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THE GEOMETRICAL FACTORS DETERMINING THE ELECTROTONIC PROPERTIES OF A MOLLUSCAN NEURONE

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SUMMARY

1. Light and electron micrographs of sections of the gastro-oesophageal giant neurone (G cell) of the nudibranch mollusc, *Anisodoris nobilis*, show that its somatic and axonal membranes are deeply infolded. The surface and volume of its soma and axon have been calculated from measurements taken at the light and electron microscope on sections of the G cell.

2. The surface of the soma is approximately 7·5 times as large as that of a sphere having the same volume. For a typical cell the soma has a volume of $1{\cdot}5 \times 10^{-5}$ cm^3 and a surface of 2×10^{-2} cm^2; the axon has a volume of 5×10^{-5} cm^3 and a surface of 5×10^{-1} cm^2.

3. Because the axon is star shaped in cross-section, its geometry cannot be described by a single parameter (diameter or radius). Furthermore, the axon is beaded, and both the area (A) and the perimeter (P) of its cross-section change from point to point.

4. However, in spite of the apparent irregularity of their cross-sections, all axons examined could be characterized by a constant A/P ratio. This ratio also remains constant when the axons are stretched.

5. According to the equations derived in the Appendix, the geometrical factor for the length constant in a folded fibre is $H = \sqrt{(A/P)}$; therefore, in the G cell the length constant (and hence the conduction velocity) should be independent of the stretch applied to the axon.

6. The geometrical factor required to calculate the axonal input conductance is $M = \sqrt{(A \,.\, P)}$. M changes in adjacent segments of the same axon; in each segment its value depends on how much the axon is stretched.

7. The input conductance of the whole axon can be calculated by

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applying a modified form of Rall's equations for dendritic trees. The results suggest that the input conductance of the G cell axon should vary with stretch and should be large in comparison to that of the soma.

INTRODUCTION

Although the giant neurones of the gastropod Molluscs are commonly used for basic neurophysiological investigations (Kandel, Castellucci, Pinsker & Kupfermann, 1970; Tauc, 1967), the relationship between the electrical and the geometrical properties of these cells has never been studied. Typically, the neurones of the Gastropods are monopolar (Hanström, 1928) and, therefore, their equivalent electrical circuit should be reduceable to the simple case of a sphere (soma) coupled to a cable (axon) (Meves, 1968). There are, however, two complicating factors. First, there are numerous and deep folds in the surface of both the soma (Amoroso, Baxter, Chiquoine & Nisbet, 1964; Borovyagin & Sakharov, 1965; Coggeshall, 1967) and of the axon (Batham, 1961; Schlote, 1957). Secondly, it is known that the axons of the Gastropods can be stretched up to 2–3 times their resting length without altering their conduction properties (Goldman, 1961). Thus, the problem is how to account for the complex and variable geometry of the molluscan neurons when considering their electrophysiological properties.

We have studied this problem in the giant neurone (G cell) of the gastro-oesophageal ganglion of the nudibranch mollusc *Anisodoris nobilis* (MacFarland). In this paper we show how the data obtained in a quantitative morphological study of both the soma and the axon can be related to the electrical properties of the cell using a general form of the cable equation (derived in the Appendix). Our results indicate that the geometry of the axon can be described by two factors. The first one, determining the conduction velocity, remains constant when the fibre is stretched. By contrast, the second, determining the input conductance of the axon, is variable with stretch. Because of its large surface to volume ratio, the axon should contribute substantially to the input conductance of the G cell; thus this important electrical parameter of the whole neurone should be regarded as a variable. A preliminary report of this study has already appeared as an abstract (Mirolli, 1970).

METHODS

The G cell of *Anisodoris nobilis* is located in a chain of small ganglia and nerves which innervate the oesophagus. The soma is found in the gastro-oesophageal ganglion, and the axon in the medial branch of the gastro-oesophageal nerve (Gorman & Mirolli, 1969).

The soma, containing a bright orange pigment, is clearly visible at the dissecting

microscope. The major (*a*) and minor (*b*) axis of its outline, measured during the dissection, provide a convenient index of the dimensions of the living cells, which can be correlated with the measurements of surface and volume taken on fixed and sectioned material. The specimens were prepared for light microscopy according to the following schedule. First, the entire oesophagus was fixed with 3·0 % glutaraldehyde in a 0·5 M solution of sucrose buffered to pH 7·5. The buffer used was Na and K phosphate with cations being present in equimolar amounts; the molarity of the fixative was 0·070 with respect to the buffer only. After a preliminary fixation of 1–2 hr, the gastro-oesophageal ganglion and selected pieces of the medial nerve were excised and further fixed overnight. They were rinsed several times with a buffered sucrose solution and post-fixed in 2 % OsO_4 (same buffer) for 1 hr. The pieces were then dehydrated with acetone, cleared in toluene, and embedded in Maraglas. During fixation and dehydration the specimens were kept in an ice bath to minimize swelling. Care was taken to properly orient the specimens in the embedding moulds so that sections could be cut in a plane perpendicular to the long axis of the nerve.

