THE RATES OF CONDUCTION OF NERVE FIBRES OF VARIOUS DIAMETERS IN CEPHALOPODS

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(With One Plate and Two Text-figures)

INTRODUCTION

All existing estimates of the relation between the diameter of nerve fibres and their rate of conduction have been made by indirect methods. In no case has it been possible to measure the conduction rates of single axons of known diameters. It is not, therefore, surprising that the most various opinions have been given about the relation. All are agreed that large fibres conduct faster than small ones, but the speed has been held to follow the diameter directly, its square, its square root, or some intermediate power (see Erlanger & Gasser, 1937, for summary of the literature).

We have tested the question using the nerves of cephalopod molluscs. These have the great advantage that they contain fibres covering a very wide range of diameters. Moreover, the diameter of the axon of the larger fibres can be measured directly in the unfixed state, thus eliminating the major errors which may result from measurement after fixation. The fibres are all remarkably similar in histological structure, in spite of their differences in size (Young, 1936*c*). None has a fatty sheath stainable with osmium tetroxide, but by the use of polarized light all can be shown to be surrounded by a thin myelin-like sheath (Bear *et al.* 1937). The large fibres are syncytia, produced by fusion of the processes of many nerve cells (Young, 1936 *a*, *b*), whereas the small fibres are probably the processes of single cells.

In addition to attempting to solve the general question of the relation of conduction rate to fibre diameter we were also interested to discover what might be the value of fibres of such large and various diameter to the animals. The giant fibres serve to cause contraction of the circular muscle fibres of the mantle, by means of which a squid or cuttlefish is propelled rapidly through the water (Young, 1938). The interesting feature of the mechanism from the present point of view is that the larger fibres run the greater distances. This suggests various possibilities. Do the large fibres conduct fast enough to allow of a significant saving of time in the reactions of the animals? Does the presence of fibres of varying diameters enable all portions of the mantle to contract at once or in some special metachronal manner?

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METHODS

The animals used were the squid (*Loligo forbesi*) and cuttlefish (*Sepia* (*Eusepia*) *officinalis*) obtained at the laboratory of the Marine Biological Association at Plymouth.[1]

Stellar nerves were dissected out in the manner already described (Young, 1938), long stretches being obtained by following the nerves into the muscles with the aid of a microscope. Sea water was used throughout as a medium.

Conduction velocities were determined by recording the action potential and estimating the difference in time of conduction from a stimulating electrode to nearer and more distant leads. Stimuli were applied repetitively by the discharges of a neon tube at frequencies of about 25 per sec. The connexions of the leading electrodes could be reversed by a switch, so that during each run several responses at each electrode position were recorded.

Both stimulating and recording electrodes were of fine platinum wire covered with platinum black.

The amplifier was a resistance-capacity coupled circuit of conventional type with a time constant of about 1 sec. The extent to which it attenuated high frequencies was unknown but was probably considerable, as no special precautions were taken to reduce the shunt capacities to ground of the input circuits. As the action potential has a sharply rising front this might introduce an appreciable error in estimating the conduction velocity from measurements of the interval between the stimulus escape and the beginning of the action potential. Other objections to this method of calculating the conduction velocity are given below. By using the difference method this source of error from frequency distortion is avoided.

The amplifier was used to feed a soft Cossor cathode-ray oscillograph. No sweep circuit was used, and the deflexions of the spot were recorded on continuously moving bromide. Time marks at intervals of 1/100 sec. were made on the paper by the light of a flash-lamp bulb interrupted by a slotted wheel driven by an electric clock motor.

In a few of the earlier experiments the conduction rate was measured by stimulating alternately through two different pairs of electrodes. This method is subject to error in that the point of stimulation is not known exactly, and its distance from the electrode will not necessarily be the same at the two cathodes. The utilization time, which may be a considerable fraction of the shock-spike interval, may also differ at the two cathodes. These errors become important in the case of the faster fibres, but a few results from the slower fibres obtained by this method have been included in the tables.

In addition to the estimates of the conduction rate obtained by measuring the differences between the times taken to reach the two electrodes it is also possible, from the same records, to estimate the conduction rate from the stimulating elec-

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trode to each lead, assuming that the impulse really starts from the cathode. In many cases these estimates agree well with the more accurate determination given by the difference method, but serious disagreements arise when the conduction distances are short.

ACCURACY OF ESTIMATES

The accuracy of our estimate of the relationship of conduction velocity to fibre diameter is affected by errors which may be classified as follows:

A. *Errors in estimation of conduction rate*

(1) *Physiological.*

The fibres may be altered in their characteristics by removal from the body to sea water, particularly since they give off branches, which must be cut during removal. The magnitude of these effects of ill-treatment cannot be assessed, but possibly all of the recorded rates are slower than those occurring in the body. The error may be systematic if the larger fibres are the more susceptible to damage.

