

## EXCITATION OF BENT NERVE.

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### INTRODUCTION.

IN a recent publication<sup>(1)</sup> an attempt was made to bring under a mathematical formula the changes in the threshold for nervous excitation which result from certain alterations in the position of the electrodes. The formula was derived from the following assumptions:

(a) The nerve is regarded as a cylinder with a relatively resistant sheath and a relatively conducting core.

(b) Nernst's assumptions regarding the dependence of excitation upon ionic concentration are accepted.

(c) Excitation is brought about by the current leaving the nerve through the cylindrical sheath, which thus constitutes Nernst's membrane.

(d) For stimulation with constant currents of fixed duration excitation will occur at a given point in the sheath when the current leaving at that point attains a certain fixed value.

The results of the mathematics were found to be in close accord with the experimental observations, namely the relation between threshold and interpolar length, and between threshold and angle between current and nerve. The foregoing assumptions therefore receive considerable support. But the whole of this analysis would be enormously strengthened if it could be shown that, without any multiplication of hypotheses, these assumptions would account for a new and wider range of observations.

The investigations in this paper, therefore, treat of a more complicated form of stimulation, and it is found that in every case there is a good agreement between observation and theory.

The mathematical treatment in this paper becomes rather technical in places, and so it was thought well to include it as an appendix at the end of the paper. The results of the mathematics can then be quoted in the text to compare with the experimental observations, and reference given to the place in the appendix where the result is obtained.

THRESHOLD FOR BENT NERVE WITH DIFFERENT  
ANGLES OF CURRENT.

In the previous paper (1) a stretch of nerve was immersed in a solution and exposed at various angles to a current flowing through the solution in parallel lines. It was shown that, when the nerve was straight, the relation between threshold and angle, plotted in polar coordinates, gave two parallel straight lines. When, however, the nerve was bent by pulling the centre a little to one side, the lines became concave to the origin, and quite changed their shape, as is shown in Fig. 6 of that paper. This rough experiment was sufficient for the matter in hand, namely to trace an error in the experiments with a straight stretch, but it seemed of interest to see what form the plotted curve assumed when the nerve was bent more accurately in some manner. The simplest cases to take are when the exposed stretch consists of two straight limbs of equal length bent in the horizontal plane at various angles.

*Apparatus.* The trough mounted on a turn-table, and the electrical apparatus, were the same as in the experiments in the former paper (Fig. 4), the only change being in the part which held the nerve. This is shown in Fig. 1.

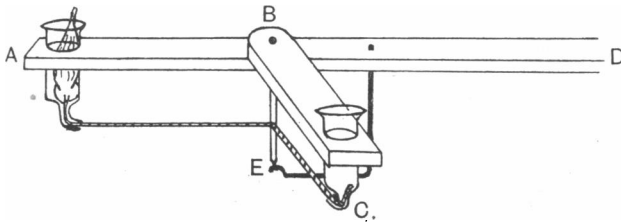


Fig. 1. Arrangement for holding the nerve.

The stand *AD* is held fast at *D*, and kept fixed throughout the experiment. The end *A* holds a glass tube containing the muscle (frog's gastrocnemius), and the sciatic is passed through the lower end of the tube, which is drawn fine and bent horizontal, pointing towards *D*. At *B*, a distance of 15 mm. from the centre of the tube *A*, is pivoted the movable arm *BC*, holding at *C* a tube similar to *A*, and equidistant from *B*. The horizontal part of the capillary end of *C* points towards *B*. The upper ends of two threads are attached to the pivot *B*, and the lower ends to *E*, a point vertically below. *E* is capable of executing a slight vertical movement, thus altering the tensions on the threads. First they are slackened and the nerve passed between them, then they are tightened



current delivered by a Lucas pendulum; the duration in this case was about 0.001 sec.

*Results.* The results are plotted in polar coordinates as in the former experiments: the distance of the plotted point from the origin is proportional to the threshold strength: the angle that the line joining the point to the origin makes with the direction  $AB$  is the angle which the current makes with the peripheral limb  $AB$ . A typical curve is shown in Fig. 2 together with a diagram showing the position of the two limbs of the nerve.

For instance, if we require the threshold when the current flows parallel to the central limb and towards the bend, we draw from the origin a line parallel to  $CB$  and in the same direction, and note the point where it cuts the experimental curve. The distance of this point from the origin is proportional to the threshold.

It is clear that to a first approximation at least the results form a triangle enclosing the origin.

In every experiment which I have made there are always three sharp discontinuities between which the curves are smooth and approximately straight. The immediate suggestion is that the three smooth lines correspond to excitation at three different points in the nerve, and that the discontinuities represent a transition from one to another of these points.

The correctness of this suggestion is a matter of the first importance in the interpretation of the results, and so I thought it worth while to prove it by several methods.

