NATURE OF THE ACTION CURRENT IN NITELLA

VI. Simple and Complex Action Patterns

By W. J. V. OSTERHOUT

(From the Laboratories of The Rockefeller Institute for Medical Research)

(Received for publication, April 15, 1946)

Successive action curves in *Nitella* may be almost or quite identical in which case the pattern may be called simple. Otherwise it may be regarded as complex.

A simple pattern[1] is shown in Fig. 1. The nature of these action curves has been discussed in previous papers.[2, 3]

An example of a complex pattern is seen in Fig. 2 which shows diagrammatically a series of changes in potential.[4]

These potentials appear to be chiefly diffusion potentials due to KCl and for convenience the effect of other electrolytes may be neglected in the discussion.

There is a potential at the outer non-aqueous protoplasmic surface, X. This potential may be called P_X. At the corresponding inner non-aqueous protoplasmic surface, Y, there is a potential which may be called P_Y. Between these two surfaces is the aqueous protoplasm, W.

[1] The experiments were made on *Nitella flexilis*, Ag., using the technique described in former papers (Hill, S. E., and Osterhout, W. J. V., *J. Gen. Physiol.*, 1937–38, **21,** 541). Regarding the amplifier see the reference just cited. In all cases two spots were recorded which were connected to a spot at the end of the cell and any changes at the latter spot could be detected because they would cause simultaneous changes at the two recorded spots. In all cases the action curves are spontaneous; *i.e.*, no stimulus is applied from without.

There was no indication of injury in these experiments.

The cells, after being freed from neighboring cells, stood in the laboratory at 15°C. ± 1°C. in Solution A (*cf.* Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*. 1933–34, **17,** 87) for several days. They belonged to Lot B (*cf.* Hill, S. E., and Osterhout, W. J. V., *Proc. Nat. Acad. Sc.*, 1938, **24,** 312).

[2] Osterhout, W. J. V., *J. Gen. Physiol.*, 1934–35, **18,** 215; 1943–44, **27,** 61. Hill, S. E., and Osterhout, W. J. V., *J. Gen. Physiol.*, 1934–35, **18,** 377; 1938–39, **22,** 91. Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1934–35, **18,** 499.

[3] This form of action curve is frequently encountered in simple patterns. The quick action curves seen in the remaining figures in this paper are observed during recovery when there is as a rule more KCl in W than when recovery is complete. This increased amount of electrolyte in W probably tends to promote quick action curves as we find that soaking the cell in 0.01 M NaCl and in other salts tends to produce quick action currents. *Cf.* Hill, S. E., and Osterhout, W. J. V., *J. Gen. Physiol.*, 1938–39, **22,** 91. Osterhout, W. J. V., *J. Gen. Physiol.*, 1942–43, **26,** 65.

[4] Regarding this see Osterhout, W. J. V., *J. Gen. Physiol.*, 1943–44, **27,** 61.

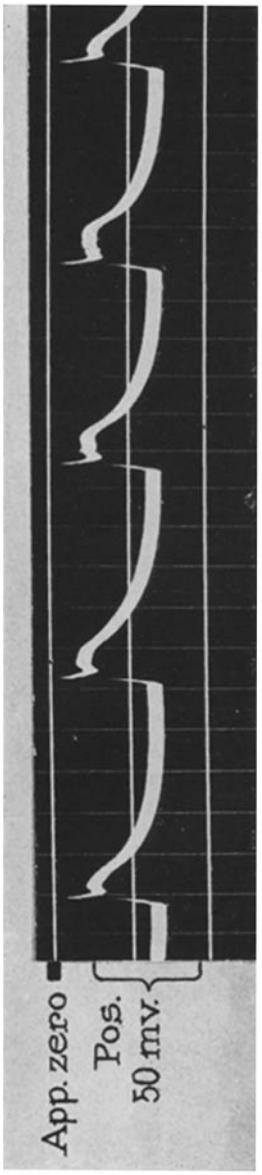

FIG. 1. Successive similar action curves. The spot recorded was in contact with 0.009 M NaCl + 0.001 M KCl and was connected to a spot in contact with 0.01 M KCl which kept the P.D. constant approximately at zero. Since the location of the zero is not exact the figure is marked "App. zero."

