tion is varied indicates that stimulation usually starts with the inner layer.[9]

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Bioelectrical Aspects of the All or None Law.

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If the all or none law holds, a muscle fibre or nerve fibre will always give the same response when stimulated so that the total electrical effect should be directly proportional to the number of fibres which react, provided the arrangement is in series rather than in parallel. But although the fibres (in a nerve or in such a muscle as the sartorius of the frog) may have a parallel arrangement they appear to behave as if they were in series since the current of action appears to increase with the number of stimulated fibres; so also cutting a muscle entirely in two gives more current of injury than when we cut only part way across.

This is explainable if we assume (as Gasser and Erlanger[1] have done in the case of nerves) that the inactive or uncut fibres act as shunts to the E.M.F. produced by those which are active or cut. Suppose, for convenience, that a group of 5 fibres may be repre-

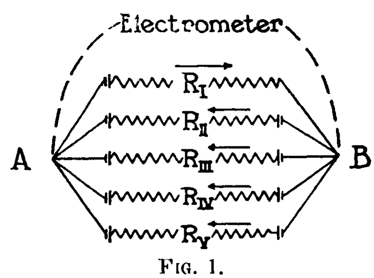

FIG. 1.

Hypothetical diagram to show electrical conditions in a group of fibres of which the uppermost (I) has been cut at the right end so that it produces the current shown by the arrows: the other fibres (II, III, IV, and V) produce no current (since the batteries in each are equal and opposite) but they act as shunts to I.

[9] Evidence will shortly be presented which indicates that the fibres of muscle and nerve may have a surface consisting of two layers, which is in harmony with the fact that the negative wave of nerve often shows two maxima and might afford a different interpretation from that given by Erlanger and Gasser (*Am. J. Physiol.*, 1927, lxxx, 522).

[1] Gasser, H. S., and Erlanger, J., *Am. J. Physiol.*, 1927, lxxx, 522.

sented as in the diagrams[2] in Fig. 1, where I represents a fibre cut at the right end and producing a current as shown by the arrows. Since in II, III, IV, and V the batteries are equal and opposite, these branches of the circuit contribute no current and act only as shunts (these may be called neutral and I may be called positive). We then have[3] P.D. $= E_1 R_N \div (R_N + R_P)$, where E_1 is the electromotive force of the battery in I, R_N is the resultant resistance of the neutral fibres taken together, and R_P is the resistance of the positive fibre (or the resultant resistance of all positive fibres taken together when there are more than 1). If each resistance equals R_0 we have $R_N = R_0 \div N$ and $R_P = R_0 \div P$, where N is the number of neutral fibres. We may then write[4] P.D. $= E_1 \left[\frac{R_0}{N} \div \left(\frac{R_0}{N} + \frac{R_0}{P}\right)\right] = \frac{E_1 P}{N + P}$. Putting $E_1 = 0.5$ we have P.D. $= \frac{(0.5)\ (1)}{4 + 1} = 0.1$.

When 2 fibres are cut the P.D. $= 0.2$; when 3 are cut the P.D. $= 0.3$, and so on. In other words, each fibre that is cut adds 0.1 to the P.D. as if the fibres were in series instead of in parallel.

To what extent we are justified in representing the situation in this way must be learned by experimental test. It is desirable for this purpose to know the P.D. produced by each fibre or cell as well as that of the entire group. Since this cannot readily be tested in muscle and nerve it may be worth while to record some experiments performed (incidental to other work) on the long multinucleate cells of the fresh-water plant *Nitella.* A group of these cells connected together at each end by a piece of moist cotton behaves like a group of fibres in a muscle in that the current of injury produced by cutting increases as more are cut. Here, however, we are able to measure the P.D. produced by each separate cell and to determine the effect produced by the uncut cells which act as shunts.

Experiments with Nitella.