#### (a) *Intuitive Analysis.*

The three points which suggest themselves as likely seats of excitation are the two extremities where the nerve enters the glass tubes and the bend in the middle. If the three regions of the curve represent stimulation at these three points, we should expect that each region would correspond to the range of angles where the point in question is at a negative potential to the rest of the nerve.

Thus the central end of the nerve should be stimulated most by a current flowing parallel to the central limb of the nerve and away from the bend. Similarly the peripheral end should be most stimulated by a current flowing parallel to the peripheral limb and away from the bend. It is seen that in precisely these two directions are the thresholds for two of the regions of the curve a minimum. Stimulation at the bend should occur when the current flows parallel to the bisector of the angle of the bend, and into the bend, since in this case the bend is cathodic

with respect to all other points in the nerve. The results show that this is also roughly the direction of the minimum threshold in the third region.

(b) *Mathematical Analysis.*

This is the same as the foregoing but put quantitatively. It will be considered later.

(c) *Variation of the Position of one Limb of the Nerve.*

If the peripheral limb is kept fixed and the position of the central limb is varied, we should expect that that part of the curve which we have already supposed to represent excitation at the peripheral end would be unchanged. Fig. 3 shows the result of an experiment to investigate

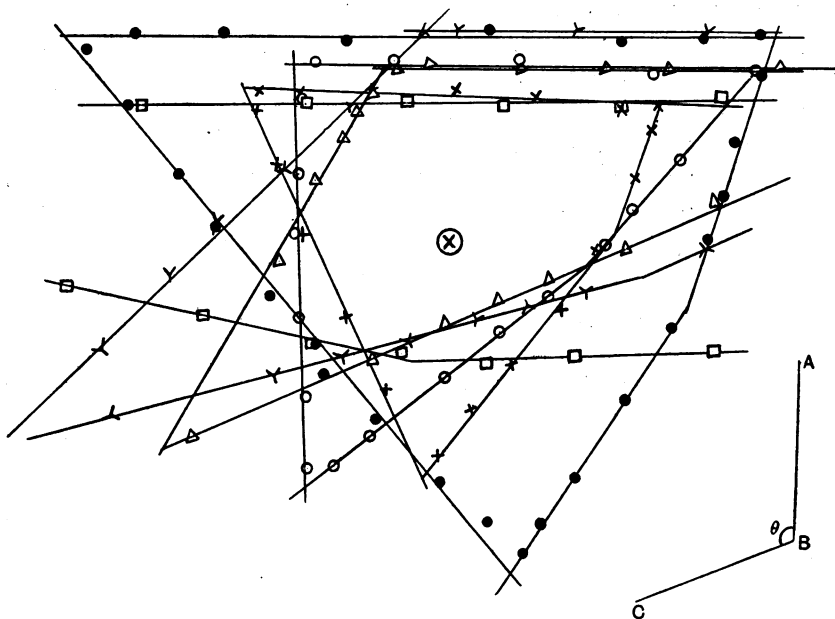


Fig. 3. Curves for nerve bent at various angles.

Order in which determinations were made:  $\square$ ,  $\theta=180^\circ$ ;  $\times$ ,  $\theta=120^\circ$ ;

$\Delta$ ,  $\theta=60^\circ$ ;  $\circ$ ,  $\theta=90^\circ$ ;  $\gamma$ ,  $\theta=45^\circ$ ;  $\bullet$ ,  $\theta=135^\circ$ .

this. Here are plotted the results of six determinations made upon the same preparation with the central limb in various positions as indicated.

The results show quite clearly that when the angle at which the nerve is bent is altered, there is a change in the direction of two out of the three lines of the curve, but the third line remains unchanged in direction, and is only altered somewhat in threshold.

The line which is unchanged is seen to be that which we have already in (a) supposed to represent excitation at the peripheral end; this is still further confirmed by the results when the angle of bend was  $180^\circ$ . In this case we merely have a single stretch, and there is hardly room for doubt that here the line represents excitation at the peripheral end.

But furthermore, from symmetry we should expect that the line representing excitation at the central end would change its direction in each experiment by an angle equal to the change in  $\theta$ , the angle at which the nerve is bent. Of the remaining lines in each curve, one is seen to make with the line that we have just identified an angle of  $180^\circ - \theta$ , the other  $\theta/2$  (roughly). The former set of lines, which meet the identified line at its left end, are therefore to be recognised as representing excitation at the central end. This is confirmed by the case when  $\theta = 180^\circ$ , wherein this line becomes the lower parallel in the case of a single stretch and certainly represents excitation at the central end.

Moreover, the lines are seen to be those which in (a) we supposed to represent excitation at the central end.

The remaining line of the three is that which in (a) we assumed to represent excitation at the bend. Its direction is seen to be symmetrical with respect to the two ends of the nerve, and thus it is not unreasonable to suppose that it does represent excitation at the bend, the one point in the nerve which is thus symmetrical.