The spikes rise almost to the zero line.

This form of curve is frequently encountered in simple patterns.

The cell was freed from neighboring cells and kept at 15°C. ±1°C. in Solution A for 40 days. An hour before the record was made the cell was placed in 0.009 M NaCl + 0.001 M KCl at 21°C.

Heavy time marks 5 seconds apart.

The potential P_Y is chiefly due to diffusion potential of KCl across Y. On one side of Y in the sap there is about 0.05 M KCl and on the other in W a lower concentration of KCl (in the complete resting state it appears to be very low). Hence we may write (for 25°C.)

$$P_Y = 59\frac{u_K - v_{Cl}}{u_K + v_{Cl}} \log \frac{a_s}{a_w}$$

where u_K and v_{Cl} are mobilities in Y and a_s and a_w are activities of KCl in the sap and in W.

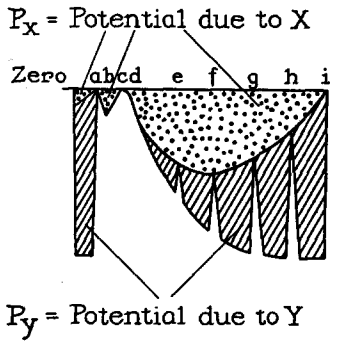

FIG. 2. Hypothetical diagram of the distribution of potential in the protoplasm which is supposed to consist of an aqueous portion W bounded by two very thin non-aqueous layers (X, at the outer surface and Y at the inner surface).

The potential is measured downward from the zero line.

When stimulation occurs Y loses its potential: hence P_Y disappears and this produces the sudden rise (spike) of the action curve at a. Potassium moves outward from the sap and on reaching X sets up some potential (b) which disappears when the potassium reaches the outside of X (at c).

The process of recovery now sets in and potassium moves back into the sap, decreasing the potassium outside of X and increasing it inside of X and thus increasing the potential across X. As potassium continues to move into the sap its concentration just inside X decreases and the potential across X decreases. Hence the potential due to X first increases and then decreases.

When stimulation occurs during recovery Y loses its potential but X does not: hence there is no response when a stimulus occurs at d, and the responses at e, f, g, and h are incomplete but they increase as recovery proceeds because the potential at Y increases.

As the potential P_X is due chiefly to diffusion potential of KCl across X we may write (for 25°C.)

$$P_X = 59\frac{u_K - v_{Cl}}{u_K + v_{Cl}} \log \frac{a_w}{a_o}$$

where u_K and v_{Cl} are mobilities in X and a_w and a_o are activities of KCl in W and in the outside solution.

The experiments indicate that when a stimulus arrives P_Y disappears but P_X is not at once affected.[5] Hence we may say that if the total potential, $P_X + P_Y$, in the resting state, is 100 mv. and the rise of the action curve is 99 mv. (stopping 1 mv. short of reaching the zero line) it means that $P_Y = 99$ mv. and $P_X = 1$ mv. We find, as a rule, that the value of P_X in the complete resting state is very small.[6]

The disappearance of P_Y might be due to physical changes including actual rupture of Y under electrical[7] or mechanical pressure,[8] or it might be due to alteration of mobilities[9] in Y as the result of chemical change. If rupture of Y occurs the value of $u_K \div v_{Cl}$ becomes equal to that in water.

As the result of stimulation Y appears to become much more permeable as indicated by the great increase in the conductivity[10] of the protoplasm and apparently K^+ moves from the sap into W.[11] When the outwardly moving K^+ reaches X it sets up a potential[12] (*b*, Fig. 2) which soon falls off as K^+ moves

[5] When the external concentration of KCl is gradually raised an action current may occur which causes the disappearance of P_Y while P_X remains unaffected. *Cf.* Hill, S. E., and Osterhout, W. J. V., *J. Gen. Physiol.*, 1937–38, **21,** 541.

