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ELECTRIC EXCITATION OF THE FIN NERVE OF *SEPIA*.

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The strength-duration curve of striated muscle depends largely upon the size and character of the stimulating cathode [Davis, 1923; Watts, 1924; Rushton, 1932 *b*, p. 467; Lapicque, 1934, p. 115]: that for medullated nerve much less [Grundfest, 1932, pp. 107, 113]. Distance between electrodes is stated somewhat to affect the chronaxie of nerve [Cardot and Laugier, 1914; Cardot, 1914] and [Lapicque, 1931] largely to affect the "pseudo-chronaxie" of muscle as measured with a fluid cathode. The final slope (at short times) of the strength-duration curve, plotted in double logarithmic co-ordination [Rushton, 1931] is, for nerve, 1 : 1 [Rosenberg, 1934 *a*; Scott, 1934; Hill, 1935], showing that the quantity of electricity required for excitation is constant: so far as published data go [Rushton, 1931, Figs. 8, 9; Rushton, 1932 *a*, Fig. 7, 1932 *b*, Figs. 4, 7, 9] the final slope for muscle is about 1 : 2, in which case the energy required for excitation is constant. It was natural to suspect that the difference between medullated nerve and muscle in all such respects might be due to the myelin sheath of the former; if so, non-medullated nerve would behave much more like muscle than medullated nerve. The object, therefore, of the present enquiry was to examine the various factors influencing electric excitation of a non-medullated nerve. (See Bugnard and Hill, 1934; Gerard 1934.)

We were introduced to the fin nerve of the cuttlefish by Mr J. Z. Young [see Young, 1932; Sereni and Young, 1932; Young, 1934], who informed us that its fibres are strictly non-medullated. The mantle-connective nerve, before entering the stellate ganglion, gives off a branch which (joined lower down by a branch from the ganglion) passes to the muscles of the fin. It can be isolated, and after washing for half an hour in aerated sea water it works well, often for long periods. It is available

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from the central nervous system downwards. The branches to and from the ganglion were cut, and one of the branches to the periphery was chosen for dissection. Stimulation was at the central end, where there are no branches and the nerve is quite uninjured; recording of the action current was from the peripheral end.

Low frequency repetitive stimulation (one-way) by commutator and condenser was employed [Hill, 1934 *a*]. The sign of activity recorded was the monophasic action current read by a moving-coil galvanometer (Zernicke Zd) connected to the nerve by calomel half-cells and filter-papers soaked in sea water. The stimulating electrodes were similar. The chamber was of paraffin wax; it was carefully washed and dried after each experiment to avoid leaks [cf. Scott, 1934; Bugnard and Hill, 1935 *b*]. Potentials were read by a voltmeter. The resistance of the discharge circuit was measured directly with a bridge. Stimuli of constant frequency were applied at approximately regular intervals, and the maximum deflection of the galvanometer was read. In constructing a strength-duration curve (log V–log RC) two or three readings were made for different voltages at each setting of the condenser, and the voltage for a given response (usually about half maximal) was obtained by interpolation. To allow for progressive changes, if any, in the nerve, each series was repeated in the reverse direction and the mean taken.

The rheobase could not usually be found, since constant current pulses, or even very long condenser discharges, were apt to lead to anomalous deflections, continuing to increase instead of reaching a maximum. These we are inclined to attribute either to summation, or to repetitive response, or both. In the absence of a rheobase the chronaxie cannot be determined[1], so we have been content to record that part of the log V–log RC curve over which normal deflections were obtained, and, as a single index of the time factor in excitation, to read off from the curve the characteristic time for minimum energy. We realize that a curve of this kind is not necessarily invariable, so that it cannot strictly be defined by a single time parameter[2]: so far, however, as a single constant can define the time factor in excitation we believe that the time for minimum energy is at least as good as any other. The asymptotes of the curve (see Fig. 1) are at slopes 0 and 1 respectively: the slope at the minimum energy point is $\frac{1}{2}$ [Rushton, 1931], and this point lies about in the middle of the curve and can be determined rather accurately. Since, however, a single quantity may not properly define the strength-duration

[1] Except indirectly as 0·694 × (time for minimum energy): see Hill (1935).

[2] Though in medullated nerve (see Hill 1935) a single constant seems to be sufficient.

curve, we have preferred, where possible, in describing the results, to give the whole curve as observed.