By "central end" of course is understood the central extremity of the exposed stretch, *i.e.* the point of entry into tube *C*, and not the actual cut end of the nerve. Similarly with the term "peripheral end."

#### (d) *Localisation by Heat.*

There is thus good evidence that two of the lines in the curve correspond to excitation at the two ends of the exposed stretch, but the evidence that the third line corresponds to excitation at the bend is not so good.

To verify this I made use of the fact that Ringer's fluid at a temperature of  $60^\circ$  C. permanently destroys the local excitability of a nerve, but the main structure is not much affected. The current may thus be supposed to distribute itself as before, but only the region of the nerve which has not been heated will be able to respond to excitation.

*Experiment.* The nerve was set up with its two limbs bent at a suitable angle, and the triangular curve determined in the usual way. Then the central end of the nerve was dipped into Ringer's fluid at  $60^\circ$  C. so that two-thirds of the central limb was immersed. After about two

minutes the nerve was withdrawn and replaced in the stimulating trough; and allowed to rest for half an hour for the destructive processes to subside. Then determinations were made as before. Again the nerve was dipped into Ringer's fluid at 60° C., this time until all but the peripheral end with half the peripheral limb were immersed. After two minutes the nerve was replaced in the trough, and after a delay of half an hour determinations were again made.

*Results.* The results are seen to be entirely confirmatory (Fig. 4).

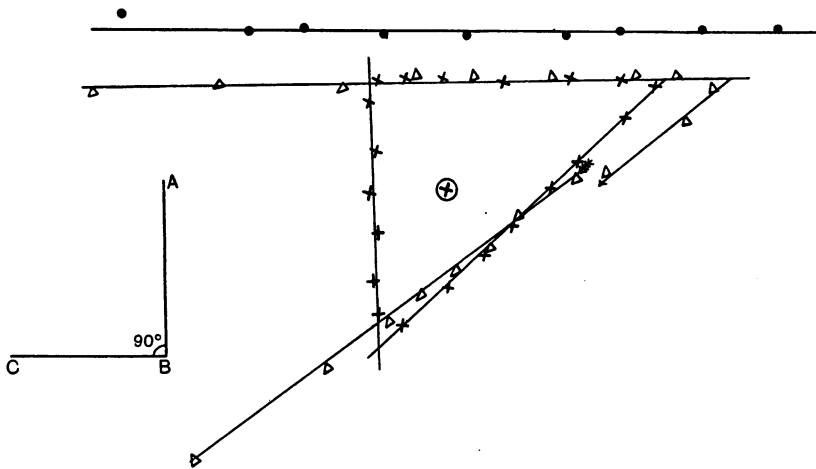


Fig. 4. Localisation by heat.

X, initial determination. Δ, after heating C. ●, after heating B.

Initially a triangle was obtained in the usual way (crosses). After heating the central end of the nerve the side corresponding to this vanished, but the other sides were practically unchanged (triangles). After heating the bend, the side corresponding to this vanished too, showing that its presence depends upon the integrity of some place in the nerve not more than about 5 mm. from the bend.

(In the figure the side corresponding to excitation at the bend appears to have a discontinuity in the curve when the central end had been heated. This is illusory. One of the points was the first of the series of determinations, the other its repetition at the end. During the course of the experiment the threshold had altered from one to the other, due no doubt to the partial recovery from the injury being incomplete at the outset of the observations.)

The curves give good evidence also that the transition from one line to another of the triangle is merely due to the experimental selection of

the lowest threshold in every case. When what was the most excitable point is destroyed, the remaining points must be excited, and the regions of the curve corresponding to these are seen to stretch out indefinitely, continuous with the short regions first observed. This is also demonstrated with the experiments with alcohol shown in Fig. 5.

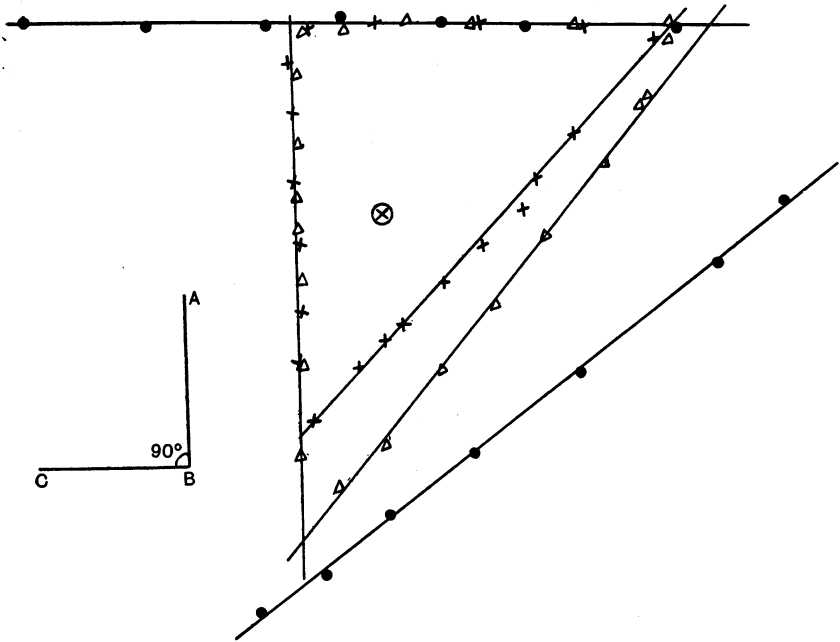


Fig. 5. Effect of application of alcohol to bend.