[6] Osterhout, W. J. V., *J. Gen. Physiol.*, 1944–45, **28,** 23.

[7] If we assume that Y is 0.01 micron in thickness the electrical pressure across Y may amount to 20,000 volts per mm. *Cf.* Osterhout, W. J. V., *J. Gen. Physiol.*, 1934–35, **18,** 221 (footnote 21).

[8] Regarding mechanical effects see Osterhout, W. J. V., and Harris, E. S., *J. Gen. Physiol.*, 1927–28, **11,** 673. Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1934–35, **18,** 369.

[9] Changes in mobilities can be produced by organic substances. Osterhout, W. J. V., *J. Gen. Physiol.*, 1938–39, **22,** 417; 1939–40, **23,** 171, 569, 749.

[10] Blinks, L. R., *J. Gen. Physiol.*, 1936–37, **20,** 229. Cole, K. S., and Curtis, H. J., *J. Gen. Physiol.*, 1938–39, **22,** 37.

[11] If there is an actual rupture of Y it is evident that KCl may pass outward freely. If there is no rupture we may assume that K^+ and Cl^- combine at the surface of X or of Y to form molecules which pass through in molecular form and dissociate on the other side. This seems probable since X and Y are non-aqueous substances immiscible with water in which KCl probably has a low dissociation constant owing to the lower dielectric constant of X and Y. *Cf.* Osterhout, W. J. V., Some models of protoplasmic surfaces, in Cold Spring Harbor Symposia on Quantitative Biology, Cold Spring Harbor, Long Island Biological Association, 1940, **8,** 51; *J. Gen. Physiol.*, 1942–43, **26,** 293.

[12] This can be true only if X is sensitive to K^+ (*i.e.*, if $u_K \div v_{Cl}$ has a fairly high value in X). If X can be made insensitive to K^+ the second peak in Fig. 2 should not appear. This can be brought about experimentally. *Cf.* Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1939–40, **23,** 743.

(Footnote continued on following page)

out through X so that the activity gradient of K^+ across X disappears (Fig. 2, *c*). Then potassium begins to move back into the sap under the influence of the forces which normally cause potassium to enter the cell from without and reach a higher concentration in the sap than in the external solution. This does not necessarily increase the concentration of K^+ in W but it first of all lessens the concentration of K^+ just outside X and this sets up an outwardly directed activity gradient of K across X and thus[13] builds up P_X (*c* to *f*). As potassium continues to move into the sap the activity of K^+ just inside X falls off and in consequence P_X falls off (*f* to *i*). In the meantime P_Y increases steadily as potassium moves from W into the sap thus increasing the outwardly directed activity gradient of K^+ across Y.

A stimulus arriving at *d* can produce no response because the value of P_Y is then zero.

A stimulus arriving at *e* causes a loss of P_Y but the response is small because at that time the value of P_Y is small. As P_Y increases the responses increase accordingly.

The experiments indicate that in the complete resting state P_X is very small and P_Y is about 100 mv. In X the value of u_K may be much greater than that of v_{Cl} so that we may have $u_K \div v_{Cl} = 40$ or more[14] and the situation is not very different in Y, for in the chain

$$\text{Sap} \mid X \mid W \mid Y \mid \text{Sap}$$

there is an inwardly directed potential of about 16 mv. which indicates that the difference between X and Y is not very great.

When stimulation occurs X appears to suffer little or no change but Y becomes very permeable and the value of $u_K \div v_{Cl}$ presumably decreases. During recovery Y regains its former state but until recovery is complete $u_K \div v_{Cl}$ may be greater in X than in Y.

In some figures in this paper the curve does not return to the complete resting level after the initial spike but remains at a higher level which may be called the incomplete resting state. Here the value of $u_K \div v_{Cl}$ in Y may be less than in the complete resting state. In that case the value of P_Y may be less than normal even if the concentration of K^+ in W falls to the normal value as potassium moves back from W into the sap.

The converse of this is seen in *Chara* where normally the second peak is absent because X is insensitive to K^+. But when it is made sensitive to K^+ by means of guanidine the second peak appears. *Cf.* Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1940–41, **24,** 9.