Unless otherwise stated the technique is that described in previous papers.[5] The cells were allowed to dip into a common beaker at the right and into separate beakers at the left. In each beaker was a

[2] In the muscle the fibres are not insulated from each other but this would not affect the result except in the case of active or cut fibres and here the effect would probably be small.

[3] It is assumed that the resistance of the measuring instrument is very high.

[4] When there are two or more positive fibres this formula holds as may be shown by setting up the usual Kirchoff equations.

[5] Osterhout, W. J. V., and Harris, E. S., *J. Gen. Physiol.*, 1927-28, xi, 673; 1928-29, xii, 167. In the present experiments the temperature ranged from 18° to 20° C.

calomel electrode: a series of switches was so arranged that the cells could be measured singly or in any desired combination.

Since the P.D. produced by cutting changes rapidly and is highly variable it seemed better to produce a more steady and uniform P.D. by using different concentrations at the opposite ends of the cell.[6] At the start with 0.01 M KCl at both ends the P.D. (average of 17 groups of 5 cells) was practically zero. With 0.001 M KCl at one end and 0.01 M KCl at the other the P.D. was 50 millivolts (average of 17 groups of 5 cells) the end in contact with 0.001 M KCl being positive. When 1 positive cell was shunted with 4 neutral cells the P.D. was 10 millivolts.[7] In other words, the shunting effect of the 4 neutral cells (cells with the same solution at both ends) reduced the P.D. of the positive cell (which has 0.001 M KCl at one end and 0.01 M KCl at the other) from 50 to 10 millivolts, as our calculations lead us to expect.

Two cells taken together gave 49 millivolts;[8] the shunting effect of the other 3 neutral cells (III, IV, and V) reduced this to 19 millivolts. We expect 20 millivolts, so that the agreement is fairly close.

When 3 cells were positive they gave (taken together as a group of 3) 46 millivolts[9] which was reduced by the shunting effect of 2

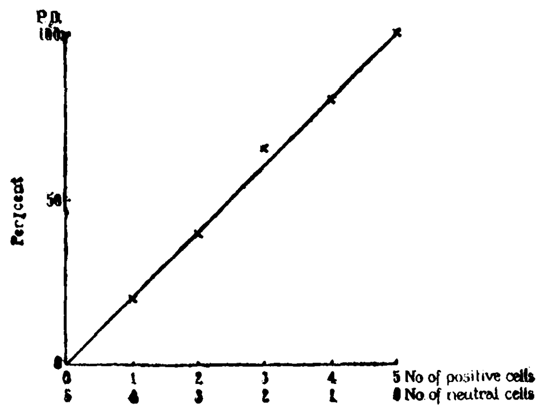

FIG. 2.

The straight line shows the calculated and the crosses the observed P.D. for each group. A group consists of 1 or more positive cells shunted by neutral cells: as the number of positive cells increases the P.D. increases as though they were in series. The ordinates represent the P.D. expressed as per cent of the P.D. observed when the shunting cells are absent.

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[6] Osterhout, W. J. V., and Harris, E. S., *J. Gen. Physiol.*, 1928-29, xii, 761.

[7] Average of 17 groups of 5.

[8] Average of 17 groups of 2.

[9] Average of 17 groups of 3.

neutral cells to 30 millivolts; in this case the expectation[10] is 28 millivolts.

When 4 cells were made positive they gave 48 millivolts;[11] on shunting with a fifth cell this was reduced to 38 which agrees with the prediction.[12]

The results are shown graphically in Fig. 2. Measurements were also made by shunting cells in other groupings. Here also the results were in accordance with prediction as is shown in Fig. 3.