The sections, 1 μm thick, were stained with *p*-phenylendiamine (0·5 % in water), and studied with a phase-contrast microscope. The cross-sections of the G cell were drawn at the camera lucida. The drawings were then inked and enlarged; the perimeter, P, was measured with a measuring wheel, and the area, A, with a polar planimeter. Complete series of the soma were obtained for eleven cells. In each series A and P were measured in every tenth section and were plotted as ordinates in graphs in which the abscissae were proportional to the distance of the section from the most rostral point of the ganglion (Text-fig. 1). From the areas bounded by the X axis and the curves P and A respectively, the surface and the volume of the soma was obtained by graphical integration (Eranko, 1956). The axons were measured in sixteen cells. Since the axon is several centimetres long, it was impractical to obtain complete serial reconstructions. Therefore only segments 1–2 mm long, cut at different distances from the gastro-oesophageal ganglion, were examined. Control electron micrographs were obtained from the same blocks used for light microscopy.

The length of the medial nerve and thus that of the G cell axon depends upon the stretch applied to the oesophagus during dissection. A first group of eight axons (unstretched) were fixed after the oesophagus was stretched just enough to eliminate the kinks in the nerve. A second group of eight axons (stretched) were fixed after further extending the oesophagus to between 1·5 and 1·8 times the length of the first group.

We have estimated the errors introduced in each step of the preparative and measuring procedures. According to our analysis, the measurements of the cell's surface should be affected by a maximum error of ± 20 % and those of the cell's volume by a maximum error of ± 30 %.

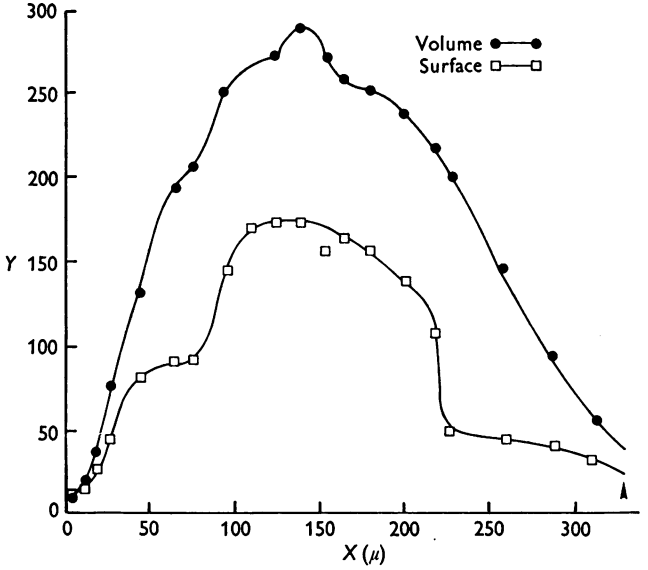
Standard statistical procedures were applied to the analysis of the data. Only the mean and S.E. of the mean are reported in the text. More specific statistical details, when needed, are given in the legends to the Text-figures.

RESULTS

(*a*) *Morphology of the G cell*

An apical region and a stem process can be distinguished in the G cell soma. The former, enveloping the nucleus, is ellipsoidal in shape (Pl. 1 *A*); its surface invaginations are relatively small (Pl. 2). Continuous with it, but lying deeper in the ganglion, is the cone-shaped stem process whose deep folds are very conspicuous (Pl. 1 *B*).

The axon, originating from the stem process, is relatively small and smooth in its initial segment, particularly at the junction of the gastro-oesophageal nerve with the ganglion (Pl. 3*A*). From here to the bifurcation of the lateral nerve, the axon increases in size; the number and the depth of its surface folds also increases, resulting in a shape which in cross-section appears similar to a multilobed star (Pl. 4). From the bifurcation of the lateral nerve to its end, the axon presents a succession of narrow segments (Pl. 3*B*, *D*, *E*) alternating with large varicosities (Pl. 3*C* and *E*). No obvious structural differences can be observed between the axoplasm of the larger and that of the narrower segments.



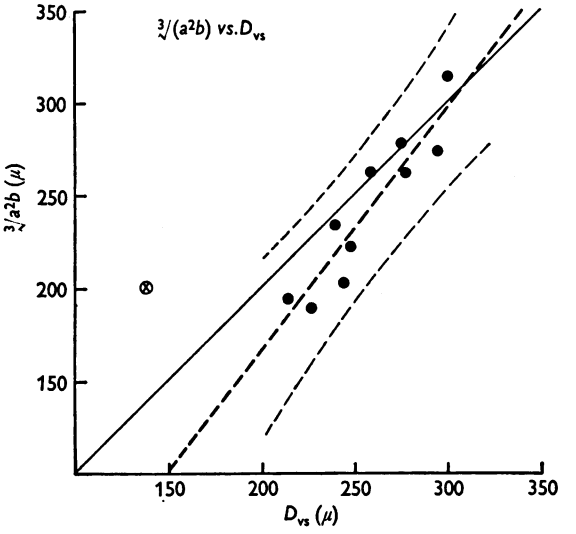
Text-fig. 1. Example of how the surface and the volume of the soma have been estimated by graphical integration from the measurements of the perimeter (squares) and area (filled circles) taken on serial sections of the same cell. The co-ordinate of each point on the X axis indicates the position of the section with respect to the longitudinal axis of the cell while its co-ordinate on the Y axis is proportional to the measurements taken: $Y = 2{\cdot}305 \times 10^{-4}$ cm^2 for the volume measurements, $Y = 6{\cdot}1 \times 10^{-1}$ cm for the surface measurements.