If recovery sets in before potassium diffuses out through X there will be no second peak: this is seen in several of the later figures.

[13] Here potassium enters against the gradient and K^+ presumably becomes less outside X than inside. *Cf.* Osterhout, W. J. V., *J. Gen. Physiol.*, 1932–33, **16,** 157.

[14] Osterhout, W. J. V., *J. Gen. Physiol.*, 1929–30, **13,** 715.

It follows that although we know the value of P_Y which is equal to the magnitude of the action curve (assuming that this involves the total loss of P_Y) we cannot tell precisely the concentration of K^+ in W when the concentration of K^+ in the sap is known because the value of $u_K \div v_{Cl}$ in Y is uncertain unless Y is similar to X, as is approximately true in the complete resting state.

A better estimate of the concentration of K^+ in W could be made from the value of P_X which depends on the outwardly directed activity gradient of K^+ across X, but with rapid action currents we cannot be sure of the concentration of KCl just outside X since some KCl may pass out through X which does not at once return to W. There may be variation in the value of P_X which is measured as the distance from the zero line to the top of the action curve, as in Fig. 2.

It follows that we may not be able to make a precise estimate of the concentration of K^+ in W. But we may say that the rise of the action curve probably signifies a movement of K^+ from the sap into W and the fall of the action curve is accompanied by a movement of K^+ from W into the sap although these movements might theoretically be due to changes in the value of $u_K \div v_{Cl}$ in Y without any movement of K^+.

If K^+ were uniformly distributed throughout W and if X and Y were closely similar we might assume that the effect of K^+ in W would be equal and opposite in X and Y and hence would cancel out. Hence the presence of K^+ in W would affect $P_X \div P_Y$ but not $P_X + P_Y$. In that case the value of $P_X + P_Y$ would depend on the value of $u_K \div v_{Cl}$ in X and in Y and on the activity of KCl in the sap and in the solution just outside X and would be independent of the concentration of K^+ in W.

Hence when the base line, corresponding to the resting state, rises we may attribute it to an increase in the concentration of KCl just outside X or to a decrease in the value of $u_K \div v_{Cl}$ in Y, since the concentration of KCl in the sap is probably not subject to much variation. (But the rise of the base line might in some cases be due to a higher concentration of K^+ in W in the region adjoining Y.)

In Fig. 2 there is a steady increase in the magnitude of the successive action curves corresponding to an orderly progress of the process of recovery whereby K^+ in W decreases regularly as K^+ moves from W into the sap. But each time a stimulus arrives during recovery some K^+ moves from the sap into W thus giving opportunity for disturbances in the process of recovery. Such disturbances take various forms, as will appear in the following pages. (See especially Figs. 3, 7, 9, and 11.)

In Fig. 2 there is steady increase in P_Y but in Fig. 3 the increase is irregular. This might be explained on the ground that the return of K^+ to the sap during recovery does not progress in orderly fashion as in Fig. 2 but is rendered irregular by the movement of K^+ from the sap into W which takes place at each stimulation.

In Fig. 4 there is a steady increase in P_X and a corresponding decrease in P_Y and the action curve declines in magnitude. We may assume that P_X and

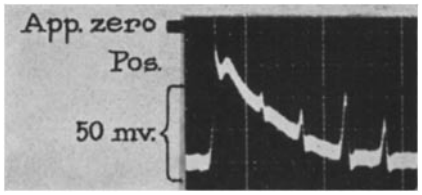

FIG. 3. Resembles Fig. 2 but the partial responses first increase and then decrease.

The recorded spot was in contact with 0.005 M NaCl + 0.0025 M $CaCl_2$. It was connected with a spot in contact with 0.01 M KCl which kept the P.D. constant approximately at zero.

The cell was freed from neighboring cells and kept in Solution A for 30 days at 15°C. ±1°C. About an hour before the record was made it was placed in 0.01 M NaCl at 22°C.

Time marks 5 seconds apart.

Cf. Osterhout, W. J. V., *J. Gen. Physiol.*, 1943–44, **27**, 61 (Fig. 2).