X, initial determination. ●, 10 min. after application of alcohol. Δ, 20 min. later.

(e) *Localisation by Alcohol.*

To confirm the results of the application of heat locally to the nerve, I tried the effect of local application of alcohol. The principle is somewhat similar, but with the difference that the change of excitability is reversible and gradual. This involves a considerable experimental difficulty because a strictly localised dose of narcotic, even if very strong, is almost completely washed out of the tissue in the half hour or so necessary for the determinations. Most things which prevent the washing out of the alcohol by the fresh solution prevent also the free passage of the stimulating current, but this experiment was made quantitatively possible by the discovery that gelatine in Ringer's fluid, to which is added about 30 p.c. alcohol, will greatly retard the washing out of the



alcohol from the nerve when it has "set" round the narcotised place. And since it has long been known that gelatine does not appreciably alter the conductivity of a solution in which it is made up, it will not appreciably alter the lines of current flow.

*Experiment.* The preparation was set up and the triangular curve obtained as usual. The nerve was then removed from the trough, and 30 p.c. alcohol in Ringer's fluid was applied to the bend, care being taken that it did not escape to other parts of the nerve. After about a minute, alcohol-gelatine-Ringer at room temperature but still liquid was applied to the same place and allowed to "set."

The nerve was then replaced in the trough and allowed to rest for ten minutes. Then the second set of determinations was made as fast as possible. After another interval of some 20 minutes the third set of observations was made.

*Results.* These also entirely confirm the earlier conclusions (Fig. 5). The first curve is the normal triangle (crosses). The second curve (dots), taken soon after the application of alcohol to the bend, shows no change in the line corresponding to stimulation at the peripheral end, a rise of threshold at the bend to about  $2\frac{1}{2}$  times the initial value, and the apparent complete inexcitability of the central end. Since, however, the central end has been no more narcotised than the peripheral end whose excitability is unchanged, the disappearance of the line corresponding to excitation at the central end must be interpreted differently. It is, in fact, due to a conduction block at the bend which prevents the propagated disturbance set up in the central limb from reaching the muscle and being indicated by it. The justification for this conclusion is derived from the third curve (triangles). It is here seen that long before the excitability of the bend has reached normal, the excitability at the central end has completely recovered. It is only necessary that the conduction block be so far lifted as to allow an impulse to pass, for the threshold for the central end to be revealed quite unaltered. The reason that the three lines corresponding to the bend are not parallel is because the threshold was diminishing during the course of the second and third determinations. The second curve (dots) was determined in a clockwise direction, the third curve (triangles) in the reverse direction, hence the opposite inclinations.

The three regions of the curve are thus seen to respond in three different and quite characteristic ways, and thus can once again be identified to confirm the former conclusions.

COMPARISON OF THE OBSERVATIONS WITH THE  
MATHEMATICAL RESULTS.

The mathematical treatment is given in the Appendix to this paper and the results only are quoted here. The capital letters refer to the section of the mathematics where the result quoted is obtained.

Now the mathematics are entirely based upon the assumptions made in the previous paper and summarised at the beginning of this one, and they merely give the quantitative results of the distribution of current in a conductor such as a nerve. In particular, the value of the current leaving the nerve through the sheath at any point is obtained, for this is the current which excites.

Now from the observations so far discussed there is very good evidence, first that they arise from three separate points on the nerve, second that these points are in the regions of the two extremities and of the bend, third that the three are quite independent so that in any position excitation will be elicited from that point where the threshold is least at the moment.

These three conclusions, which are entirely drawn from the experimental results, lend good support to the mathematical theory since they may be exactly deduced from the original assumptions.

It is found (*A*, *C*) that there are in the whole nerve stretch, three points such that the current leaving through the sheath at one or other of them is always greater than at any other point whatever, and hence excitation will always occur at one of these three points with a lower threshold than at any other. It is found, moreover, that the position of these points is exactly where we have supposed them, namely at the bend and at the points of entry of the nerve into the tubes. Finally, since the excitation is assumed to be dependent upon the current leaving the nerve locally, it will be quite independent of local changes of excitability elsewhere.

Since experiment and calculation agree as to the nature of the three portions of the curve obtained, it will be legitimate to go further and to calculate the exact form of the curves.

It is found (*B*) that each of the three portions should be a straight line, and hence the results should be strictly a triangle.