It is possible to go to quite high frequencies (*e.g.* 100 per sec.) in stimulating this nerve. For the present purpose, however, low frequencies

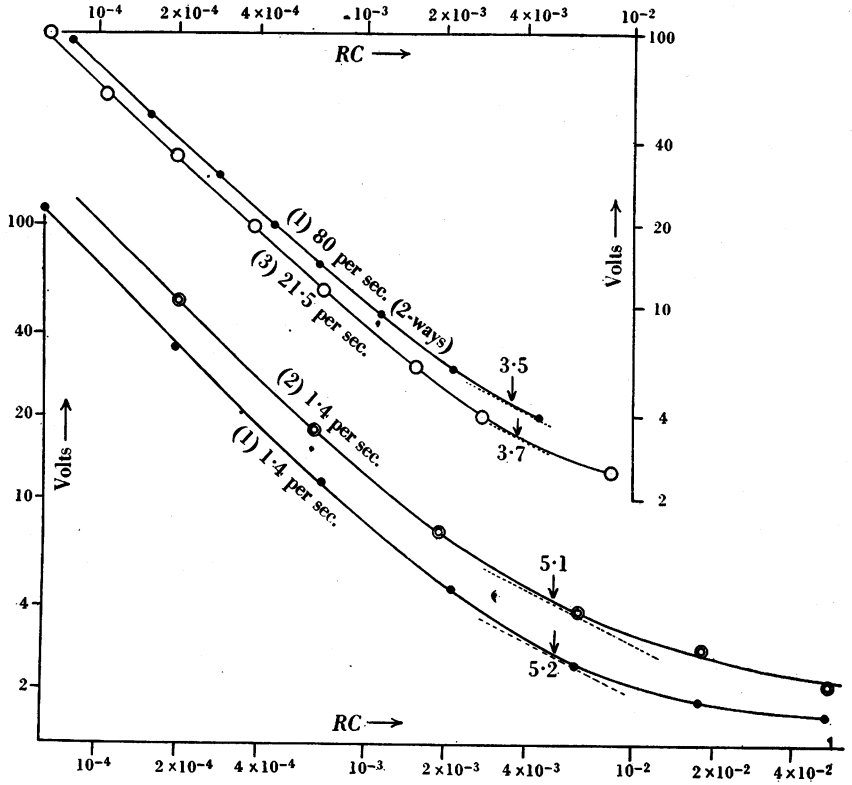

Fig. 1. Strength-duration (log V – log RC) curves for repetitive electric excitation of the fin nerve of *Sepia* at about 20° C. (August and September, 1934). Nerve (1) at 1·4 shocks per sec. (25 p.c.) and at 80 shocks per sec. (10 p.c.); nerve (2) at 1·4 shocks per sec. (33 p.c.); nerve (3) at 21·5 shocks per sec. (40 p.c.). (The numbers p.c. in brackets indicate the response taken, as a fraction of maximum.) The curves for higher frequency cannot be continued to the right. The only curve for which a rheobase was approximately obtainable is No. 1 at 1·4 per sec., where the rheobase is the horizontal axis. The points of minimum energy (slope $\frac{1}{2}$) are given by the arrows: the corresponding times are shown in msec. The final slopes of the curves are close to 45° C., the quantity of electricity required for excitation becoming constant.

had to be used. The strength-duration curve was wanted up to discharge times of 50 msec., and this prohibited the use of frequencies greater than about 3 per sec. At a high frequency only a restricted portion of the curve can be observed (see Fig. 1).

At the short-time end of the curve high voltages are required. If these are too high leaks will occur and spoil the results. We have avoided voltages greater than about 100. We were able, however, without risk, to go sufficiently far to the left to get on to the final straight part of the curve.

The experiments were made at room temperature (about 20° C.); the nerves were in air (not oxygen). The circuit used for the experiment of Fig. 1 consisted of a 10,000 ohms shunt, 12,500 ohms in series with the nerve, nerve and electrodes about 2500 ohms. The discharge resistance R was about 6000 ohms (directly measured). For all other experiments the shunt was 10,000 ohms, the series resistance 20,000 ohms and the total discharge resistance (directly measured) about 7000 ohms. No significant difference in the discharge resistance was found when the distance between, or the size of the electrodes, was altered.