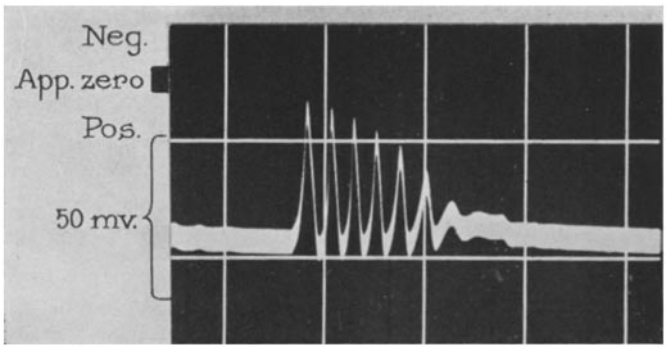

FIG. 4. Shows a regular increase in the potential at the outer protoplasmic surface and decrease in the magnitude of the action curve. For explanation see Fig. 5.

The recorded spot was in contact with 0.01 M ammonium acetate at pH 7. It was connected with another spot in contact with 0.01 M ammonium acetate.

The cell was freed from neighboring cells and kept in Solution A at 15°C. ± 1°C. for 29 days. Half an hour before the record was made the cell was placed in 0.01 M ammonium acetate at 22°C.

Time marks 5 seconds apart.

P_Y change as shown in Fig. 5. This behavior might be accounted for on the ground that after each action current the return of K^+ to the sap is incomplete so that the concentration of K^+ in W steadily increases.

In some cases we see a steady decrease in P_Y while (after the first spike) P_X does not show much change (Fig. 6). In such cases it would seem that the

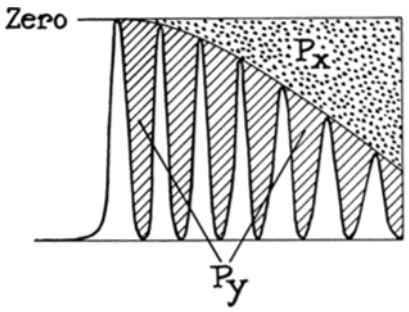

FIG. 5. Diagrammatic representation of Fig. 4 showing that P_X increases and P_Y decreases. Each time an action current arrives P_Y temporarily disappears. (This differs from Fig. 4 in having the first response go to zero as though P_X were zero at the start.)

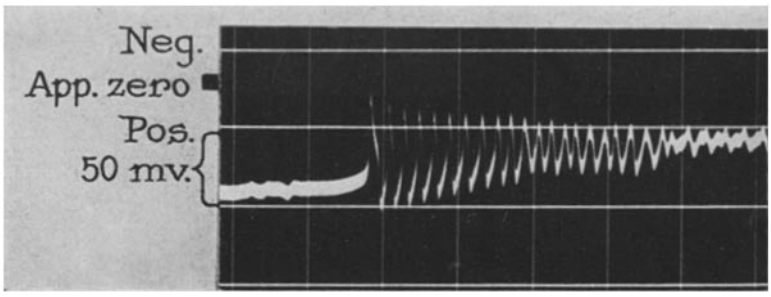

FIG. 6. Shows a regular decrease in the magnitude of the action curve which appears to be due to the falling off of potential at the inner protoplasmic surface since the base line rises: this is presumably due to a decrease in the mobility of K^+ in the inner protoplasmic surface layer.

After the first spike, which goes nearly to zero, the potential (P_X) at the outer protoplasmic surface increases and then remains relatively constant since the distance between the zero line and the top of the action curve shows no great change.

The recorded spot was in contact with Solution A and was connected to another spot in contact with 0.01 M KCl which kept the P.D. constant approximately at zero.

The cell was freed from neighboring cells and kept in Solution A for 30 days at 15°C. ± 1°C. The cell was placed in 0.01 M guanidine chloride at 22°C. for 22 minutes before the record was made.

Heavy time marks 5 seconds apart.

concentration of K^+ in W does not change much but the value of $u_K \div v_{Cl}$ in Y falls off.