As an analogy to action currents we may consider the effect of cutting which produces in *Nitella* a transitory "negative variation"[13]

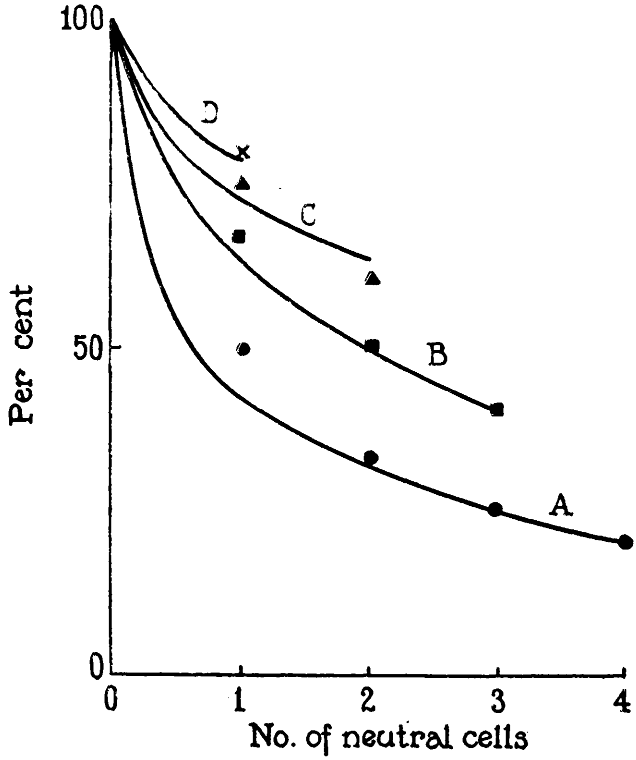

FIG. 3.

The curves show the calculated and the circles the observed P.D. for each group. Curve *A* for 1 positive cell shunted by 1, 2, 3, or 4 neutral cells; Curve *B* for a group of 2 positive cells shunted by 1, 2, or 3 neutral cells; Curve *C* for a group of 3 positive cells shunted by 1 or 2 neutral cells; Curve *D* for a group of 4 positive cells shunted by 1 neutral cell.

[10] The prediction is that the shunting effect will reduce the P.D. from 50 to 30, *i. e.*, to 60% of the original; in this case we start with 46 and 60% of this is 27.6 which is taken as 28.

[11] Average of 17 groups of 4.

[12] *i. e.*, that the reduction will be to 80% of 48 or 38.4.

[13] Osterhout, W. J. V., and Harris, E. S., *J. Gen. Physiol.*, 1928-29, xii, 167, 355.

the time curve of which somewhat resembles the current of action of muscle and nerve. If we arrange a group of *Nitella* cells with 0.001 M KCl at both ends and cut only 1 cell we obtain a much smaller P.D. than as if no shunting cells were present. On the other hand, if we cut all of them simultaneously we obtain about the same P.D. as if we cut 1 by itself. This is in accordance with expectation but no attempt was made to arrive at exact quantitative relations because the negative variation produced by cutting is so variable.

Experiments with Muscle.[14]

Since the fibres cannot be separated for experimental purposes no quantitative work was attempted. A normal muscle, short-circuited by a dead muscle (touching the leads) gives, of course, less current of action than when there is no shunt. The results of cutting the sartorius muscle of the frog are very irregular but when a sufficient number of experiments are averaged there is a rough proportionality between the number of fibres cut and the observed current of injury. If the muscle is completely cut across and a median longitudinal cut is made which partially or completely isolates the 2 halves it is found that each half gives approximately the same current of injury as was observed before the longitudinal cut was made. This is, of course, in accordance with expectation.

Other things being equal it would follow that if all the fibres are cut (or stimulated) a muscle or nerve with a small number of fibres should give as much current of injury (or current of action) as one with a greater number.

Summary: That the fibres of muscle or nerve, despite their parallel arrangement, act electrically as though in series may be explained by assuming that the inactive or uncut fibres act as shunts to those which are stimulated or cut. Experiments on *Nitella* support this assumption.

[14] We employed the sartorius or gastrocnemius of the frog (*R. catesbiana* and *R. pipiens*), leading off with Ringer's solution.