Some experiments (Figs. 2, 4, 5) gave this to a very good approximation, but some (especially the earlier ones) did not. The deviation, when it occurred, was always in the direction of a concavity towards the

origin. It is necessary to discover whether this effect when present indicates a fallacy in the theory, or an experimental error.

We may consider first the lines corresponding to stimulation at the ends of the nerve. The case here is very similar to that of a single straight stretch, and it was natural to suppose that the cause of the deviation in both experiments was the same, namely that the stretch was not quite straight. In confirmation of this it was found that if both the limbs of the nerve were kept stretched rather tightly, the two regions corresponding to excitation at the extremities were exactly straight (Fig. 6).

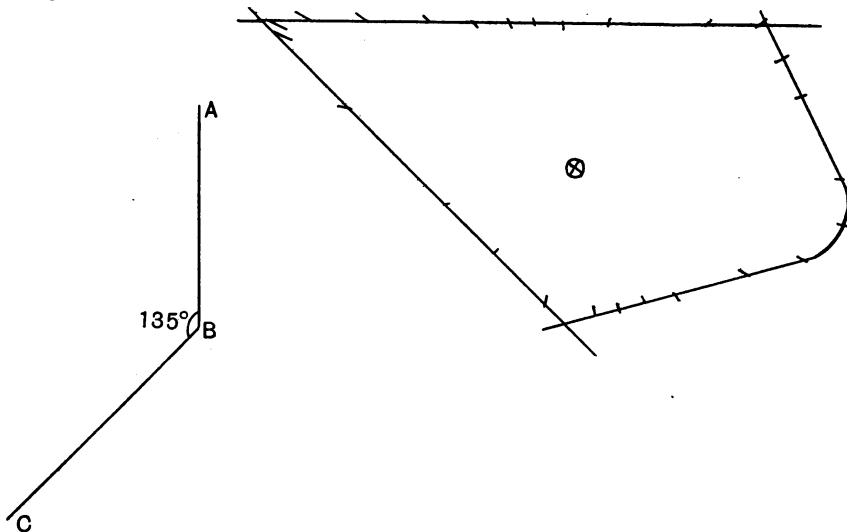


Fig. 6. Nerve constricted at bend.

Stimulation at the bend, however, cannot have the deviation explained in quite the same way. At first I thought that the explanation lay in the fact that the nerve did not bend at a point (as the calculation assumed) but round the arc of a small circle. To diminish this I bent the nerve round a fine silk thread and stretched both limbs. The results showed, however (Fig. 6), that this procedure, far from diminishing the deviation from a straight line, greatly increased it, and at the same time clearly defined the form of it. This region of the curve had split up into two straight lines deviating by a considerable angle: in the case shown this is greater than a right angle.

I observed the bend through a powerful dissecting microscope, and found that the inner edge was greatly compressed by the thread and the outer edge flattened by the pull of the nerve, so that it was constricted

exactly like a badly bent glass tube. It is evident that it is to this constriction that the anomaly was due.

I have calculated the effect of constricting a nerve fibre at the point where it is bent, and it is easy to show that the results in this case are two straight lines instead of one. The deviation between the lines is greater, the greater the constriction, reaching a maximum value equal to  $\theta$ , the angle of the bend.

This matter may be of interest in experiments investigating the action of striction, but it is beyond the scope of the present paper, and I have not thought it worth while to include the above calculation in the Appendix. The only present value of the observation is that on the one hand it indicates that not even these results are necessarily beyond the scope of the theory, and on the other, it confirms the suggestion that the deviation from a straight line is due to the constriction at the bend. Fig. 3 affords other examples of the region of the bend breaking up into two straight lines. In this experiment, again, the nerve was stretched, as was necessary if the peripheral limb was not to change position when the central limb was altered.

It thus appears that the condition for straight lines on two sides of the triangle (namely stretching of the nerve) is opposed to that for the third side. It is therefore a matter of some delicacy to adjust the exact degree of tension to realise all the conditions of the mathematics at once, but it is easy to verify the calculation at will either for the bend or for the extremities in any preparation by having the nerve loose or tight respectively, and in this way it is always possible to get a very good agreement between observation and calculation.

Since the experimental results have been shown to be strictly composed of straight lines, we may finally enquire whether the directions of them are also in conformity with the calculation.

From (C) we find that if  $\theta$  is the angle of the bend, the two lines of the results corresponding to excitation at the ends meet at an angle of  $(\pi - \theta - \cdot 1 \sin \theta)$  measured in radians.

Thus instead of this angle being supplementary to  $\theta$  as was supposed in the intuitive argument above, we find that it is less than this by  $\cdot 1 \sin \theta$  radians which amount to

$$\begin{array}{ll} 4^\circ & \text{when } \theta = 90^\circ \pm 45^\circ, \\ 5^\circ & \text{,, } \theta = 90^\circ \pm 30^\circ, \\ 6^\circ & \text{,, } \theta = 90^\circ. \end{array}$$

When this result is compared with those curves which do not exhibit the striction phenomenon, the angle in question is seen to be always a

little less than  $180^\circ - \theta$ , and the amount less is very close to the required values. The matter cannot be pressed too far, for the method of bending the nerve admits of a zero error of one or two degrees in the reading of  $\theta$ .