The results of four experiments (on three nerves) are given in Fig. 1. Two were at low frequency, and of these one (the lowest curve) was the only experiment in which an approximate determination of the rheobase could be made. Two were at high frequency, so were limited to shorter times. The characteristic time for minimum energy is given by the tangent of slope $-\frac{1}{2}$ and is indicated by an arrow and the value of RC in msec. on each curve. The final slope to the left is nearly enough -1, showing that, as in medullated nerve, the quantity of electricity required for excitation becomes constant at short times. This quantity can be calculated from the curves of Fig. 1; for the submaximal responses there considered it is about $2{\cdot}5 \times 10^{-8}$ coulomb, through the nerve itself, per impulse. This is ten times the quantity required for a frog's sciatic [Bugnard and Hill, 1935 *a*, *b*], which, however, is of much smaller section. The chief part of the current, in the present case, must have been short-circuited through tissue spaces, and through the fibres of the mantle-connective nerve which pass to the ganglion and do not return to the fin nerve.

The results of Fig. 1 were obtained with the nerve resting on the edges of strips of moist drawing-paper about 2 cm. apart, the cathode being nearer to the galvanometer. The next step was to see whether the distance between the electrodes had any effect on the strength-duration curve. The chamber was provided with four stimulating electrodes, E_1, E_2, E_3 and E_4, E_1 (nearest to the galvanometer) being a fixed cathode, the anode being variable between the other three. At each capacity and voltage, observations were made for each electrode distance, and after a complete series in one direction another was made in the opposite direction. In this way an exact comparison is possible. Of the three electrode distances, E_1E_2, E_1E_3, E_1E_4, the first, E_1E_2, was as small as possible, while E_1E_3 and E_1E_4 were of the order of 1 and 2 cm. respectively. The

diameter of the nerve being of the order of 1·8 mm.[1], there was no sense in making E_1E_2 much less than that quantity, and moreover if E_1 and E_2 were too close, fluid would collect between them and short-circuit the shocks. It was soon found that no difference at all could be detected between E_1E_3 and E_1E_4, so in the later experiments two distances alone, the shortest and the longest, were compared. These two gave so nearly the same result that the difference has been tabulated and a mean result given in Fig. 2.

TABLE I. Effect of inter-electrode distance on the log V–log RC relation.

Sept. 10. E_1E_2=1·7 mm.: mean of E_1E_3 (13 mm.) and E_1E_4 (19 mm.). 6 shocks per sec.

log RC	$\bar{4}$·515	$\bar{4}$·870	$\bar{3}$·165	$\bar{3}$·56	$\bar{3}$·855	$\bar{2}$·32
log V (E_1E_2)	1·500	1·295	1·125	0·96	0·875	0·80
log V (E_1E_3, E_1E_4)	1·530	1·315	1·150	0·97	0·880	0·78
Difference	−0·030	−0·020	−0·025	−0·01	−0·005	+0·02

Sept. 10. E_1E_2=1·3 mm.: mean of E_1E_3 (13 mm.) and E_1E_4 (19 mm.). 6 shocks per sec.

log RC	$\bar{4}$·515	$\bar{4}$·870	$\bar{3}$·165	$\bar{3}$·56	$\bar{3}$·855	$\bar{2}$·320
log V (E_1E_2)	1·415	1·120	0·900	0·71	0·610	0·540
log V (E_1E_3, E_1E_4)	1·380	1·085	0·855	0·66	0·540	0·465
Difference	0·035	0·035	0·045	0·05	0·060	0·075

Sept. 12. E_1E_2=1·5 mm.; E_1E_4=20 mm.; 8·5 per sec.

log RC	$\bar{5}$·87	$\bar{4}$·16	$\bar{4}$·515	$\bar{4}$·875	$\bar{3}$·165	$\bar{3}$·560	$\bar{3}$·855	$\bar{2}$·32
log V (E_1E_2)	1·85	1·52	1·260	1·970	0·875	0·735	0·650	0·54
log V (E_1E_4)	1·89	1·54	1·275	1·060	0·880	0·720	0·600	0·50
Difference	−0·04	−0·02	−0·015	+0·010	−0·005	+0·015	+0·050	+0·04

Sept. 13. E_1E_2=2·0 mm.; E_1E_4=19½ mm.; 3·7 per sec.