In other cases (Fig. 7) there is a steady increase in the magnitude of the action curve such as we see in Fig. 2 (p. 49). This is followed by a steady decrease of P_Y while P_X does not change much: the latter part of the pattern resembles Fig. 6.

In Fig. 8 the magnitude of the action curve soon becomes approximately constant, indicating a relatively constant value of P_Y in the resting state. This may continue for several minutes.

Fig. 9 presents an interesting case where after a complex pattern the curve rises and does not return to the complete resting state: after this it is evident that P_X remains small since the distance between the zero line and the top of the action curve is small, and P_Y is also small as shown by the magnitude of the

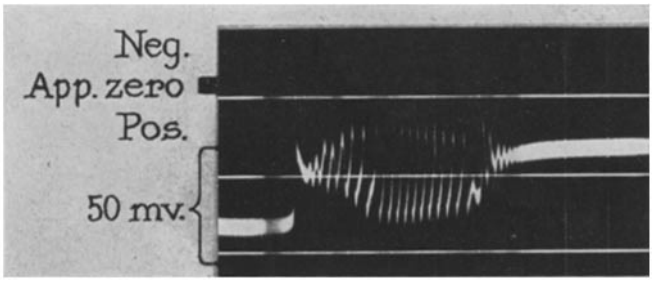

FIG. 7. After the first spike (which goes nearly to zero) there is a decrease and then a gradual increase in the magnitude of the action curve as in Fig. 2. This is followed by a gradual decrease in magnitude during which the potential at the outer protoplasmic surface shows little change. Since the base line rises we may assume that the mobility of K^+ in the inner protoplasmic surface falls off, as in Fig. 6.

The recorded spot was in contact with 0.01 M NaCl and was connected to another spot in contact with 0.01 M KCl which kept the P.D. constant approximately at zero.

The cell was freed from neighboring cells and kept in Solution A for 40 days at 15°C. ± 1°C. An hour before the record was made the cell was placed in 0.01 M NaCl at 25°C.

Time marks 5 seconds apart.

action curve. The rise of the base line is presumably to be explained in the same manner as in Fig. 6.

In Fig. 10 the curve after the first spike fails to return at once to the complete resting state, but in a short time there are 5 action curves and then 2 very small responses during which P_Y has a low value. Since P_X also has a low value we cannot ascribe the low value of P_Y to the presence of K^+ in W but we may assume that the mobility of K^+ in V is relatively small.

Some additional features of these curves call for comment. It will be observed that the double peak seen in Figs. 1 and 2 is lacking in some of the slow action curves and in all of the quick action curves. This is to be expected if

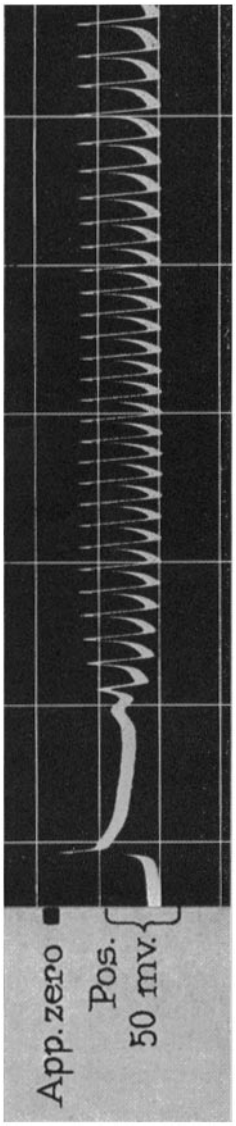

FIG. 8. After the first spike (which goes nearly to zero) the magnitude of the action curve falls off but later increases and becomes approximately constant. The potential (P_X) at the outer protoplasmic surface also becomes approximately constant as shown by the distance from the apex of the action curve to the zero line.

The recorded spot was in contact with 0.01 M NaCl. It was connected with a spot in contact with 0.01 M KCl which kept the P.D. constant, approximately at zero.

The cell was freed from neighboring cells and kept in Solution A for 41 days at 15°C. ± 1°C. Two and a half hours before the record was made it was placed in 0.01 M NaCl at 25°C.

