohm}^{-1} \text{cm.}^{-2}$

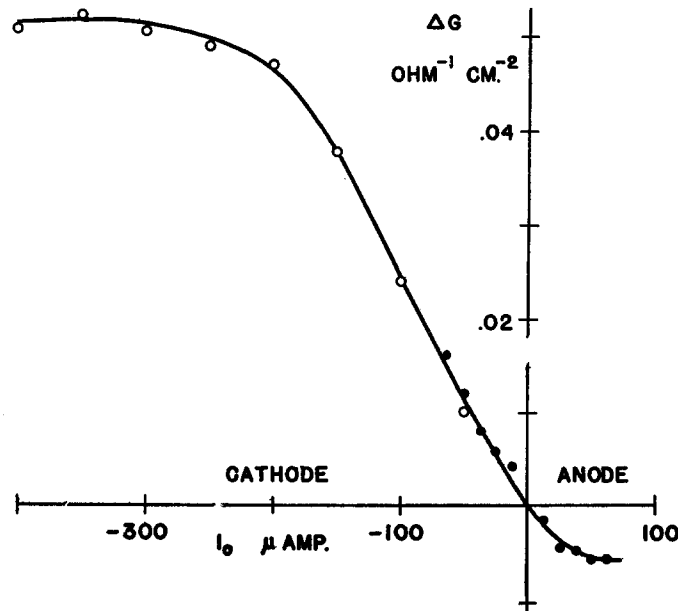


FIG. 9. Change of membrane conductance, ΔG_4 , vs. total current flow, I_0 , from two experiments on the same axon.

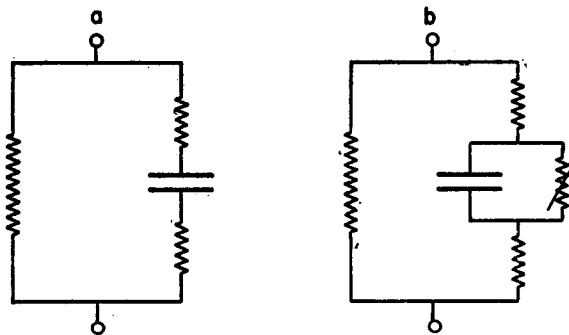


FIG. 10. Equivalent circuits for transverse impedance of axon. (a) Theoretical circuit neglecting membrane conductance. (b) Theoretical circuit with a variable membrane conductance depending upon current flow.

The variation of ΔG with polarizing current is usually obtained from data at a single frequency. The impedance for each value of the polarizing current may be extrapolated to zero frequency and the conductance

change calculated as above, but the impedance change is usually sufficiently small to be proportional to the conductance change (Cole and Curtis, 1939). The impedance change is then computed by

$$|\Delta Z| = \sqrt{(\Delta R_0)^2 + (\Delta X_0)^2}$$

or from photographic records, and $\Delta G = -K|\Delta Z|$, where the factor of proportionality, K , is obtained from one or two extrapolations. A curve of ΔG vs. I_0 (Fig. 9) shows values obtained by both methods and is typical of data on eleven axons.

DISCUSSION

To justify the interpretation of the observed impedance change on polarization as a change of membrane conductance, we proceed as before (Cole and Curtis, 1938). The circular path followed by the impedance of the resting fiber as the frequency is varied, seen in Fig. 7, and called the resting locus, is the characteristic result of many biological impedance measurements. On the assumption of a negligible membrane conductance we may calculate from theory (Cole and Curtis, 1936) the equivalent circuit shown in Fig. 10 *a*, where the condenser represents the capacity of the axon membrane. If the membrane capacity *alone* were to change, the impedance at each frequency would merely move along the resting locus; if the resistance of the axoplasm varied, only the infinite frequency extrapolation would be altered; and changing either the volume of the cell or the resistance of the sea water would vary both the infinite and zero frequency extrapolations. Since Figs. 7 and 8 do not allow any single one of these possibilities, we turn to a variation of the membrane conductance as indicated in Fig. 10 *b*. It has been shown (Cole and Curtis, 1938, 1939) that with a variation of this conductance alone, the impedance would follow a circular arc tangent to the resistance axis at the infinite frequency extrapolation. This is seen to be approximately true at each frequency in Fig. 7 and on an enlarged scale at 20 kc. in Fig. 8, it is found to represent the data to within the limits of experimental accuracy. We are thus entitled to conclude from these data that the impedance change during polarization may be interpreted as a change of the membrane conductance alone, and that there is an increase of the membrane conductance at the cathode and a decrease at the anode. When we assume that the membrane conductance is proportional to the ion permeability of the membrane, the results demonstrate an increase of permeability at the cathode and a decrease at the anode.