log RC	$\bar{4}$·515	$\bar{4}$·875	$\bar{3}$·165	$\bar{3}$·560	$\bar{3}$·855	$\bar{2}$·14	$\bar{2}$·540
log V (E_1E_2)	1·610	1·300	1·105	0·875	0·770	0·68	0·605
log V (E_1E_4)	1·595	1·290	1·060	0·805	0·705	0·58	0·510
Difference	0·015	0·010	0·045	0·060	0·065	0·10	0·095
log V (E_1E_2)	1·79	1·495	1·310	1·08	0·930	0·830	0·745
log V (E_1E_4)	1·80	1·490	1·265	1·05	0·915	0·835	0·725
Difference	−0·01	+0·005	+0·045	+0·03	+0·015	−0·005	+0·020

Interpolating for the value $\bar{2}$·32 on September 13, the following mean differences can be calculated.

log RC	$\bar{4}$·515	$\bar{4}$·875	$\bar{3}$·165	$\bar{3}$·560	$\bar{3}$·855	$\bar{2}$·320
Difference log V	−0·001	+0·008	+0·021	+0·029	+0·037	+0·050

There clearly is a small difference between the far and the near electrodes, the excitability being the same at short times, but greater for the distant electrodes at long times. The difference, however, is very small,

[1] Actually as it lay on an electrode its thickness was about 1·5 mm.

being only 12 p.c. (log 1·12 = 0·05) at a discharge time of 21 msec. It is probably to be associated with the fact that with electrodes close together the current lines are very curved, and we shall show later that excitation by electrodes straight across the nerve has a comparatively large effect in the same sense. The mean curves for close and for distant electrodes are given in Fig. 2; the time for minimum energy is 2·5 msec. for the former, 3 msec. for the latter.

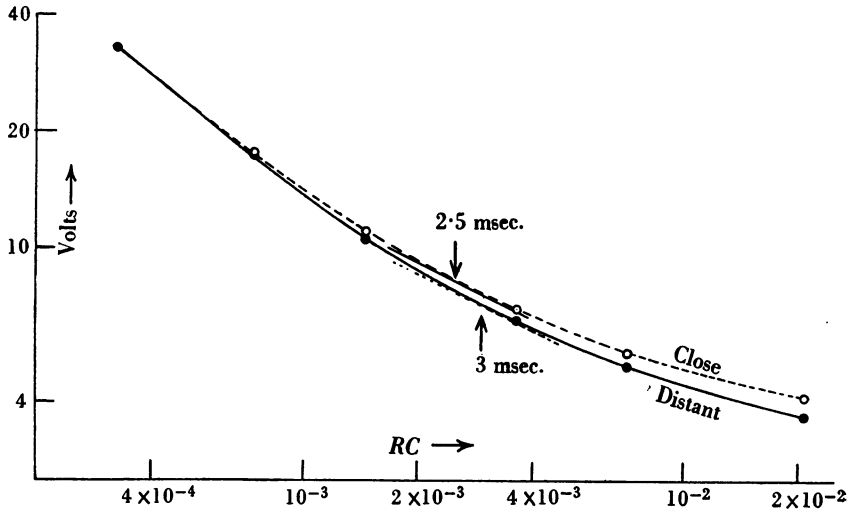

Fig. 2. Mean curves (log V − log RC) for excitation of *Sepia* fin nerve by close and by distant electrodes.

The electrodes used in the experiments described so far were "linear," *i.e.* the sharp edges (about 0·2 mm. wide) of filter- or drawing-paper, soaked in sea water. We next examined the effect of using a large flat electrode as cathode. In this case, in order to ensure a comparison uninfluenced by any progressive alteration in the nerve, four series were made in each experiment as follows, and the mean taken.

Series 1 with decreasing capacities: linear electrode.
Series 2 with increasing capacities: large electrode.
Series 3 with decreasing capacities: large electrode.
Series 4 with increasing capacities: linear electrode.

Keeping $E_1E_4 = 22$ mm., E_1 the cathode was extended to E by a pad of filter-paper soaked in sea water, where E was either towards, or away from, E_4. The nerve lay upon this wet pad. For the comparison, the usual linear electrode was used at E_1 as cathode.

TABLE II. Effect of electrode size on the log V– log RC relation.