(2) *Temperature.*

As will be seen from the table, the air temperature during the experiments was between 19·5 and 22·1° C. Actual nerve temperatures will depend on humidities and there may be considerable sources of error in this factor. There is no reason to think that they affect the results systematically.

(3) *Lengths between electrodes.*

These were measured with calipers to the nearest 0·5 mm. The measurements are subject not only to errors of reading but also to those due to the fact that the nerve does not always run straight. These errors are not systematic and should not exceed ± 2 % of each observation.

(4) *Conduction times.*

The estimates of these depend on measurement, on the photographs, of the distances between the deflexions of the oscillograph produced by the "escape" of the stimulating current and the beginning of the action potential. Measurements were taken with a travelling scale and vernier reading to 0·1 mm. There is sometimes considerable difficulty in judging the point of inflexion of the record. Errors of as much as ± 10 % of the conduction rate are possible with individual readings, but in all cases successive responses, usually 10–15 at each electrode, were measured, and the difference between the mean times to each electrode taken as the time for conduction between the electrodes. The errors of measurement of time are thus greatly reduced and do not exceed ± 2 % and are not systematic.

B. *Errors in estimation of diameter*

The diameter of the giant fibres, one of which occurs in each of the stellar nerves of *Loligo* (Pl. I, fig. 1), can be measured directly in the fresh state with an ocular micrometer. Measurements were made from the inside of the sheath (Bear *et al.* 1937) and therefore represent the diameter of the axon itself. A serious difficulty is that the diameter of the fibres is not constant. In *Loligo* they increase as they emerge from the stellate ganglion, rapidly reach a maximum and then taper peripherally. In *Sepia* the increase is progressive over a considerable distance. In few cases was the diameter constant over the length whose conduction velocity was measured. Diameters were therefore measured at intervals of 3 mm. along the length of the axon, and the mean diameter of the stretch of nerve between the electrodes was taken for purposes of correlation with the conduction rate. The fluctuation over the portion used was of the order of ± 10 % of the mean, and considerable and unavoidable errors may enter the calculation if the mean value taken does not accurately represent the average diameter of the stretch of nerve used. Such errors would not, however, be systematic.

Besides the giant fibre, each stellar nerve also contains numerous small axons (Pl. I, fig. 1), and measurement of the conduction rate of these greatly extends the range of fibre sizes studied. A serious difficulty arises, however, from the fact that it is not possible to study the rate and diameter of individual fibres. The procedure has therefore been to assume that the rate calculated by measuring to the beginning of the rise of the action potential produced by these fibres as a group is that of the largest fibre in the group. Since the fibres can be measured only in cross-section the nerves were fixed after each experiment in saturated picric acid dissolved in sea water. They were then embedded in celloidin-paraffin, sectioned and stained with Mallory's technique. With this procedure the fibres are excellently preserved, and the degree of shrinkage can be determined by comparing the diameter of the giant fibre measured in the fresh state and in the sections. In this way a good estimate of the diameter of the largest of the small fibres can be obtained, erring probably on the side of being too high, since the giant fibre is likely to shrink proportionately more than the smaller fibres. Further, it must be remembered that there is no guarantee that the largest fibre seen in the section was actually responsible for the beginning of the rise of the recorded action potential.

TOTAL EFFECT OF ERRORS

From consideration of all of these sources of error it may be expected that estimates of the relationship of conduction rate to fibre diameter will differ from the theoretical value by ± 5 % on account of observational errors. The only serious systematic sources of error are the possible damage to the fibres produced by removal from the body, and the estimate of the diameter of the smaller fibres.

SHAPE OF THE ACTION POTENTIAL OF STELLAR NERVES

The action potential resulting from the application of a strong stimulus to a stellar nerve of either *Sepia* or *Loligo* consists of an initial fast wave followed by a later hump, which itself often contains two maxima (Pl. I, figs. 2, 5). If the giant fibre be crushed the fast wave no longer appears. There can therefore be no doubt that the fast wave is produced by the giant fibre, the later waves by the small fibres in the nerve. The threshold for the giant fibre is usually much lower than for the small fibres (see Young, 1938), so that the former can be stimulated separately.

In *Sepia* each stellar nerve, where it leaves the ganglion, contains several large fibres which may run together throughout the nerve. In some cases we have been able to recognize the existence of two fibres by their different thresholds. It is usually possible to find a stretch at the periphery in which only one large fibre is present.

SHAPE OF THE ACTION POTENTIAL OF SINGLE FIBRES

With two leads on intact portions of the nerve the action potential of single giant fibres is of the usual diphasic form (Pl. I, fig. 2*a*). Very often, however, in addition to the main spikes and crests, various intermediate oscillations of potential are recorded (Pl. I, figs. 2*b*, 3*b*, 4*b*). The pure diphasic potentials are generally obtained when the leads are close together and the most complex pictures when they are farthest apart. This makes one suspect that the intermediate oscillations are in some way due to branches which occur at intervals of a few millimetres along the giant axons of *Loligo*, becoming more frequent towards the periphery.