With regard to the third side of the triangle, when straight, it appears from (C) that it should meet the other two lines at approximately equal angles. The difference of angles should not exceed  $\theta/15$ . In Fig. 1 this value is somewhat exceeded, but in Figs. 4 and 5 the results are well within the limits.

The more the nerve is constricted at the bend, the less will each extremity be influenced by the condition of the remoter half of the nerve, and the more will the angle first considered approximate to  $180^\circ - \theta$ . This is seen to be actually the case in those curves exhibiting the striction effect. All the curves which indicate great striction give an angle sensibly equal to  $180^\circ - \theta$ , while all the curves showing no striction give an angle sensibly less.

Within the limits of the experiments, therefore, there is a good accord between the calculated and observed values of the angles of the various lines, and the theory put forward in the previous paper is, without any further hypothesis, found to be justified quantitatively in its three main deductions:

(a) The results show three different regions corresponding to the three definite places on the nerve discussed above.

(b) For each region the results, plotted in polar coordinates, are straight lines.

(c) The direction of each line is as predicted.

## APPENDIX.

### MATHEMATICAL TREATMENT OF CURRENT DISTRIBUTION.

In the former paper<sup>(1)</sup> the distribution of current in a nerve was calculated for the simple case where the ends of the nerve were in equipotential solutions, and the intermediate region was exposed to a uniform potential gradient. Since then I have been able to make a considerable advance in the mathematical treatment, and the formula which will be derived in the sequel is superior to the previous one both with regard to its very wide scope, and to the great ease with which it can be applied in most practical cases. It has, moreover, the advantage that it may be deduced from first principles in a few lines.

*Definitions.*

These are the same as in the former treatment, but we may mention

*Analytical Unit of Length* is the length of cylinder which has the same resistance to currents passing axially down the core as it has to currents passing radially through the sheath, and this resistance is defined as the *Analytical Unit of Resistance*.

$x$  = length measured along the nerve in analytical units.

$V$  = potential of core at any point  $x$ .

$U$  = potential applied to outside of sheath at  $x$ .

$$U' = \frac{\partial U}{\partial x^2}, \quad U'' = \frac{\partial^2 U}{\partial x^2}.$$

Then current leaving the core at  $x$

$$= \frac{\partial^2 V}{\partial x^2} = V - U.$$

*Analysis.*

Now the complete primitive of this differential equation, as can easily be verified by differentiation, is

$$2V = 2U + e^{-x} \int_{-\infty}^x e^x U'' dx + e^x \int_x^{\infty} e^{-x} U'' dx + ae^{-x} + be^x. \dots\dots\dots(1)$$

The arbitrary constants may be evaluated from the following assumptions. Both ends of the nerve are in equipotential solutions, the end  $x = -p$  is closed by a membrane of resistance  $r_1$ , the other end  $x = q$  by a membrane of resistance  $r_2$ . Then

$$\left(\frac{\partial^2 V}{\partial x^2} / \frac{\partial V}{\partial x}\right)_{-p} = r_1, \quad \left(\frac{\partial^2 V}{\partial x^2} / \frac{\partial V}{\partial x}\right)_q = -r_2.$$

From (1) we obtain

$$\left(\frac{\partial^2 V}{\partial x^2}\right)_{-p}, \quad \left(\frac{\partial V}{\partial x}\right)_{-p}, \quad \left(\frac{\partial^2 V}{\partial x^2}\right)_q, \quad \left(\frac{\partial V}{\partial x}\right)_q,$$

noting that

$$\left(\frac{\partial U}{\partial x}\right)_{-p} = 0 = \left(\frac{\partial U}{\partial x}\right)_q.$$

Also since  $U$  is assumed to be constant between  $x = -\infty$  and  $-p$ , and between  $x = q$  and  $\infty$ ,

$$\int_{-\infty}^{-p} e^x U'' dx = 0 = \int_q^{\infty} e^{-x} U'' dx.$$

$$\therefore a = \frac{r_1 - 1}{r_1 + 1} e^{-2p} \left[ b + \int_{-\infty}^{\infty} e^{-x} U'' dx \right], \quad b = \frac{r_2 - 1}{r_2 + 1} e^{-2q} \left[ a + \int_{-\infty}^{\infty} e^x U'' dx \right].$$

$$\begin{aligned} \therefore a + b &= \frac{r_1 - 1}{r_1 + 1} e^{-2p} \int_{-\infty}^{\infty} e^{-x} U'' dx + \frac{r_2 - 1}{r_2 + 1} e^{-2q} \int_{-\infty}^{\infty} e^x U'' dx \\ &+ \frac{r_1 - 1}{r_1 + 1} \cdot \frac{r_2 - 1}{r_2 + 1} e^{-2(p+q)} \left[ a + b + \int_{-\infty}^{\infty} (e^x + e^{-x}) U'' dx \right]. \end{aligned}$$