Sept. 3. 6 shocks per sec. Large cathode 14 mm. along the nerve, symmetrically placed over E_1: compared with linear cathode at E_1.

log RC	$\bar{4}$·520	$\bar{4}$·84	$\bar{3}$·170	$\bar{3}$·47	$\bar{3}$·77	$\bar{2}$·15	$\bar{2}$·45
log V large	1·825	1·58	1·320	1·14	1·01	0·88	0·82
log V linear	1·675	1·43	1·185	1·01	0·87	0·76	0·68
Difference	0·150	0·15	0·135	0·13	0·14	0·12	0·14

Sept. 10. 6·2 shocks per sec. Large cathode 13 mm. along the nerve away from E_4.

log RC	$\bar{4}$·51	$\bar{4}$·78	$\bar{3}$·060	$\bar{3}$·340	$\bar{3}$·64	$\bar{3}$·90	$\bar{2}$·22
log V large	1·27	1·04	0·825	0·645	0·50	0·42	0·34
log V linear	1·18	0·93	0·730	0·540	0·41	0·33	0·25
Difference	0·09	0·11	0·095	0·105	0·09	0·09	0·09

Sept. 10. 6·2 shocks per sec. Large cathode 11 mm. towards E_4.

log RC	$\bar{4}$·51	$\bar{4}$·78	$\bar{3}$·06	$\bar{3}$·34	$\bar{3}$·640	$\bar{3}$·90	$\bar{2}$·22
log V large	1·22	1·00	0·80	0·63	0·495	0·40	0·33
log V linear	1·06	0·84	0·62	0·41	0·310	0·25	0·18
Difference	0·16	0·16	0·18	0·22	0·185	0·15	0·15

Sept. 11. 8·5 shocks per sec. Large cathode 13 mm. towards E_4.

log RC	$\bar{4}$·51	$\bar{4}$·83	$\bar{3}$·165	$\bar{3}$·560	$\bar{3}$·855	$\bar{2}$·240	$\bar{2}$·54
log V large	1·41	1·19	0·955	0·780	0·680	0·580	0·49
log V linear	1·72	1·48	1·255	1·055	0·950	0·885	0·82
Difference	−0·31	−0·29	−0·300	−0·275	−0·270	−0·305	−0·33

Results are given in Table II. There is clearly no difference at all, in the form of the curve, between large and small electrodes, the tabulated difference of log V remaining constant over the whole range. In the first experiment the large electrode required about 35 p.c. more voltage than the linear electrode throughout the whole range of times, in the second about 25 p.c. more; in the third 50 p.c. more; in the fourth 50 p.c. less. The variation in excitability may depend upon the actual point of impact of the current in the several cases: it does not disguise the fact that the time-factor in excitation is quite unaltered when the stimulating cathode changes from a line 0·2 mm. wide to a flat plate in contact with the nerve for more than 1 cm. The mean value of the characteristic time for minimum energy, read from curves drawn from the results of Table II, is 2·7 msec. for each.

Lastly we come to the comparison of transverse with longitudinal excitation. In exp. (1) (September 24), shown in Fig. 3, the electrodes were, for longitudinal excitation, the usual filter paper edges 23 mm. apart: for transverse excitation, anode, a filter paper edge, cathode, a drawing-paper point exactly opposite the anode. The discharge resistances directly measured were 7300 and 7750 ohms respectively. In exp. (2), Fig. 3 (September 25, frequency 6·1 per sec.), the longitudinal electrodes were

filter-paper edges 22 mm. apart ($R=7500$ ohms); the transverse electrodes were two drawing-paper edges exactly opposite one another ($R=7400$ ohms). There is clearly a large difference between longitudinal and transverse excitation, the nerve being about four times as quick for the latter as for the former. This is not a matter of distance between electrodes, since we have already shown that that has little effect. At short times