RELATION OF CONDUCTION RATE TO FIBRE DIAMETER

Forty-five estimations of conduction rate were made, and Table I shows the thirty-nine of them which have been selected for consideration. The remaining six readings were aberrant for known reasons, one being made on a nerve taken from a dead animal, two on very short pieces of nerve and three on fibres found subsequently to be damaged.

Conduction rates range from 2·2 to 22·8 m./sec. and diameters from 30 to 718μ. The larger fibres evidently conduct faster than the smaller, and in favourable cases it was sometimes possible to show that in one and the same fibre the thicker regions conduct more rapidly than the thinner. As would be expected from the analysis of sources of error summarized on pp. 455, 456, there are considerable deviations: fibres of the same diameter often seem to differ considerably in conduction rate. In order to discover what relation the data enable us to suggest for conduction rate to diameter the regression coefficient, b, of the logarithm of the conduction rate, y, on the logarithm of the diameter, x, was calculated from

$$b = \frac{Sy\,(x - \bar{x})}{S\,(x - \bar{x})^2}.$$

This was done first using all the data from nerves of *Sepia* and *Loligo* together, and the coefficient found is $0{\cdot}614 \pm 0{\cdot}027$. The corresponding plot and regression lines are shown in Text-fig. 1, and it will be seen that a straight line fits the data reasonably well, though the large *Sepia* fibres conduct somewhat slowly. We are making a great assumption in treating together not only the giant and small fibres, which have different functions, but also fibres from such differing animals as *Sepia* and

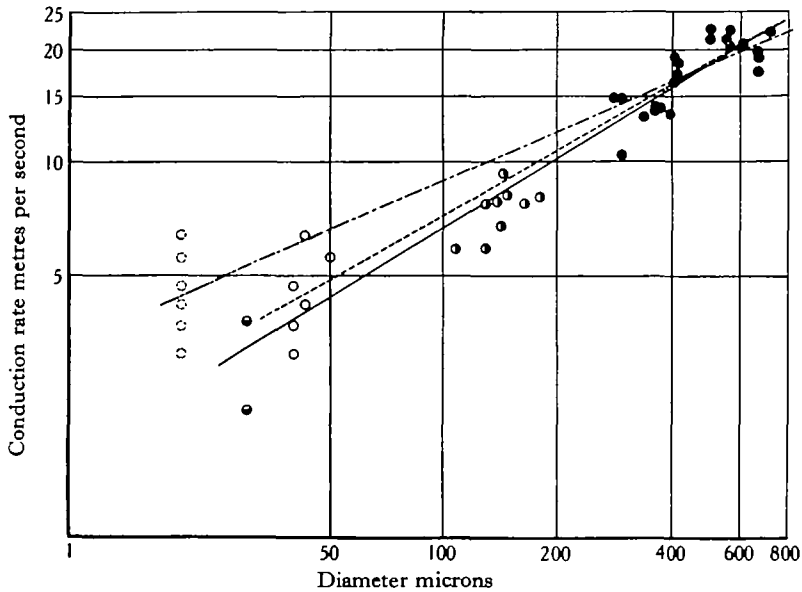
Table I. *Conduction rates and fibre diameters*

Animal	Position of nerve	Diameter μ	Velocity m./sec.	$T°$ C.
Loligo AAIai	Ultimate	718	22·3	21·7
Loligo AAKaii	Ultimate	669	19·1	21·7
Loligo AAKbi	Ultimate	667	17·6	21·7
Loligo AAKai	Ultimate	665	19·9	21·7
Loligo AAIaii	Ultimate	610	20·8	21·7
Loligo AADai	Ultimate	567	20·5	21·2
Loligo AAGa	Ultimate	567	22·6	22·1
Loligo AACaii	Ultimate	554	21·4	20·5
Loligo AABai	Ultimate	503	22·8	20·5
Loligo AABaii	Ultimate	503	21·3	20·5
Loligo AAFa	Ultimate	415	18 6	21 2
Loligo AADb	Penultimate	413	17·4	21·2
Loligo AACb	Penultimate	409	19·3	20·5
Loligo AADcii	Antepenultimate	403	16·5	21·2
Loligo AAHc	Antepenultimate	394	13·5	19·5
Loligo AAHdii	Penultimate	371	14·0	19·5
Loligo AACc	Antepenultimate	360	14·1	20·5
Loligo AAHb	Penultimate	357	13·8	19·5
Loligo AAHe	Antepenultimate	336	13·3	19·5
Loligo AAGd	Preantepenultimate	294	11·0	22·1
Loligo AAFb	Penultimate	292	14·9	21·2
Loligo AAEbi	Penultimate	280	15·0	22·0
Sepia KD	Ultimate	180	8·1	19·7
Sepia IO	Ultimate	164	7·8	21·0
Sepia IRa	Ultimate	148	8·2	21·2
Sepia IRb	Ultimate	145	9·4	21·2
Sepia IXb	Ultimate	143	6·8	21·0
Sepia IXa	Ultimate	139	7·9	21·0
Sepia IM	Ultimate	130	5·9	21·0
Sepia IT	Ultimate	130	7·8	22·1
Sepia IU	Ultimate	108	5·9	20·5
Loligo AADaii	Small fibres	50	5·6	21·2
Loligo AAEa	Small fibres	43	4·2	22·0
Loligo AAEb	Small fibres	43	6·4	22·0
Loligo AAEd	Small fibres	40	3·7	22·0
Loligo AAFb	Small fibres	40	4·7	21·2
Loligo AAGb	Small fibres	40	3·1	22·1
Sepia ICc	Small fibres	30	3·8	20·8
Sepia IM	Small fibres	30	2·2	21·0