But since  $p + q = \text{total length of nerve} > 6 \text{ units}$

$$e^{-2(p+q)} < 1/160,000.$$

The last term is therefore negligible, and substituting in (1), where  $x$  is put zero, we obtain

$$2 \left( \frac{\partial^2 V}{\partial x^2} \right)_{x=0} = 2(V-U)_{x=0} = \int_{-\infty}^0 e^x U'' dx + \int_0^{\infty} e^{-x} U'' dx + \frac{r_1 - 1}{r_1 + 1} e^{-2p} \int_{-\infty}^{\infty} e^{-x} U'' dx + \frac{r_2 - 1}{r_2 + 1} e^{-2q} \int_{-\infty}^{\infty} e^x U'' dx. \dots\dots(2)$$

Now in all the cases to be considered  $U$  is made up entirely of straight lines, hence  $U''$  vanishes except where two lines meet, and this greatly simplifies the integration.

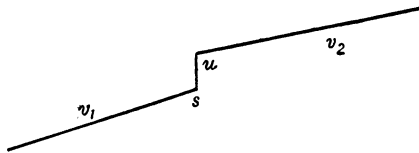


Fig. 7.

If  $U$  is the function shown, such that for values of  $x < s$ ,  $U' = v_1$ ; for  $x > s$ ,  $U' = v_2$ .

Also if  $U_{s+\Delta x} - U_{s-\Delta x} \rightarrow u$  when  $\Delta x \rightarrow 0$ ,

then 
$$\int_{s-\Delta x}^{s+\Delta x} e^{-x} U'' dx = e^{-s} (v_2 - v_1 + u), \int_{s-\Delta x}^{s+\Delta x} e^x U'' dx = e^s (v_2 - v_1 - u), \dots\dots\dots(3)$$

as can be proved by twice integrating by parts.

It thus becomes a matter of the greatest simplicity to integrate (2) by merely applying (3) in turn to each junction of the lines within the range of the integral.

(A) Localisation of Excitation.

The nerve is stimulated by the current leaving it,  $\frac{\partial^2 V}{\partial x^2}$ , and this may be calculated for any function  $U$ , at the point  $x = 0$  from (2). Since the outer limits of the integrals are infinite, we may change the origin, and cause the point  $x = 0$  to coincide with any place on the nerve whatever. In practice, however, we are interested only in that point where the excitation is greatest. For a nerve in a uniform condition this will be the place where  $\frac{\partial^2 V}{\partial x^2}$  is greatest. We proceed to show that if  $U$  is linear between  $x = s_1$  and  $x = s_2$ , then  $\left| \frac{\partial^2 V}{\partial x^2} \right|$ , either at  $s_1$  or at  $s_2$  will be greater than at any intermediate point.

For if we consider (1) it immediately appears that whatever value  $x$

assumes within the range under consideration, the coefficients of  $e^x$  and  $e^{-x}$  are unaltered. We thus obtain

$$2 \left( \frac{\partial^2 V}{\partial x^2} \right)_x = A e^x + B e^{-x} \equiv C \sinh \overline{x + \kappa}, \quad \text{or} \quad C \cosh \overline{x + \kappa},$$

where  $\kappa$  is a constant, and these hyperbolic functions in any range have the value at one extreme numerically greater than all other values in the range.

We thus conclude that the excitation need only be considered at the junctions of the lines which compose  $U$ .

(B) *Application to Experiment with Bent Nerve.*

In the previous paper it was shown that the diameter of a single nerve fibre is so small, and the resistance of its sheath so large, that no sensible error would be introduced in assuming that in any transverse section the potential was uniform over the whole of the core, and over the outside of the sheath. We are, in fact, justified in speaking of the potential of the core, or the potential applied to the sheath, at a certain distance along the axis.

Thus if  $ABC$  is the nerve bent at an angle  $\theta$ , and if the lines of current

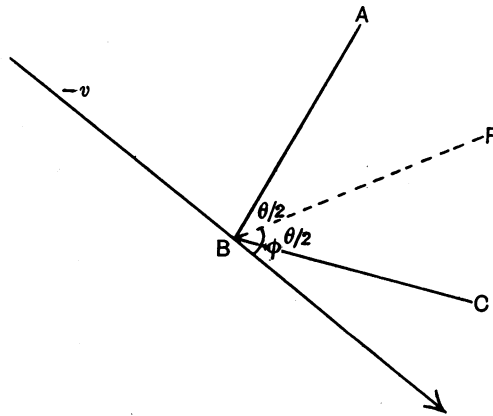


Fig. 8.

flow are in the direction of the arrow, making an angle  $\phi$  with the bisector  $BF$  of the angle  $ABC$ , then the effect on the nerve is found by resolving parallel to the two lines  $AB, BC$ .