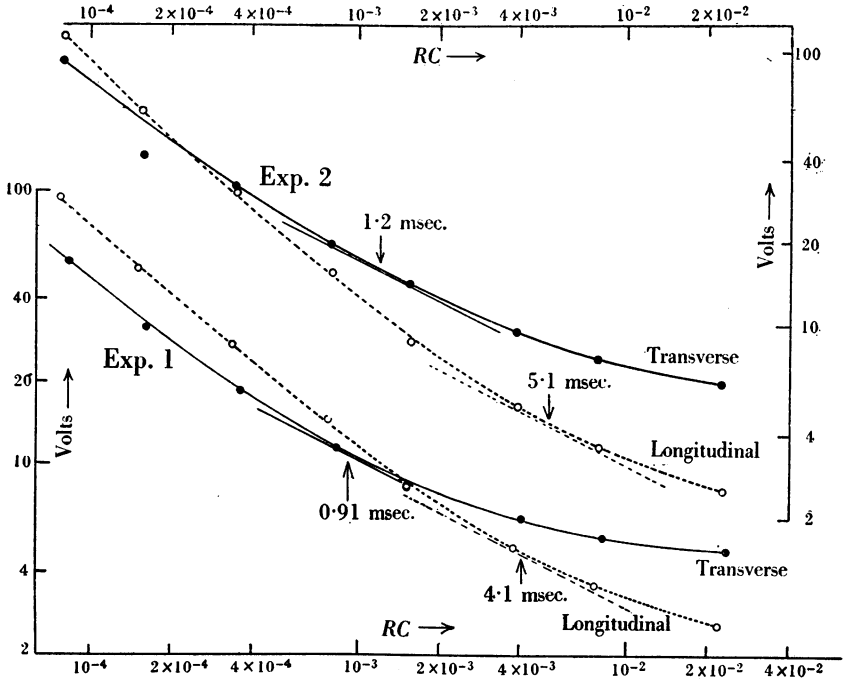

Fig. 3. Comparison of transverse and longitudinal excitation of *Sepia* fin nerve. Exp. 1, fluid point cathode; Exp. 2, fluid linear cathode: in both cases immediately opposite fluid linear anode. Longitudinal excitation by linear fluid electrodes 23 mm. apart. Time for minimum energy shown by arrows.

transverse excitation is more effective, at long times, longitudinal excitation. In Fig. 2 the difference between close and distant electrodes is in the same sense as, but much smaller than, that between transverse and longitudinal excitation (Fig. 3); it seems likely that it is due to the fact that with near electrodes the current lines are so curved that an appreciable transverse effect occurs.

It has long been known that with medullated nerve, transverse excitation is much less effective [see Rushton, 1927]. Rushton's experiments were made with parallel current lines in a bath of Ringer's

fluid; the present experiments with narrow linear or point electrodes placed opposite one another across the nerve. The conditions, therefore, are not the same. The curves in Fig. 3, however, are a warning against taking any fixed time and comparing excitabilities to transverse and longitudinal currents for that time alone. For a short time one result may be found, for a long time the opposite. It would be interesting, but unfortunately we had no time, to repeat the experiments of Fig. 3 with parallel current lines along and across the nerve.

Which, if either, of the curves of Fig. 3 corresponds to that which would be obtained by using, as cathode, a silver wire coated with AgCl

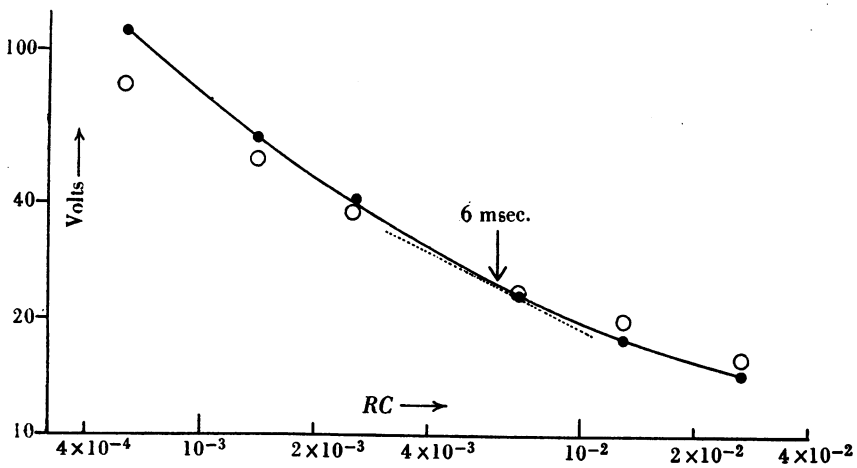

Fig. 4. Response of muscle fibres causing colour change in *Sepia*. Solid circles and curve, log V–log RC relation for skin intact on animal: hollow circles, isolated skin. About 17° C.

thrust into the tissue is not certain. Possibly the latter would give a curve somewhere between the two, variable according to the position of the wire in relation to the tissue excited.