Loligo. This assumption is shown to be reasonable by calculating the regression coefficient of log. conduction rate on log. diameter for *Loligo* alone. This gives b, $0{\cdot}575 \pm 0{\cdot}028$, a figure which is not significantly different from that for the two animals together. The corresponding regression line is shown dotted on Text-fig. 1. The data, therefore, do not show that the fibres of *Sepia* differ from those of *Loligo* in the relation which conduction rate bears to diameter. This is of course not proof that there is no such difference, but certainly it cannot be large. It is striking that

the conduction rates of such varied fibres, from animals belonging to different suborders, should be expressible as a single function of the diameter.

Before we can make a final estimate of the relation of conduction rate to diameter it is necessary to consider the possible effects of the sources of systematic error considered on p. 456. There was seen to be reason to suppose that the diameters of the small fibres were overestimated. In order to test the maximum possible effects of this error the regression coefficient of log. conduction velocity on log. diameter was calculated, for *Loligo*, on the assumption that the small fibres responsible were



Text-fig. 1. Plot of logarithm of diameter of fibres against logarithm of conduction velocity. ● *Loligo*, giant fibres: ○ *Loligo*, small fibres; ◑ *Sepia*, giant fibres; ◒ *Sepia*, small fibres. —— regression line using all of the data: b, 0·614; a, −0·401. ---- *Loligo* points only: b, 0·574; a, −0·285. ·---· *Loligo*, calculated on the assumption that all of the small fibres have diameter 20μ: b, 0·439; a, +0·074.

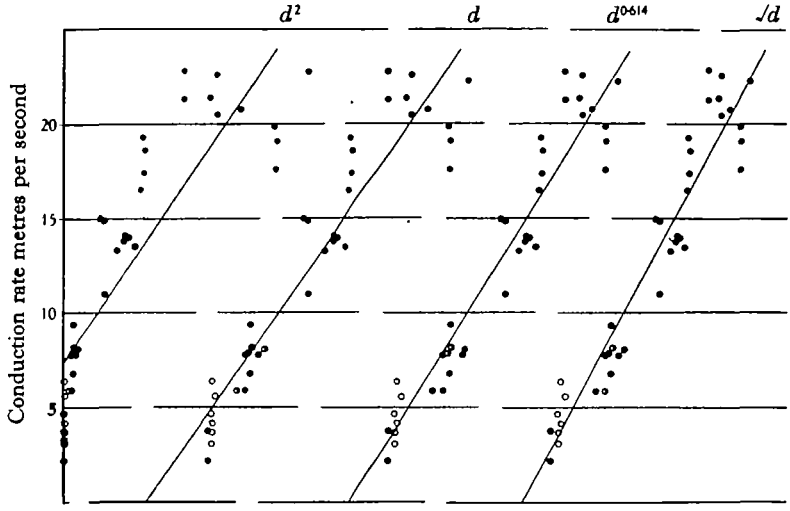
of diameter 20μ in every case, which is certainly an underestimate. The regression coefficient is $0{\cdot}439 \pm 0{\cdot}074$, a result significantly different from that previously obtained. The corresponding line is shown with dots and dashes on Text-fig. 1. It will be seen that if this were the correct line for *Loligo* it would no longer be possible to fit the data for the two animals, even approximately, by a single line.

The data show then that, for *Loligo*, the conduction velocity increases approximately as the square root of the diameter. In order to express this result graphically, and to show the failure of other hypotheses to fit the data, the regression coefficients of conduction velocity have been calculated for various powers of the diameter, namely, 0·5, 0·61, 1, 2. In each case the residual variance of the speed, i.e. that part of it which is not due to the regression, has been calculated, and is of course least for the best fit:

Power	0·5	0·614	1	2
Residual variance ...	135·95	133·09	168·48	467·66

The total variance of the velocity as found in these data is 1658·06, and the minimum residual after the best line has been fitted is 8 % of the total, which is approximately what would be expected in view of the known sources of non-systematic error listed on p. 455.