Heavy time marks 5 seconds apart.

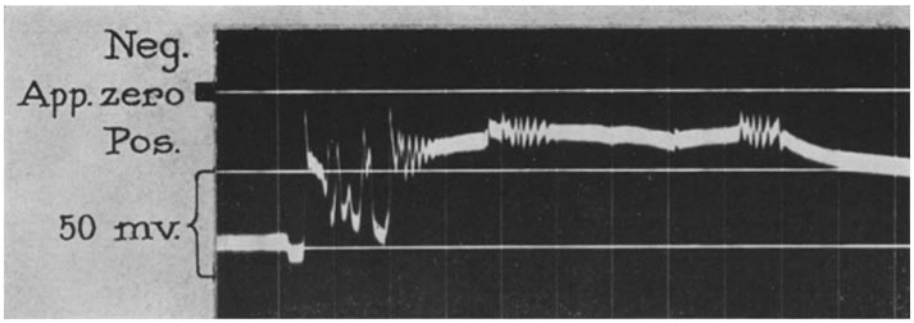

FIG. 9. After a preliminary complex pattern the curve rises and does not return to the complete resting state. After this happens the magnitude of the action curve is small and the potentials at the inner and outer protoplasmic surfaces are small. The rise of the curve is presumably due to the falling off in the mobility of K^+ in the inner protoplasmic surface layer, Y.

The recorded spot was in contact with 0.01 M NaCl and was connected to a spot in contact with 0.01 M KCl which kept the P.D. constant approximately at zero.

The cell was freed from neighboring cells and kept for 40 days in Solution A at 15°C. ± 1°C. About 3.5 hours before the record was made the cell was placed in 0.01 M NaCl at 25°C.

Heavy time marks 5 seconds apart.

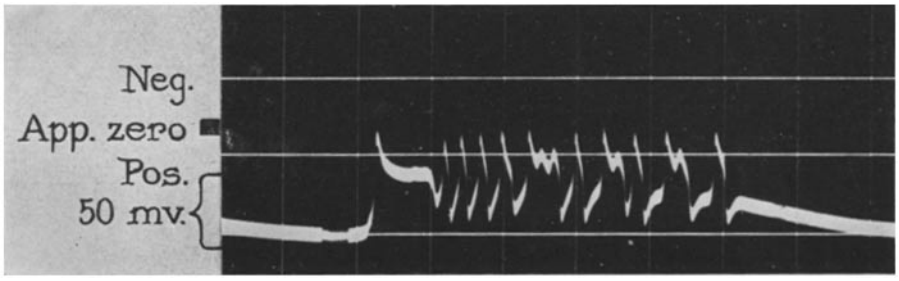

FIG. 10. After the first spike (which goes nearly to zero) the curve remains in the incomplete resting state for a time. Then 5 action curves follow. After this there are 2 very small responses during which P_X and P_Y have a low value: as the base line is then high we may assume that the value of $u_K \div v_{Cl}$ in Y is also small.

The recorded spot was in contact with Solution A and was connected with a spot in contact with 0.01 M KCl which kept the P.D. constant approximately at zero.

The cell was freed from neighboring cells and kept in Solution A for 30 days at 15°C. ± 1°C.: 40 minutes before the record was made it was placed in 0.01 M guanidine chloride at pH 7 at 22°C.

Heavy time marks 5 seconds apart.

recovery sets in and potassium begins to move back into the sap before potassium has time to diffuse out through X.[15]

If we assume that the all-or-none law holds and that each stimulus causes a complete disappearance of P_Y we must likewise assume that in some cases rapid changes take place in P_X (as shown by the distance between the top of the action curve and the zero line) as well as in the value of P_Y in the resting state. A good example of this is seen in Fig. 11. Here we see that an action curve which goes nearly to zero is regularly followed by 2 responses of small magnitude. This might be explained on the ground that after each full response the movement of K^+ from W into the sap is too slow to increase the

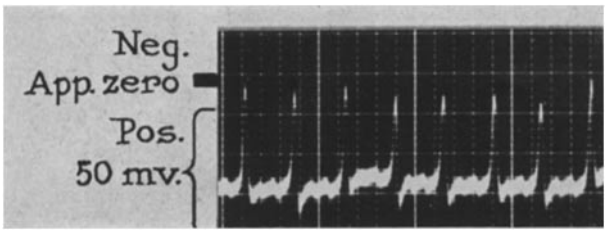

FIG. 11. Shows rapid changes in the potential at the outer protoplasmic surface and in the magnitude of the action curve. A complete response (which goes nearly to zero) is followed by 2 incomplete responses: the latter are presumably due to incomplete recovery.