A few observations were made on the electric stimulation of the muscle fibres which extend the chromatophores of the animal's skin. (For references see Fuchs, 1914; Parker, 1930.) The colour change was recorded with a photo-cell connected to a galvanometer [see Hill and Solandt, 1934]. Single condenser discharges were used, and a small constant response was taken as indicator of constant excitation. In Fig. 4 the mean results of four series on two different animals (decapitated and eviscerated) are given by solid circles. On one animal two series were made on the dorsal, one on the ventral side: on another animal one series was made on

the dorsal side. Calomel electrodes were used for stimulation, the cathode making contact with the skin by a cotton-wool wick soaked in sea water: the change of colour recorded was around the cathode. The total resistance was 13,500 ohms, 10,000 of this being a "grid leak" in series with the electrodes, no shunt being used.

The curve of Fig. 4 is practically identical with the curves shown in previous figures for the fin nerve, being slightly to the right, perhaps owing to the fact that in these experiments (September 26) the temperature was rather lower (about 17° C.). It is probable that the nerve fibres running to the muscles of the chromatophores were in fact being stimulated, not the muscles themselves. Two series were made on strips of isolated dorsal skin extended on a cork. The mean result of these is given by the hollow circles. It is somewhat different from that for the skin still in place on the animal; perhaps in the isolated skin the muscle fibres themselves are being stimulated. Certainly if the skin be kept isolated for some time, more intense currents are required to excite it, which may be due to the death of injured nerve fibres and the consequent necessity of stimulating the muscle fibres directly.

An attempt was made to find whether frequency of stimulation affects the time factor in excitation. The difficulty is that, although the nerve will respond to quite high frequencies, the significant portion of the strength-duration curve is at durations so long that a high frequency is impossible. It is necessary, for example, in order to get a proper idea of the curve, to go to discharge times of 20 msec.; this, however, prohibits a frequency of more than 10–20 per sec. If the intervals are diminished between shocks of such duration, anomalies are apt to occur, due perhaps to summation of stimuli. The result, so far as it is significant, is that no important difference is produced by varying the frequency. For example, in one experiment the characteristic time for minimum energy was: 1·4 per sec., 2·5 msec.; 9·5 per sec., 2·65 msec.; 40 per sec., 2·9 msec. In another it was: 1·4 per sec., 2·8 msec.; 9·5 per sec., 3·3 msec. In view of the smallness of the effect, if any, of frequency, the matter was not followed up.

The relation between total electric response and frequency is of the usual kind, with a maximum beyond 100 shocks per sec.

The effect of potassium ions was investigated, (*a*) in making the fin nerve inexcitable, (*b*) in decreasing the injury potential, and (*c*) on the strength-duration curve before the limit of inexcitability was reached. The results of (*a*) and (*b*) were similar to those of Cowan [1934], but it was necessary to soak the fin nerve for some time in the solution containing

an excess of potassium in order to obtain the full effect. This is presumably due to the fact that the fin nerve, unlike the limb nerve of *Maia*, is surrounded by a firm connective tissue sheath, so that the ions can penetrate only by diffusion. As Cowan found, the effects are reversed on washing in normal sea water.

The nerve, for the first 2 or 3 cm. below the brain, in a large animal, has no branches, and can be prepared without damage. The injury potential was measured in this region. The nerve was injured by crushing as directed by Cowan [1934, p. 232].

The maximum injury potential was about 20 mV. This was reduced to 5–10 mV. on soaking in ten times the usual potassium-ion concentration; the initial value was largely, but not fully, recovered by soaking

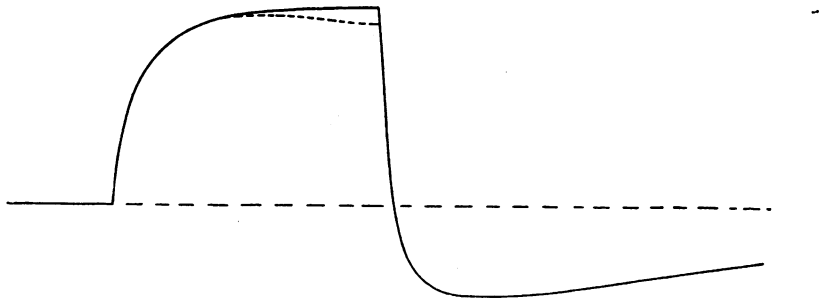

Fig. 5. Response of fresh rested fin nerve to short tetanus. Horizontally time: vertically action current (galvanometer deflection).

in normal sea water. A correspondingly smaller reduction of injury potential was effected by soaking in a less concentrated potassium solution. The injury potential is smaller than Cowan found for *Maia* nerve (about one-half); the effect of potassium is also less. It may be that with the much more solid nerve of *Sepia* it is more difficult both to get the true value of the resting potential at the cell membrane and also to cause potassium-ions to permeate the trunk.