Both the soma and the axon of the G cell are completely enveloped by glia which penetrate into and fill the surface folds (Pls. 2 and 4). However, at no point do the G cell and the glia form close junctions; the entire surface of the G cell (as well as that of the other neurones present in the ganglion) is bounded by a regular space approximately 200 Å wide which is continuous with the extracellular space found between the glial cells, both inside and outside the invaginations (Mirolli & Crayton, 1968). Small ions

can diffuse freely from the solutions bathing the ganglia to the G cell (Mirolli & Gorman, 1973). Thus both the morphological and the physiological evidence point to the conclusion that the invaginations do not represent regions where the flow of ionic currents is particularly restricted, and for this reason, the entire surface, inclusive of that of the folds, was included in our measurements.

(*b*) *Surface and volume of the soma*

In the eleven somata studied the volume (V) ranged from $1{\cdot}4 \times 10^{-6}$ to $14{\cdot}6 \times 10^{-6}$ cm^3. If the soma was a sphere its diameter would be given by the expression $D = \sqrt[3]{[(6/\pi).V]}$. D can be correlated with a function of the cell's two axis, a and b, measured at the dissecting scope. For cells of



Text-fig. 2. Regression of d *vs.* D. The expected relationship between d and D is indicated by the line passing through the origin of the graph. The line best fitting the data (dashed line: $d = -102 + 1{\cdot}33\ D$) deviates considerably from this theoretical relationship indicating that the cell shape changes with size. The standard errors of the estimates a (intercept) and b (regression coefficient) are ± 49 and $\pm 0{\cdot}17$ respectively. Note that the datum of the smallest cell (crossed circle) which does not cluster with the others, has not been considered in calculating the regression line.

medium and large size D is a linear function of $d = \sqrt[3]{(a^2.b)}$, indicating that the soma has approximately the shape of an oblate spheroid (Text-fig. 2; see legend).

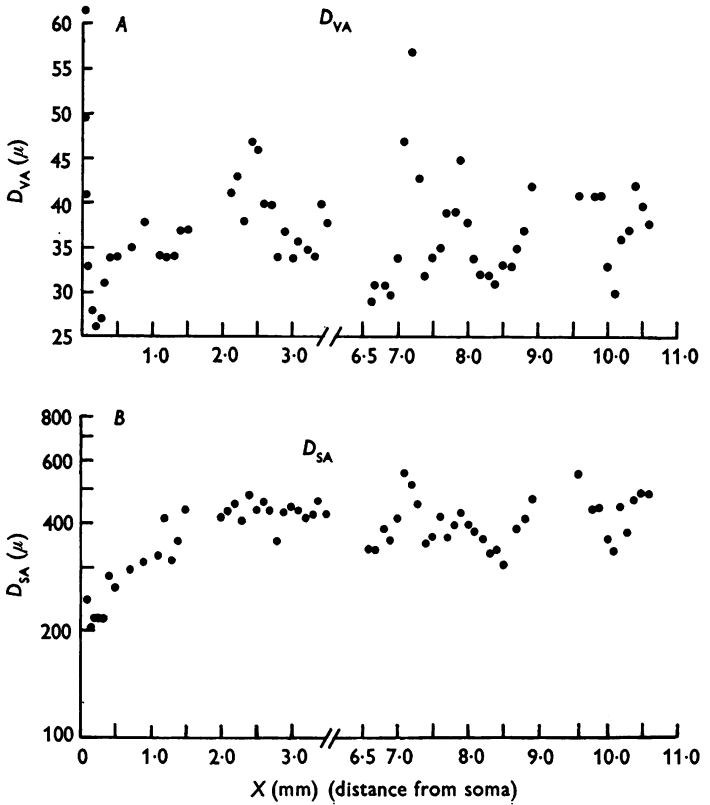
The total surface area of the soma (S) ranged from $0{\cdot}4 \times 10^{-2}$ to $2{\cdot}1 \times 10^{-2}$ cm^2. The average ratio between the calculated soma surface and that of a

sphere having a diameter equal to $d(S')$ is $7{\cdot}5 \pm 0{\cdot}4$. The ratio S/S' is approximately constant for cells of medium and large size, and thus can be used directly as a correction factor to obtain the true soma surface according to the expression

$$S \approx 7{\cdot}5.\pi.d^2 \approx 23{\cdot}5.d^2.$$

(*c*) *The geometrical factors for the length constant and input conductance of the axon*

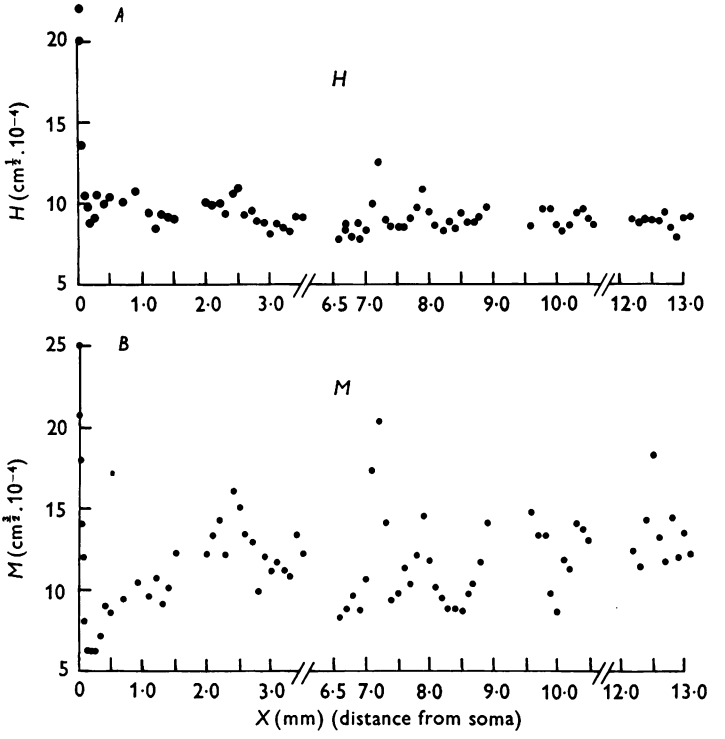
As explained in the Appendix, the properties of the axon as a conducting cable depend on two different functions of its surface and volume. For any axonal segment of constant dimensions, the geometrical factor for the length constant, H, is the square root of the ratio between the surface area (A) and the perimeter (P) of the cross-section [$H = \sqrt{(A/P)}$], and the geo-