In Text-fig. 2 there are plotted the points relating conduction rate to each of the suggested powers. It will be seen that the hypothesis that the speed varies with the square of the diameter is quite untenable for these fibres, the rate of increase of speed with diameter being far too slow. The hypothesis that the relationship is to the first power of the diameter would also require a greater increment of speed with diameter than is actually found. The difficulty of fitting a line with a slope of



Text-fig. 2. Plots of conduction velocity against various functions of the diameter of the fibres. Symbols as in Text-fig. 1. The lines are the corresponding regression lines, arithmetically calculated.

45° to the points of Text-fig. 1 also shows this very clearly. The square root hypothesis, though it gives slightly too small an increment of speed with diameter, is not excluded by the data.

There remain to be considered the possible systematic errors which result from removal of the nerves from the body. It is possible that the large fibres are slowed in conduction more than the small. If the fastest of the larger fibres alone were considered, the increment of speed with diameter would be somewhat greater than that given by the above calculations, but even so would not reach as high as the first power. With all of these qualifications, therefore, we are still able to say that in these cephalopods the conduction rate varies approximately as the square root of the diameter of the fibres.

RATE OF CONDUCTION AND THICKNESS OF MYELIN SHEATH

None of the previous observations on the rates of nervous conduction in cephalopods have been made on nerves which contain very large fibres.[1] Arvanitaki *et al.* (1936) used the visceral nerve of *Sepia* which contains axons of 50μ in diameter (Young, unpublished), and found maximum rates of 4 m./sec. Bogue & Rosenberg (1934) found 4·0–6·9 m./sec. in the fin nerve of *Sepia*, whose largest fibres approach 50μ (Young, 1936*c*), while Jenkins & Carlson (1902) found 4·3 m./sec. in the corresponding nerve of *Loligo pealii*, whose fibres are somewhat larger. Various workers have studied the mantle connective of octopods and reported conduction rates up to 5·5 m./sec. (Winterstein, 1913). The values obtained during the present work for the conduction velocity of fibres up to 50μ therefore agree with those of others as closely as differences of technique and temperature would lead one to expect. It seems not unlikely that the conduction rate of all the nerve fibres of cephalopods can be expressed as a single function of the diameter. Indeed, it is possible that a single relation applies to all molluscs, since the nerves of lamellibranchs and gastropods, which conduct at rates of 0·5 m./sec. or less, contain very small fibres.

The velocity of conduction in other groups of animals cannot however be forecasted from the data for molluscs. The differences may be due to a variety of factors, but it seems that the main variable between the fibres of different groups is the thickness of the myelin sheath. Animals seem to differ in their capacity to lay down oriented layers of lipoids around the axons, possibly as a result of fundamental differences in diet or chemical make-up.

In cephalopods the myelin-like sheath is always very thin, not more than 1 % of the diameter of the axon (Bear *et al.* 1937), and it cannot be revealed by staining with osmium tetroxide (Young, 1936*c*). In these animals, therefore, increase in conduction velocity has been obtained by great increase of size of the fibres. The giant fibres of earthworms are smaller than those of cephalopods (about 100μ in diameter), and are also divided into segments, yet they conduct at rates of 17–25 m./sec. (Eccles *et al.* 1932). This relatively faster conduction may well be due to the presence of sheaths which stain with osmium tetroxide, are negatively birefringent and occupy about 5 % of the diameter of the axon (Friedlaender, 1889).

Among the Crustacea some groups contain fibres which are surrounded by thick, negatively birefringent myelin sheaths (Retzius, 1888; Nageotte, 1922; Göthlin, 1913). The conduction velocity of these fibres is not known, and the leg nerves of the forms commonly used for investigation are mostly positively birefringent. However, they can be shown by the metatropic reaction to contain oriented lipoids in the inner sheath (Bear & Schmitt, 1937), and this lipoid is just

[1] During the summer of 1936 the nerves of *Loligo pealii* were studied briefly by Dr H. K. Hartline and J. Z. Y. If a drop of sodium citrate (1–10 %) is placed on the end of the nerve a series of impulses is set up in the giant fibre, which continues to discharge for some minutes at a frequency of about 200 per sec. By leading diphasically, the rates of conduction of the impulses in these discharges were approximately determined. The values found, though irregular, were similar to those in the present series, for instance a fibre of 532μ conducted at 21 m./sec., and some small fibres in a stellar nerve at 3·8 m./sec.

detectable histologically by the darker staining of these layers with osmium tetroxide (Young, 1936*c*). The myelin-like layer is estimated by Bear & Schmitt to be about 5 % of the diameter of the axon. Now the largest axons of *Maia* (10–20μ, excluding the outer sheaths) conduct at 3–5 m./sec. at 20° C. (Lullies, 1934; Auger & Fessard, 1934; Bogue & Rosenberg, 1936). Those of the crayfish conduct at 3–4 m./sec. (du Buy & Coppée, 1936),[1] and of *Homarus*, in which the sheath may sometimes be negatively birefringent (Bear & Schmitt, 1937), considerably faster, up to 9 m./sec. (Monnier & Dubuisson, 1932; Auger & Fessard, 1934). As Lullies has pointed out, these rates of crustacean nerves are slower than those of fibres of similar diameter in vertebrates. But they are somewhat *faster* than would be expected for such fibres in cephalopods, whose sheaths are thinner.