It will be noticed in Fig. 8 that the point of maximum impedance change

during the passage of a distantly initiated impulse is close to the theoretical locus but does not lie on it. This is the type of departure found in the previous work (Cole and Curtis, 1939) and was believed then to be caused by the amplifier characteristics. This hypothesis has been supported, although not yet proven, by further work, and even if it is not valid, the difference between this aspect of cathode polarization and propagated activity is very slight.

On the basis of the local circuit theory of excitation and propagation, at least a part of the membrane conductance increase during activity may be a result of membrane current flow, but in the previous discussions (Cole and Curtis, 1938, 1939) the implications of this possibility were avoided. Since a membrane conductance change is brought about by current flow and independently of excitation, it is now necessary to consider the method of measurement more carefully. As a result of a current flow, i , the potential difference across the membrane is altered in some way by an amount, v . When $v = Ri$ the membrane obeys Ohm's law and R is its resistance. The alternating-measuring current, i_a , and the direct-polarizing current, i_d , were applied simultaneously in these experiments and the resulting alteration of the potential difference across the membrane at any time depends upon the instantaneous sum of these two currents, so $v = f(i_d + i_a)$. If now the maximum value of the conduction component of the alternating current, i_a , is small compared to the direct current, i_d , we have by Taylor's expansion, approximately

$$v = v_d + v_a = f(i_d) + \frac{df(i_d)}{di_d} \cdot i_a$$

where the part of the potential difference caused by the polarizing current is v_d and by the measuring current is v_a . Since we are considering only the conduction component of the measuring current we have

$$v_a = \frac{df(i_d)}{di_d} \cdot i_a = \left(\frac{dv}{di} \right)_{i=i_d} \cdot i_a = r(i_d) \cdot i_a$$

where r is the "variational" resistance of the membrane as measured by a small alternating current. If now the membrane obeys Ohm's law, $v = ri$, we have $v_d = ri_d$; $v_a = ri_a$, and r is independent of the current. In graphical form, for Ohm's law, we have a straight line relation between the current and voltage and the variational resistance, or the slope of the line, remains unchanged for all values of current. In the present case, r , or the slope, depends upon the current, i , and Ohm's law certainly is not valid except as an approximation for the small variations of current which we have applied by the bridge.

Since we have now found that the membrane does not follow Ohm's law, some specifications of its conductive properties must be given in place of the resistance. The most obvious possibility is the potential difference as a function of the current which is obtained by the integration

$$v = f(i) = \int_0^i r(i) di,$$

for both anode and cathode. Our present data, however, only give changes of the membrane conductance such as Fig. 9 and it is necessary to have the resting conductance before the integration can be carried out. The value of 1000 ohm cm.² obtained by other measurements (Cole and Hodgkin, 1939) could be used, but there is another difficulty. The polarizing membrane current density in the region between the impedance electrodes is also needed, and must be calculated from the total polarizing current. This may be done easily on the basis of the simple cable theory, if a constant membrane resistance can be assumed, but the process is quite tedious for the present problem where this assumption cannot be made. Since these results will be very dependent upon the value assumed for the resting conductance and the information may be obtained more directly from another type of experiment (Cole and Curtis, 1941), the calculations have not been carried out. However the general form of $f(i)$, or the v vs. i curve, is quite apparent. At the origin its first derivative, or slope, is given by the resting resistance, and on the anode side this slope increases with increasing current until a large limiting slope is reached. On the cathode side, the slope continually decreases until a small limiting slope is obtained for large currents. Then for a potential applied across the membrane with the anode outside, the current flow will be less than for the same potential with the cathode outside. It is then perfectly obvious that the axon membrane not only acts as a rectifier but probably also as a rather efficient rectifier.