Text-fig. 3. Variability of the cross-sectional area (A) and perimeter (P) in successive segments of axon no. 176. The data plotted are the diameters of the circles corresponding to A and P, respectively: $D_{VA} = \sqrt{(4A/\pi)}$; $D_{SA} = P/\pi$. If the axon had a circular cross-section, then $D_{VA} = D_{SA}$.

metrical factor for the input conductance, M, is the square root of the product between these two quantities [$M = \sqrt{(A \,.\, P)}$].

Although both A and P change greatly in adjacent segments of the same axon (Text-fig. 3), their ratio, and therefore the factor H, is remarkably constant (Text-fig. 4A). For each axon examined the average H factor, $\bar{H}$, estimated from a sample of ten sections selected at random, differs by

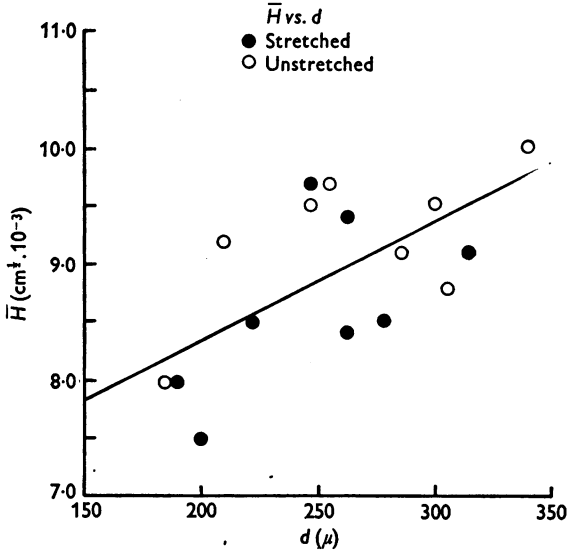


Text-fig. 4. Variability of the functions H and M in successive segments of axon no. 176. Both H and M were calculated from the data reported in Fig. 3.

no more than 2 % from the true average calculated from all the sections available (at least fifty). The $\bar{H}$'s of the sixteen axons studied (eight stretched and eight unstretched) are plotted *vs.* d in Text-fig. 5. It is evident, by inspection of the data, that there are only minor differences (note ordinate scale). The statistical analysis (see legend to Text-fig. 5) makes clear that these differences are all absorbed by a small, but significant, dependence of H on size (d). There is no measurable difference between the $\bar{H}$'s of the stretched and those of the unstretched axons.

In contrast to H, M changes greatly from segment to segment of the same axon. Text-fig. 4B is representative of our findings in all the sixteen

axons examined. In all cases the smallest value of M, M_0, is found in the initial segment of the axon, and in all cases the variability of M is very large, reflecting the variability of both A and P. For each axon the average M factor, $\bar{M}$, estimated from a sample of ten sections selected at random, is only within 10% of the mean value calculated from all the available sections. The plots of $\bar{M}$ and M_0 *vs.* d are shown in Text-fig. 6*A* and *B*. It is clear, by inspection, that their magnitude is directly related to cell size. It is also clear that both M_0 and $\bar{M}$ are smaller in the more stretched axons. This difference is statistically significant (see legend to Text-fig. 6). As shown in the Appendix, a single value for the factor M of each fibre can be obtained by applying a modified form of Rall's equations for branched



Text-fig. 5. Plot of $\bar{H}$ *vs.* d for stretched and unstretched axons. For each axon $\bar{H}$ was calculated from ten sections selected at random. The analysis of the variance of the data give the following information. (1) The difference between cells is highly significant ($F = 7{\cdot}91$, 15 d.f.). (2) The difference between stretched and unstretched axons is not significant ($F = 2{\cdot}1$, 1 d.f.). (3) Most of the variability is absorbed by the regression of $\bar{H}$ *vs.* d. The regression is linear; the best-fitting line drawn through the data has the following equation: $\bar{H} = 6{\cdot}42 + 0{\cdot}0098\ (\pm 0{\cdot}0032).d$.

cylinders. This equivalent M factor, M_e, is obtained by properly weighing each segment according to its dimensions, its length and its distance from the soma. The detailed anatomical information required for calculating M_e was available for only six out of the sixteen axons studied. In all these six cases M_e was larger than M_0 and smaller than $\bar{M}$. The average values were $M_0 = 6{\cdot}7$, $M_e = 9{\cdot}3$, and $\bar{M} = 11{\cdot}7$. On this basis M_0 and $\bar{M}$ can be

considered adequate estimates of the lower and upper limits of M_e and accordingly used to estimate the limits of the input conductance of the axons, even in those cases where the calculation of M_e was not possible.

DISCUSSION

We shall first examine the problem of the determination of the passive electrical properties of the G cell and then discuss some more general physiological implications of our data.