Among the vertebrates, where the sheath occupies about 25 % of the axon diameter, the conduction is relatively much faster than in any of the above groups. Schmitt & Bear (1937) suggest that the larger fibres also have relatively the thicker sheaths. Unfortunately it has not yet been possible to discover the relationship between diameter, sheath proportion and conduction velocity in vertebrates. However, from the above analysis of the data for various groups it is already clear that, as suggested by Bear & Schmitt, relative thickness of sheath is an important factor in determining the conduction velocity. We can recognize a series in which the relative thickness of the myelin-like layer and the conduction velocity of fibres of a given size increase together, thus: Cephalopoda < Annelida = Crustacea < Vertebrata. The occurrence of this parallelism can hardly be accidental, and although more accurate data are needed for quantitative treatment it seems clear from the information which we have that the layer of oriented lipoids serves to accelerate the propagation of the nerve impulse in proportion to its thickness.

VALUE OF THE GIANT FIBRES TO THE ANIMAL

It is possible to assess roughly the saving of reaction time which the possession of giant fibres makes possible for the squid. Measurements of the total reaction time are not available, but the shortest pathways from the receptor to the muscles of the mantle are known to involve six synapses from the eye and three from the statocyst (Young, unpublished). In the stellate ganglion of *Eledone* Fröhlich (1910) found a synaptic delay of 10 msec., and the data of Bogue & Rosenberg (1934) indicate a much shorter one for the giant fibres of the same ganglion of *Sepia*. In *Loligo* the synaptic delays are almost certainly shorter still, but if we take 5 msec. we shall have an outside estimate and may then neglect the delay in the receptor cells themselves, and in the short intracentral pathways. The time from the occurrence of a movement in the visual field to the starting of the impulses in the stellar nerves will therefore be not more than 30 msec.; for impulses coming from the statocyst the figure is probably as low as 15 msec.

[1] It will be noticed that these fibres of fresh-water animals conduct at rates of the same order as those of their marine relatives. Unfortunately, the diameters and rates of the fibres are not properly known in either case.

The length of the longest stellar nerve of a large squid is about 30 cm., along which conduction at 22 m./sec. would take 13·6 msec. Thus, allowing for a peripheral delay of 10 msec. (Young, 1938, almost certainly an overestimate), we find that the squid begins to get under way not more than 55 msec. after a movement in the visual field, or 39 msec. after a disturbance of the statocyst; probably it starts even sooner. The corresponding figures for a large *Sepia*, assuming 23 cm. of mantle length and 12·2 m./sec. conduction rate (see Table III) are 59 and 44 msec.

These figures may prove to be inaccurate, but they are not likely to be too low; yet they show that the proportion of the total reaction time occupied by conduction in the longest stellar nerve is for optic reflexes 25 % in *Loligo* and 32 % in *Sepia*, and for static reflexes 35 and 43 % respectively. Assuming that the squid had no fibres larger than 50μ, conducting at say 5 m./sec., the delay in the nerves would be 60 msec. and the reaction time 100 msec. for optic stimuli. A squid therefore saves at least half of the time which an animal without giant fibres would spend in starting.

It is clear that this saving is likely to be of very considerable survival value. When the above estimates of the reaction time can be replaced by actual observations it may be possible to assess exactly the advantage which would accrue with a further increase in speed, and to explain why selection seems to have stopped in *Sepia* with fibres much smaller than those of *Loligo*.

SIGNIFICANCE OF PRESENCE OF FIBRES OF DIFFERENT DIAMETERS

In a medium-sized squid the lengths of each of the stellar nerves was measured from the ganglion to the midventral line (i.e. to the limit of its distribution) and the diameter of its giant fibre determined. Assuming conduction rates calculated from the *Loligo* regression line of Text-fig. 1 we obtain Table II.

Table II

Diameter μ	Conduction rate m./sec.	Length mm.	Time to edge msec.	Time at 5 m./sec. msec.	Time at 20 m./sec. msec.
83, 116, 150	9·0	19	2·1	3·8	0·9
150	9·0	22	2·4	4·4	1·1
217	11·4	37	3·2	7·4	1·8
283	13·5	36	2·7	7·2	1·8
317	14·3	48	3·4	9·6	2·4
350	15·0	63	4·2	12·6	3·1
440	17·5	82	4·7	16·4	4·1
583	20·5	115	5·6	23·0	5·7

In the last two columns there have been calculated the times at which the impulses would arrive if all of the fibres conducted at 5 and 20 m./sec. respectively. Of course all of the calculations oversimplify and perhaps falsify the situation in that they suppose the fibres to be of uniform diameter throughout their length.

It is clear from Table II that although the presence of fibres of varying diameters does not quite ensure that all parts of the mantle shall contract together, yet it does considerably reduce the differences which would occur if no giant fibres were present. If all of the fibres were of equal and *large* diameter the absolute differences in time of contraction of the various muscles would be a little greater than it actually is, the relative time differences would be considerably greater.