If the potential gradient in the direction of the arrow is  $-v$ , then the value in the direction  $AB$  is  $(v \cos \overline{\phi + \theta/2})$ , and in the direction  $BC$  it is  $(-v \cos \overline{\phi - \theta/2})$ .



The whole nerve stretch is thus exposed from the end to *A* in an equipotential region.

*A* to *B* in a region of gradient  $v \cos \overline{\phi + \theta/2}$ .

*B* to *C* in a region of gradient  $-v \cos \overline{\phi - \theta/2}$ .

*C* to the end in an equipotential region.

$AB = BC = s$ .

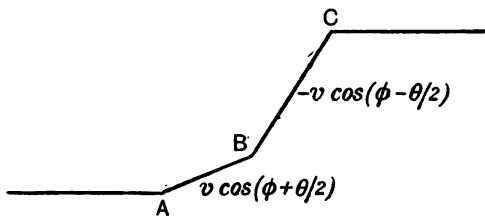


Fig. 9.

Now in (*A*) it was shown that to calculate the threshold excitation we need only consider the points *A*, *B* and *C*, thus we obtain the theoretical result simply by applying formula (2) to the function *U* shown in Fig. 9, where the origin is made to coincide successively with *A*, *B* and *C*.

To obtain numerical values we note that  $s = 3$  units,  $q > 6$  units, hence  $e^{-s} = \cdot 05$  and terms in  $e^{-2s}$  and in  $e^{-q}$  are negligible.

After this simplification we obtain

$$\left(\frac{\partial^2 V}{\partial x^2}\right)_A \propto \cdot 95v \cos \overline{\phi + \theta/2} - \cdot 05v \cos \overline{\phi - \theta/2}, \quad \text{similarly} \quad \left(\frac{\partial^2 V}{\partial x^2}\right)_C;$$

$$\left(\frac{\partial^2 V}{\partial x^2}\right)_B \propto -v \cos \overline{\phi - \theta/2} \left[1 - e^{-s} - \frac{r_2 - 1}{r_1 + 1} e^{-2q+s}\right] - v \cos \overline{\phi + \theta/2} \left[1 - e^{-s} - \frac{r_1 - 1}{r_1 + 1} e^{-2p+s}\right],$$

where the factors of proportionality do not involve  $\phi$ .

Making use of the trigonometrical identity

$$a \cos \overline{\phi + \theta/2} + b \cos \overline{\phi - \theta/2} \equiv c \cos \overline{\phi + \psi/2},$$

where 
$$c^2 = a^2 + b^2 + 2ab \cos \theta, \quad \tan \psi/2 = \frac{a - b}{a + b} \tan \theta/2;$$

$$\left(\frac{\partial^2 V}{\partial x^2}\right)_A \propto v \cos \overline{\phi + \psi/2}, \quad \text{where} \quad \psi/2 = \theta/2 + \cdot 05 \sin \theta \text{ radians (approx.).}$$

(*C*) Thus the experimental results, plotted in polar coordinates  $v, \phi$ , should give two straight lines corresponding to stimulation at the two extremities *A* and *C*, and these lines meet at an angle  $(\pi - \theta - \cdot 1 \sin \theta)$  in circular measure.

Analysing in a similar way the expression for  $\left(\frac{\partial^2 V}{\partial x^2}\right)_B$  we obtain, when  $\theta < 140^\circ$ ,

$$\left(\frac{\partial^2 V}{\partial x^2}\right)_B \propto -v \cos \overline{\phi + \psi}, \quad \text{where} \quad \psi \pm \theta/30.$$

The third side of the triangle is therefore also straight, and within narrow limits its direction is perpendicular to the bisector of the angle of the bend.

#### SUMMARY.

(1) A nerve consisting of two straight stretches bent at an angle was stimulated by a current flowing in parallel lines, and for various values of this angle the relation was found between the threshold and the angle between current and nerve.

(2) Excitation was found to occur at one of three points in the nerve, namely at the bend or at one or other extremity of the exposed region, and the excitatory process at any one of these points was found to be quite independent of the process elsewhere.

(3) The results, plotted in polar coordinates, form a triangle each side of which corresponds to excitation at one of the three points mentioned in (2).

(4) All the results obtained can be deduced theoretically without any new hypothesis from the assumptions made in a previous paper<sup>(1)</sup> and summarised at the beginning of this one.

(5) In the Appendix the mathematical treatment is developed in a form very suitable for application to most questions of the dependence of threshold upon the arrangement of the electrodes.

In conclusion I wish to express my thanks to Dr Adrian for his valuable criticism.

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#### REFERENCE.

1. W. A. H. Rushton. *This Journ.* 63, p. 357. 1927.