We assume that the somatic and the axonal membranes have the same specific conductance G_m, and that the entire soma behaves as a single isopotential compartment. These assumptions, both reasonable on the basis of the evidence available at present (Gorman & Mirolli, 1972), result in the model for the G cell geometry given in Text-fig. 7. With respect to a current source coupled either to the soma or to the initial part of the axon, the input conductance of the entire cell, G_T, is given by the sum of the input conductance of the soma, G_S, and that of the axon, G_A. G_S is simply the product of the soma surface, S, times the membrane specific conductance, G_m. G_A depends on the dimensions and the electrical characteristics of both the conducting core of the axon and those of its surface membrane, according to the equation $G_A = M\sqrt{(G_m . G_i)}$ (see Appendix), where G_i is the specific axoplasmic conductance, and the geometrical factor M ($cm^{\frac{3}{2}}$) takes into account both the surface and the volume of the fibre. Since our data permit us to estimate the lower and upper limit of M, the G cell total conductance can be approximated by the following expression:

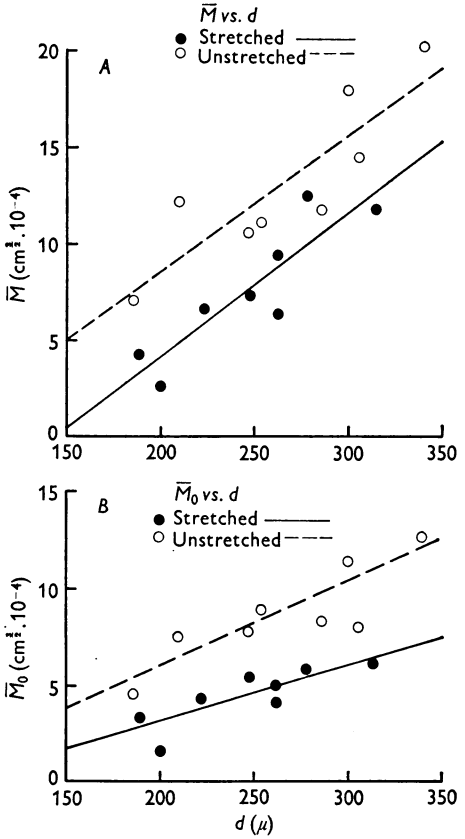
$$G_m . S + M_0\sqrt{(G_m . G_i)} < G_T < G_m . S + \bar{M}\sqrt{(G_m . G_i)}.$$

G_T is a quantity that can be measured experimentally. The values of M_0 and $\bar{M}$ to be used depend on the value of d (Text-fig. 6) as well as on whether the axon was stretched or relaxed during the experimental determination of G_T. This expression allows us to calculate G_M and consequently the ratio (ρ) between the axonal and the somatic conductances. ρ can also be calculated from the shape of the voltage transients (Rall, 1959). With either method ρ is estimated to be between 4 and 8 (Gorman & Mirolli, 1972; Marmor, 1971) and this satisfactory agreement confirms the validity of our analysis.

The most interesting anatomical characteristic of the G cell axon is the constancy of its H factor. In a given fibre the value of H remains approximately the same, in spite of the remarkable differences that can be observed between the absolute dimensions of adjacent segments (Pl. 3), even when the fibre is stretched at different lengths. Because H determines the length constant, the invariance of this factor implies that the velocity with which a spike is conducted should be uniform and independent of stretch

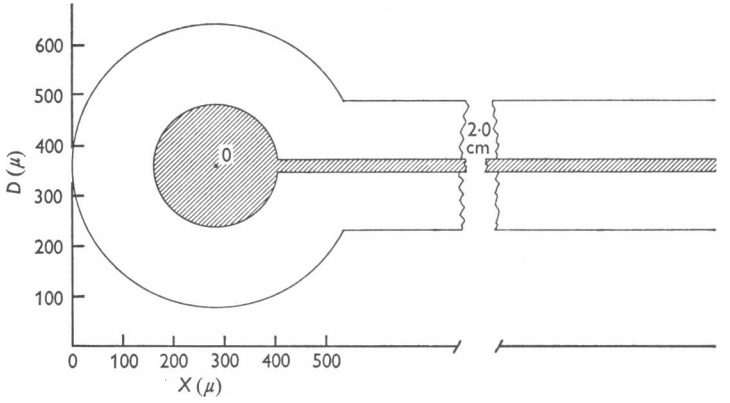
(see Appendix), a fact confirmed experimentally (M. Mirolli & A. L. F. Gorman, unpublished results).

The non-dependence of conduction velocity on stretch can be observed in a number of invertebrate nerve fibres (Bullock, Cohen & Faulstick, 1950; Goldman, 1961, 1963; Jenkins & Carlson, 1904; Turner, 1951) and also in vertebrate muscle fibres (Martin, 1954). Hodgkin (1954) has shown that this interesting phenomenon can be explained without assuming any change in the local electrical properties of the axoplasm and the membrane



Text-fig. 6. Plot of $\bar{M}$ (A) and M_0 (B) *vs.* d for stretched and unstretched axons. $\bar{M}$ was calculated, for each axon, from ten sections selected at random. M_0 is a single value, corresponding to the narrowest segment of the axon. The difference between the stretched and unstretched axons, which is appreciable by inspection, was confirmed by analysis of the variance ($F = 8{\cdot}004$, 1 d.f.). The equation of the lines fitted to the data are as follows: $\bar{M}$ (stretched) $= -10{\cdot}51 + 0{\cdot}0733\ (\pm 0{\cdot}0161).d$. $\bar{M}$ (unstretched) $= -5{\cdot}73 + 0{\cdot}0711\ (\pm 0{\cdot}0170).d$. M_0 (stretched) $= -2{\cdot}71 + 0{\cdot}0292\ (\pm 0{\cdot}0080).d$. M_0 (unstretched) $= -2{\cdot}92 + 0{\cdot}0446\ (\pm 0{\cdot}0139).d$.

if the geometry of the fibre is such that the ratio between volume and surface, per unit length, (v/a) is not changed by stretching. Since the constancy of H implies the constancy of v/a, our results can be considered as direct experimental evidence of the validity of Hodgkin's argument.