Sepia is much broader relative to its length than is *Loligo*, so that the stellar nerves are more nearly equal in length. The giant fibres are also more nearly similar in diameter. Measurements corresponding to those of Table II have been made for a very large *Sepia*, and are given in Table III.

Table III

Diameter μ.	Conduction rate m./sec.	Length mm.	Time to edge msec.	Time at 3 m./sec. msec.	Time at 12 m./sec. msec.
234	11·2	46	4·1	15	3·8
100	6·6	60	9·1	20	5·0
167	9·1	84	9·2	28	7·0
184	9·6	82	8·5	27	6·8
167					
150					
134					
150	8·5	81	9·5	27	6·8
200	10·2	83	8·1	28	6·9
184					
167					
117					
117					
284	12·6	83	6·6	28	6·9
250	11·7	87	7·4	29	7·2
200					
117					
100					
284	12·6	96	7·6	32	8·0
250					
200					
167					
83					
184	9·6	125	13·0	42	10·0
216	10·6	140	13·2	47	11·6
200					
150					
267	12·2	192	15·8	64	16·0

Since there is often more than one giant fibre in each stellar nerve it has been assumed for calculation that the largest fibre in the trunk is the one which reaches to the ventral limit of the territory innervated by that nerve.

It will be noticed from the tables that the *Sepia* chosen was actually longer than the *Loligo*, but that the latter had the larger fibres. Evidently the saving of time, by itself, is not the only reason for the presence of the large fibres. In the *Sepia* table it will be seen that the diameters do not vary in any very regular manner with the lengths of the nerves in which they run, and they do not ensure that all of the muscles contract together, though their presence does reduce the discrepancies which would exist in an animal with no large fibres. It seems, therefore,

that in *Sepia*, with it rounder shape, selection has not operated to produce fibres of sizes which vary in a regular manner, and that this latter arrangement has developed only in the long-bodied squids.

SUMMARY

1. The rates of conduction of nerve fibres of *Sepia* and *Loligo* varying from 30 to 718μ in diameter have been estimated from records of their action potentials. The limits of conduction velocity were found to be 2·2–22·8 m./sec. at 20° C.

2. Although the fibres examined have different functions, and come from animals which differ considerably in structure and mode of life, yet the conduction rates of all of them can be approximately expressed as a single function of the diameter. These fibres, therefore, do not differ greatly from each other in any respect but size.

3. Calculation of the regression coefficient of the log. of the conduction rate on the log. of the diameter of the fibres shows that the rate increases with the power $0{\cdot}614 \pm 0{\cdot}027$ of the diameter. On account of various sources of error however the exact relation does not necessarily lie within these limits, but it is not likely to be very far from the square root.

4. The possession of giant fibres produces a significant saving of time for the animal, it being calculated that the reaction time of a squid is about half that of a similar animal without giant fibres.

5. The presence of rapidly conducting fibres is probably also an advantage in that it decreases the discrepancies between the times of contraction of parts of the mantle at varying distances from the central nervous system. In *Loligo* there is a graded series of fibres with the larger in the longer nerves, and this is apparently a further device for ensuring more nearly simultaneous contraction.

6. The relative thickness of the myelin-like sheath increases from about 1 % of the diameter of the axon in cephalopods to 5 % in Crustacea and annelids and 25 % in vertebrates: the conduction velocity of fibres of a given size also increases in the same series. This parallelism provides strong support for the view that the layer of oriented lipoids increases the velocity of propagation of the nerve impulse in proportion to its thickness.

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EXPLANATION OF PLATE I

Fig. 1. Photograph of transverse section of stellar and fin nerves of *Loligo pealii*. Fixed picroformol, embedded celloidin-paraffin and stained with Masson's stain. *f.n.* fin nerve; *g.f.* giant fibre; *st.n.* stellar nerve.

Fig. 2. This and figs. 3 and 4 are action potentials from stellar nerves of *Loligo forbesi*. All read from left to right, the first deflexion being the stimulus artefact. (*a*) Record with earthed electrode *E*(2) more distant from cathode, (*b*) with earthed electrode *E*(1) nearer to cathode. Distances in mm.:

Cathode ... 14·8 ... Earth 1 ... 12·2 ... Earth 2 ... 4·7 ... Grid.

Conduction rates between *E*(1) and *E*(2) are therefore 14·9 m./sec. for the fast fibre (diameter 292μ) and 4·7 m./sec. for the beginning of the slow wave. Nerve *AAFb*.

Fig. 3. Showing complex changes of potential between electrodes placed far apart. (*a*) Earthed lead far from cathode, (*b*) close to cathode. Distances in mm.:

Cathode ... 12·0 ... Earth 1 ... 14·2 ... Earth 2 ... 10 ... Grid.

Nerve *AAGc*.