Returning to the conductance change, it is seen that the maximum increase under the cathode (Figs. 8 and 9) is of the same order of magnitude as that found during the passage of an impulse. This conclusion may be of considerable significance, but it should not be emphasized at the present time because the cathode polarization currents necessary to give the maximum conductance change were used in only a few experiments. The maximum decrease of conductance at the anode in Fig. 9 is about 0.005 ohm⁻¹ cm.⁻² and this is close to the average value found for four axons. If the resting membrane resistance were 200 ohm cm.², corresponding to a conductance of 0.005 ohm⁻¹ cm.⁻², such a change would mean that the membrane becomes non-conducting under the anode and if the resting resistance

were greater than 200 ohm cm.² and, consequently, the conductance less than 0.005 ohm⁻¹ cm.⁻², the resistance calculated during current flow would be negative. Since we are not prepared to deal with the latter concept, we should conclude that the resting resistance was less than 200 ohm cm.². This is, however, much lower than the values of 400 to 1100 ohm cm.² obtained by longitudinal measurements (Cole and Hodgkin, 1939), and no reason can be given for this discrepancy. The axons used for the transverse measurement were apparently in as good condition and survived at least as well as those used for the longitudinal measurements. The types of analysis used for the interpretation of the data are very dissimilar in the two cases, but no fundamental errors of assumptions or derivation have as yet been uncovered. It is felt, at present, that this disagreement is probably not a serious matter and that the results may be taken to indicate a very low limiting conductance under the anode.

On the basis of the present data, any discussion of the mechanisms of excitation and propagation is little more than speculation, but attention may be called to a few observations. One of these is the oscillation of the impedance change seen in Fig. 4 *a*, just below threshold. This is a characteristic of the responses at the cathode, down to about half threshold, and is not found at any anode polarization. There is then the further observation that the first maximum of this oscillation clearly becomes the all-or-nothing response at threshold (Fig. 4 *b*).

The change of membrane conductance has been determined as a function of the current in the steady state, but we have no evidence at present to indicate that this relation between current flow and membrane conductance remains unaltered during excitation and recovery. However, let us assume for the moment that with these data we may calculate the current flow through the rectifier element from the conductance change during the passage of an impulse. There is no change up to the point of inflection of the rising phase of the action potential. This corresponds to no current flow through the element and requires that the change of membrane potential difference occur elsewhere in the membrane. Such a conclusion seems reasonable and can probably be verified by a careful consideration of the conductance change after the application of a polarizing current. On the other hand, the increased conductance after the point of inflection would require an outward current flow in the rectifier element during all of the time that the total membrane current flow is inward and this will involve more detailed assumptions. Indeed from the steady state characteristics one would say that the only current flow through this element during the entire action would be outward, which would correspond to a net transport

of positive ions outward across the membrane. This is in the proper direction to recharge the membrane during the recovery phase and might lead us to conclude that the conductance increase is concerned primarily with recovery. Such a conclusion would agree with the observation that an axon nearly always failed to conduct soon after the impedance change during the passage of an impulse became too small to measure. However, these conclusions are not justified unless it can be shown that during excitation and recovery the dependence of the membrane conductance on current is the same as for a constant current flow.

SUMMARY

The change in the transverse impedance of the squid giant axon caused by direct current flow has been measured at frequencies from 1 kc. per second to 500 kc. per second. The impedance change is equivalent to an increase of membrane conductance at the cathode to a maximum value approximately the same as that obtained during activity and a decrease at the anode to a minimum not far from zero. There is no evidence of appreciable membrane capacity change in either case. It then follows that the membrane has the electrical characteristics of a rectifier. Interpreting the membrane conductance as a measure of ion permeability, this permeability is increased at the cathode and decreased at the anode.

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