Text-fig. 7. A model of the G cell of *Anisodoris nobilis*. The model emphasizes the difference between the dimensions of the conducting core of the cell (inner area, shaded) and those of its membrane (area enclosed by the outer line). Abscissae: distance from the most rostral point of the soma. Ordinates: diameter of the cell's cross-section. The model does not take into account either the narrowing of the initial segment of the axon or the dependence of the axonal dimensions on stretch.

The finding that the M factor is dependent on stretch suggests that the efficiency of the synaptic input to the G cell could be partially controlled by the stretch applied to the axon. This possibility is best illustrated by considering the effect of a synaptic current I_0 localized at the initial segment of the axon (Gorman & Mirolli, 1970). In this case the amplitude of the post-synaptic potential E_0 is approximately given by the expression

$$E_0 = \frac{I_0}{G_A + G_S}$$

and since G_A is several times larger than G_S (Gorman & Mirolli, 1972; Marmor, 1971), E_0 should be significantly larger when the axon is stretched. In addition, stretching should also result in longer lasting synaptic potentials since the rate of decay of E_0 depends on the magnitude of the input conductance of the cell.

Our conclusions are not limited to the particular case of the G cell but are generally valid for those cells which are subjected, in physiological conditions, to a variable stretch and whose shape, therefore, is also variable. For these cells the simplest and most efficient geometrical solution to the problem of a conducting cable, that of a circular cylinder (for which both

conduction velocity and input conductance are constant) is ruled out. The evolution of a shape which will make the conduction velocity independent of stretch is possible; however, the input conductance will necessarily be dependent on stretch. Whether or not stretch will be of importance in modulating the synaptic input of a cell will depend on the localization of the synaptic input and on the conductance ratio between the different cell's compartments.

We are grateful for comments on an earlier draft of this paper by Drs A. L. F. Gorman, M. F. Marmor and W. Rall. In addition, one of us (M. M.) wishes to thank Dr W. Rall for several stimulating conversations and a number of useful suggestions concerning the material presented in the Appendix to this paper.

APPENDIX

By Maurizio Mirolli

A general form of the equations for the distributions of passive electrotonic potential in nerve and muscle fibres

The classical mathematical theory for passive electrotonus (Davis & Lorente de Nó, 1947; Hodgkin & Rushton, 1946; Rall, 1959) has been developed for fibres obeying the condition of circular symmetry. There are, however, a number of cases where this condition is clearly not respected (see the accompanying paper). Assuming that these fibres also behave as a leaky co-axial cable, the problem is to find an explicit expression for the geometrical factors that should appear in the equations defining their length constant and their input conductance.

The solution presented here was suggested by the result obtained by Hodgkin (1954), who has shown that the conduction velocity depends on the ratio between the fibre volume, v, and surface, a, per unit length. Since an action potential is propagated by an electrotonic wave (Hodgkin, 1937) a geometrical factor equivalent to v/a should also appear in the expression for the length constant of the fibre.

The constancy of the ratio v/a is a particular case of the more general condition $\mathrm{d}(A/P)/\mathrm{d}x = 0$ where A and P are the area and the perimeter of a general cross-section of the fibre and x is its length measured from a reference point. Consider the steady-state situation in the nth section of a general segment of length $\Delta x = \overline{a-b}$ when a constant source of electromotive force is applied at $x = 0$. The axial current in this section is given by

$$I_{\mathrm{Ax,\,n}} = -\frac{A_{\mathrm{n}}}{R_{\mathrm{i}}}\left(\frac{\mathrm{d}V}{\mathrm{d}x}\right)_{\mathrm{n}}, \tag{1}$$

where R_{i} is the resistivity of the cytoplasm (Ω.cm). Because of this axial current a potential difference V will be established across the membrane

annulus limiting the nth section. If the membrane has constant thickness and constant specific resistance ($R_m[\Omega.cm^2]$) the current density for any point of this membrane annulus is given by

$$J_{m,n} = \frac{V}{R_m}, \tag{2}$$

and the total membrane current in the segment of length $\overline{a-b}$ is

$$I_m = -\frac{1}{R_m}\int_a^b P.V.dx. \tag{3}$$

If $\overline{a-b}$ is small, P can be considered constant so that

$$\frac{dI_m}{dx} = -\frac{P_n V}{R_m}. \tag{4}$$

Because of the continuity of the current gradient this expression must be equal to the derivative of (1). After substituting and rearranging we obtain

$$\left(\frac{A}{P}.\frac{R_m}{R_i}\right)\frac{d^2V}{dx^2} - V = 0. \tag{5}$$

The coefficient of the second differential has been assumed to be constant and therefore eqn. (5) describes the distribution of electrotonic potential in the entire fibre. The square root of this coefficient is the characteristic length λ (cm) of the fibre

$$\lambda = \sqrt{\left(\frac{A}{P}\right)}.\sqrt{\left(\frac{R_m}{R_i}\right)} = H.\sqrt{\left(\frac{R_m}{R_i}\right)}; \tag{6}$$

H ($cm^{\frac{1}{2}}$) is a pure geometrical factor.