Excitability disappears rapidly with five times the normal potassium-ion concentration; even with three times it disappears too fast to allow a strength-duration curve to be made. With twice the normal concentration the excitability is diminished (greater voltage required for a given response) but a strength-duration curve could generally be made. The result was that doubling the potassium had no significant effect upon the time factor in excitation.

Fatigue and after potentials. Like the limb nerve of *Maia* [Levin, 1927; Furusawa, 1929] the fin nerve of *Sepia* is fatigable and shows

prolonged electrical after-effects of stimulation. In detail, however, there are considerable differences; the fin nerve is much less rapidly fatigued, and the after-effect of a few seconds' stimulation is normally to increase, not to decrease, the injury potential. Prolonged stimulation (4 or 5 min., say, at 10–20 shocks per sec.) reduces the response to a fraction of its initial value (*e.g.* to 1/4), and the injury potential considerably (*e.g.* to 7/10). Both are restored by rest in air.

The after-effect of a few seconds' tetanus to a fresh nerve is sketched in Fig. 5. The deflection of the galvanometer is maintained to the end of the stimulus, or slightly decreases. Then a rapid movement occurs to the opposite side of the base line, to which return is slow. There is no "retention of action current" [Levin, 1927] as in *Maia* nerve, but exactly the opposite. These and similar effects could be better studied by the combined use of an oscillograph and a sensitive galvanometer, and we have not investigated them further.

Summary.

1. Some of the differences observed, in respect of electric excitation, between striated muscle and medullated nerve might be attributed to the myelin sheath of the latter, to nodes of Ranvier, etc. It was desirable, therefore, to examine the electric excitation of non-medullated nerve, where these do not exist.

2. The fin nerve of the cuttlefish, which is entirely non-medullated, makes a very suitable preparation. Its action current was measured with a moving-coil galvanometer, in response to low-frequency repetitive stimulation.

3. For constant response, the strength-duration (log V– log RC) curve is of the usual type, with an asymptote at short times at a slope of 1 : 1, showing that there the quantity, not the energy, required for excitation, is constant. At 20° C. the characteristic time for excitation by minimum energy is 3–5 msec., about ten times that for the frog's sciatic.

4. Distance between electrodes has little effect on the strength-duration curve within the range 1·5–20 mm.

5. Size of stimulating cathode has no effect.

6. Frequency of excitation has little or no effect.

7. Transverse excitation with linear fluid electrodes has a large effect, giving a time factor which is only one-quarter of that for longitudinal excitation.

8. Stimulating the skin with single discharges, and recording the colour change with photo-cell and galvanometer, one can make a strength-

duration curve for the response of the radial muscle fibres of the chromatophores. The relation is almost identical with that for nerve: probably the nerve fibres are being excited.

9. The injury potential of the fin nerve is about 20 mV. This can be reversibly reduced by soaking the nerve in sea water with a greater concentration of potassium ions. Increased potassium-ion concentration leads to reversible inexcitability, but, so long as the nerve remains inexcitable, to no change in the strength-duration curve.

10. The nerve can be fatigued, and its injury potential diminished, by prolonged stimulation. Recovery occurs in air.

11. In the limb nerve of the crab, also non-medullated, the after-effect of a short stimulus is to reduce the injury potential: in the fin nerve of the cuttlefish, the first after-effect is to increase it considerably.

Similar experiments with the limb nerve of the spider crab were performed at Plymouth in August, before these by us in September, by Dr R. W. Gerard. We knew of his results, which will be reported later [see also Gerard, 1934], and are indebted to him, as we are to Dr W. A. H. Rushton, for much discussion. At Plymouth also, analogous experiments, with single shocks, were made by Rosenberg [1934 *b*] on *Maia* and on *Sepia* nerve; while Bogue and Rosenberg [1934] studied the electric response of both with an oscillograph: these results also will be reported in detail later.

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