Fig. 4. Complex changes of potential with the final wave the smaller. (*a*) Earthed lead far from cathode, (*b*) close to cathode. Distances in mm.:

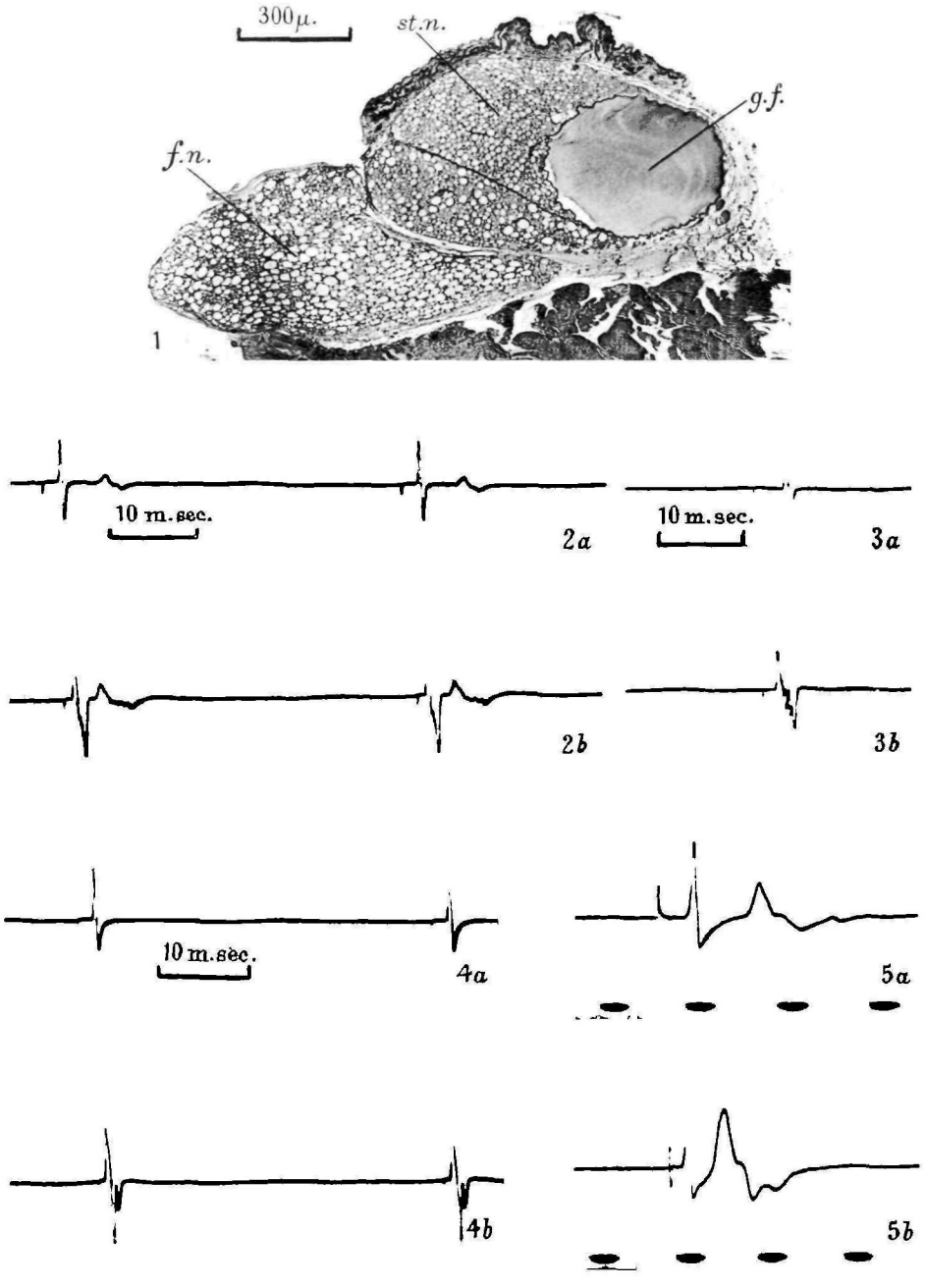
Cathode ... 11 ... Earth 1 ... 16·2 ... Earth 2 ... 13 ... Grid.

Nerve *AAFa*.

Fig. 5. Action potentials of stellar nerve of *Sepia officinalis*, stimulated by two pairs of electrodes. (*a*) Stimulating electrode more distant from earthed lead, (*b*) nearer to earthed lead. Distances in mm.:

Cathode 1 ... 11·3 ... Cathode 2 ... 7 ... Earth ... 4 ... Grid.

Conduction rates between *C*(1) and *C*(2) are therefore 5·9 m./sec. for the giant fibre (diameter 130μ) and 2·2 m./sec. for the front of the slow wave. Time intervals 10 msec. Nerve *IM*.



PUMPHREY AND YOUNG.—THE RATES OF CONDUCTION OF NERVE FIBRES OF VARIOUS DIAMETERS IN CEPHALOPODS (pp. 453—466).