The input conductance of a fibre, G_A, is defined as the ratio between input current, I_0, and input voltage, V_0. For a fibre of semi-infinite length, G_A is obtained by differentiating the general solution of eqn. (5) and substituting in eqn. (1) for $x = 0$:

$$G_A = \sqrt{(A.P)}.\sqrt{(G_m.G_i)} = M\sqrt{(G_m.G_i)}; \tag{7}$$

M ($cm^{\frac{3}{2}}$) is a pure geometrical factor.

In the particular case of a monopolar neurone having both the H factor and the M factor constant, we can immediately obtain an expression for the specific conductance of the membrane G_m ($\Omega^{-1}.cm^{-2}$). The total neurone conductance is

$$G_T = SG_m + G_A, \tag{8}$$

where S (cm^2) is the surface of the soma (Rall, 1959). Substituting from eqn. (7) and solving, we have

$$\sqrt{G_m} = \frac{-M\sqrt{G_i} + \sqrt{(M^2G_i + 4SG_T)}}{2S}. \tag{9}$$

A more general case is that of fibres in which H and M are not constant. These fibres can always be thought of as made up of a series of successive segments, each of length l_n and each characterized by a constant ratio A/P. For each nth segment, therefore, the characteristic length factor, H_n, and conductance factor, M_n, can be defined. Thus, it is possible to extend to these fibres the results that Rall (1959, 1960) has obtained for a branching cable. Each nth segment is considered equivalent to the entire set of the nth branches. Rall's equations can now be directly applied in a stepwise procedure, satisfying the boundary conditions. Note the relation between the terms B, C and D used by Rall (on the left) and those used here:

$$C = \tfrac{1}{2}\pi R_i^{-\frac{1}{2}};$$

$$\tfrac{1}{2}\pi D^{\frac{3}{2}} B_0 = M_0 B_0 = M_e. \tag{10}$$

B_0 is a factor expressing the input conductance of the initial (0th) segment as a fraction of the conductance of a fibre having a constant M factor equal to M_e but semi-infinite length (see Rall, 1959).

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EXPLANATION OF PLATES

PLATE 1

A: low power light micrograph of the gastro-oesophageal ganglion of *Anisodoris nobilis*. The soma of the G cell is on the left of the Figure; the neuropile of the ganglion on the right. The section shows both the apical region (surrounding the nucleus), and the stem process. At this magnification the indentations of the apical region are not clearly visible. *B*: higher power of the stem process of the same cell shown in *a*.

PLATE 2

A: Low power electron micrograph of the apical region of the G cell. CS, connective sheath of the ganglion; OGL, outer glial layer; GCS, G cell soma. Note the infoldings of the G cell plasma membrane, two of which are marked by arrows. *B*: Higher power electron micrograph of the outer glial layer.