The recorded spot was in contact with 0.01 M NaCl and was connected with a spot in contact with 0.01 M KCl which kept the P.D. constant approximately at zero.

The cell was freed from neighboring cells and kept in Solution A for 30 days at 15°C. ± 1°C. About an hour before the record was made the cell was placed in 0.01 M NaCl at 22°C.

Heavy time marks 5 seconds apart.

Cf. Osterhout, W. J. V., *J. Gen. Physiol.*, 1943–44, **27,** 61 (Figs. 1 and 2).

value of P_Y (and decrease the value of P_X) sufficiently to permit a full response during the next 2 stimuli.[16] A more gradual change of this sort is seen in Fig. 4.

An alternative explanation would be that the incomplete responses are due to incomplete disappearance of P_Y. On this basis we should not have to assume such rapid changes in the concentration of K^+ in W and correspondingly rapid changes in P_X.

It is evident that the action currents of *Nitella* vary much more than those of such highly specialized cells as muscle and nerve which give stereotyped responses. The variations found in *Nitella* are largely due to irregularities in the process of recovery. These in turn depend on lack of uniformity in the move-

[15] *Cf.* Osterhout, W. J. V., *J. Gen. Physiol.*, 1943–44, **27,** 61.

[16] *Cf.* Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1938–39, **22,** 115. Osterhout, W. J. V., *J. Gen. Physiol.*, 1942–43, **26,** 457.

ments of potassium and on changes in the mobility of ions in the non-aqueous protoplasmic surfaces: it seems probable that such changes in mobility can be produced by metabolism since they can be brought about by organic substances.[17] These variations occur chiefly in connection with quick action currents brought about by previous treatment with such reagents as NaCl[18] and guanidine.[19] It seems possible that these reagents act by increasing the conductivity of *W*. Untreated cells usually give simple action patterns with slow recovery, such as we see in Fig. 1.

The situation in *Nitella* suggests that here is an excellent opportunity for the experimental control of the action current.

SUMMARY

The experiments indicate that the protoplasm of *Nitella* consists of an aqueous layer *W* with an outer non-aqueous surface layer *X* and an inner non-aqueous surface layer *Y*.

The potential at *Y* is measured by the magnitude of the action curve and the potential at *X* by the distance from the top of the action curve to the zero line. These potentials appear to be due chiefly to diffusion potentials caused by the activity gradients of KCl across the non-aqueous layers *X* and *Y*. The relative mobilities of K^+ and Cl^- in *X* and in *Y* can be computed and an estimate of the activity of KCl in *W* can be made. In the complete resting state the mobilities of K^+ and Cl^- in *X* are not very different from those in *Y*.

The action curve is due to changes in *Y* which suddenly becomes very permeable, allowing potassium to move from the sap across *Y* into *W*, and thus losing its potential. A gradual loss may be due to changes in ionic mobility in *Y*.

When recovery is incomplete and *Y* has not yet regained its normal potential a stimulus may cause a loss of the potential at *Y* giving an action curve of small magnitude. The magnitude may vary in successive action curves giving what is called a complex pattern in contrast to the simple pattern observed when recovery is complete and all the action curves are alike. Complex patterns occur chiefly in cells treated with reagents. Untreated cells usually give simple patterns.

A variety of complex action patterns is discussed. It is evident that the cells of *Nitella* show much more variation than such highly specialized cells as muscle and nerve which give stereotyped responses.

In some cases it may be doubtful whether the all-or-none law holds.

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