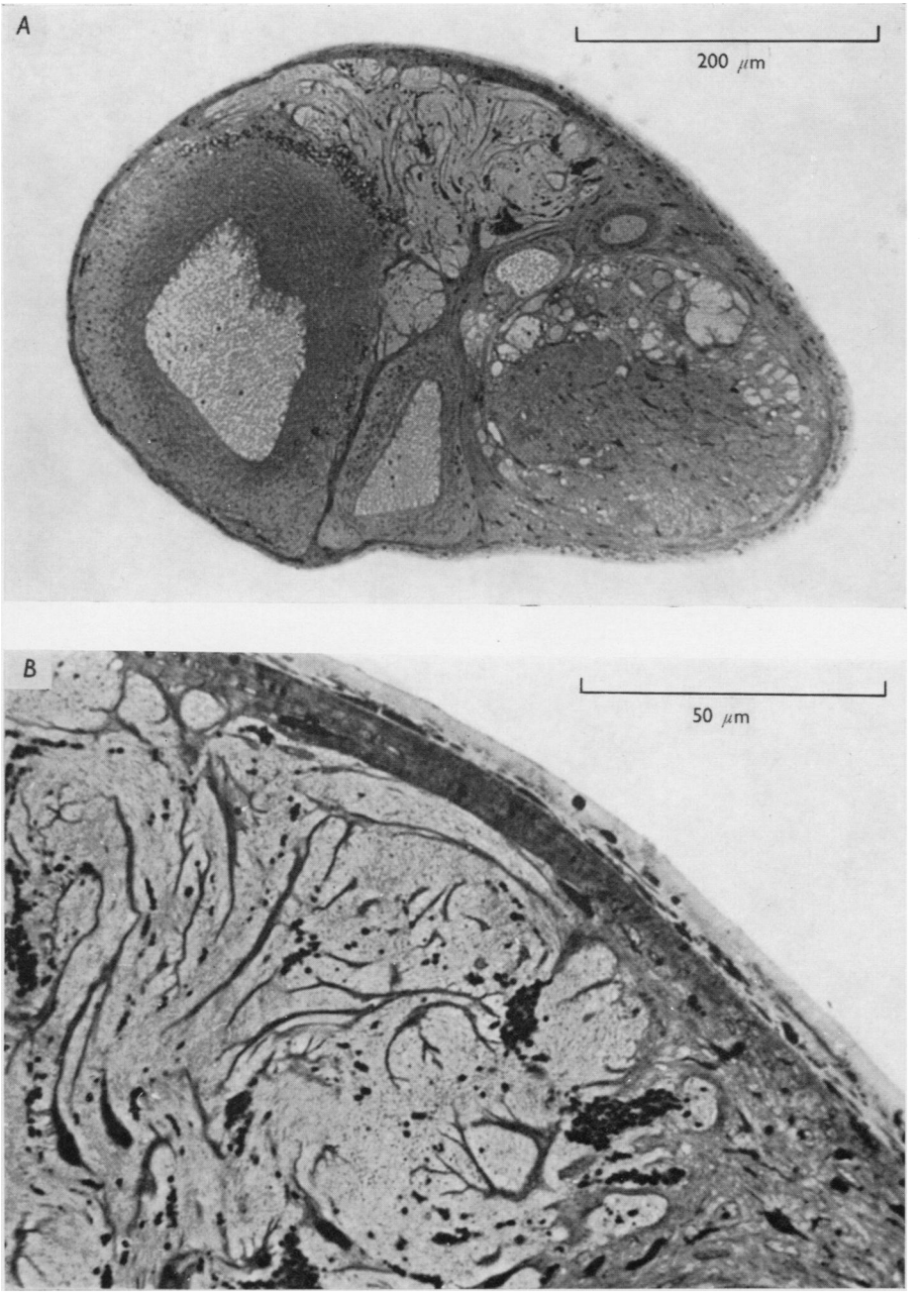
PLATE 3

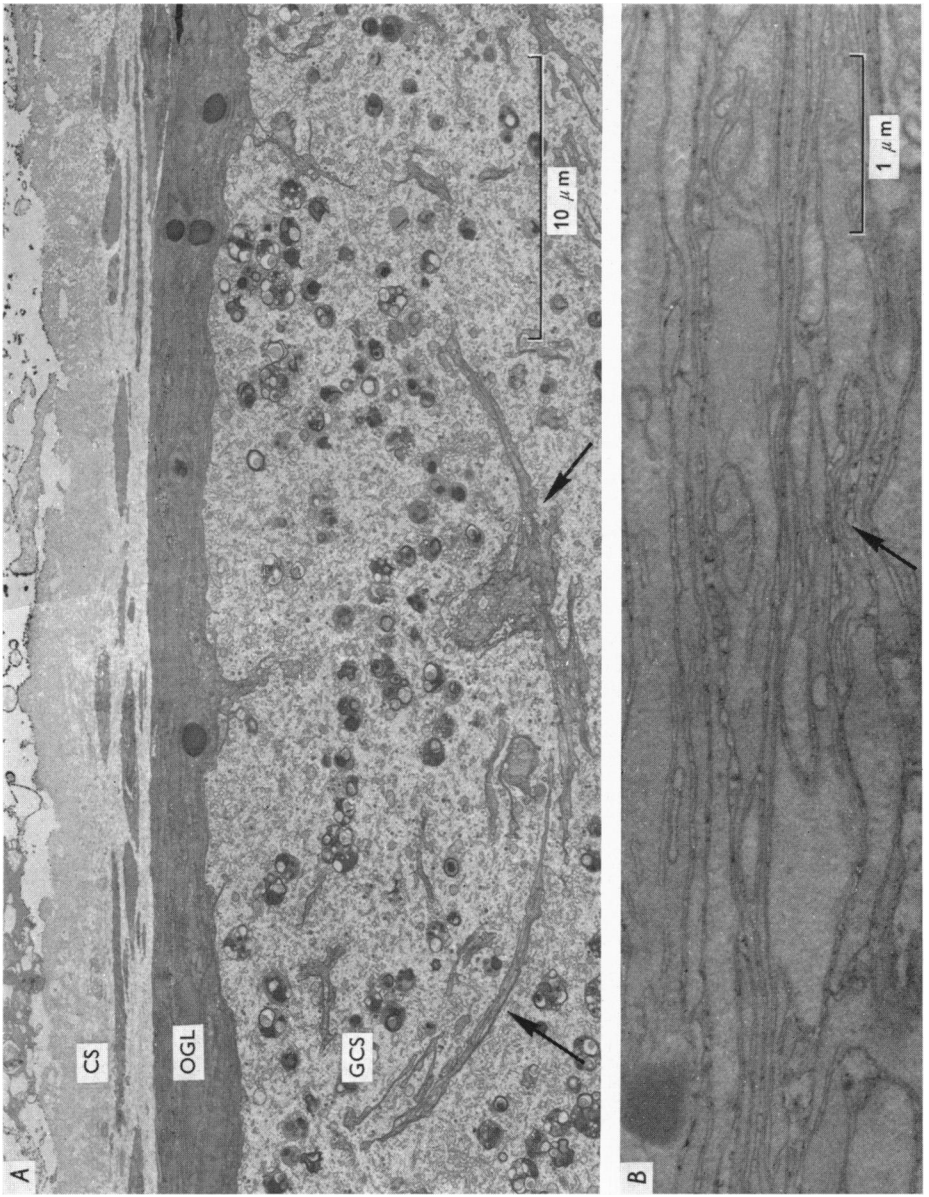
Light micrographs of the axon no. 176 cut at different distances (X) from its origin. All the sections were cut in a plane perpendicular to the axon's longitudinal axis.

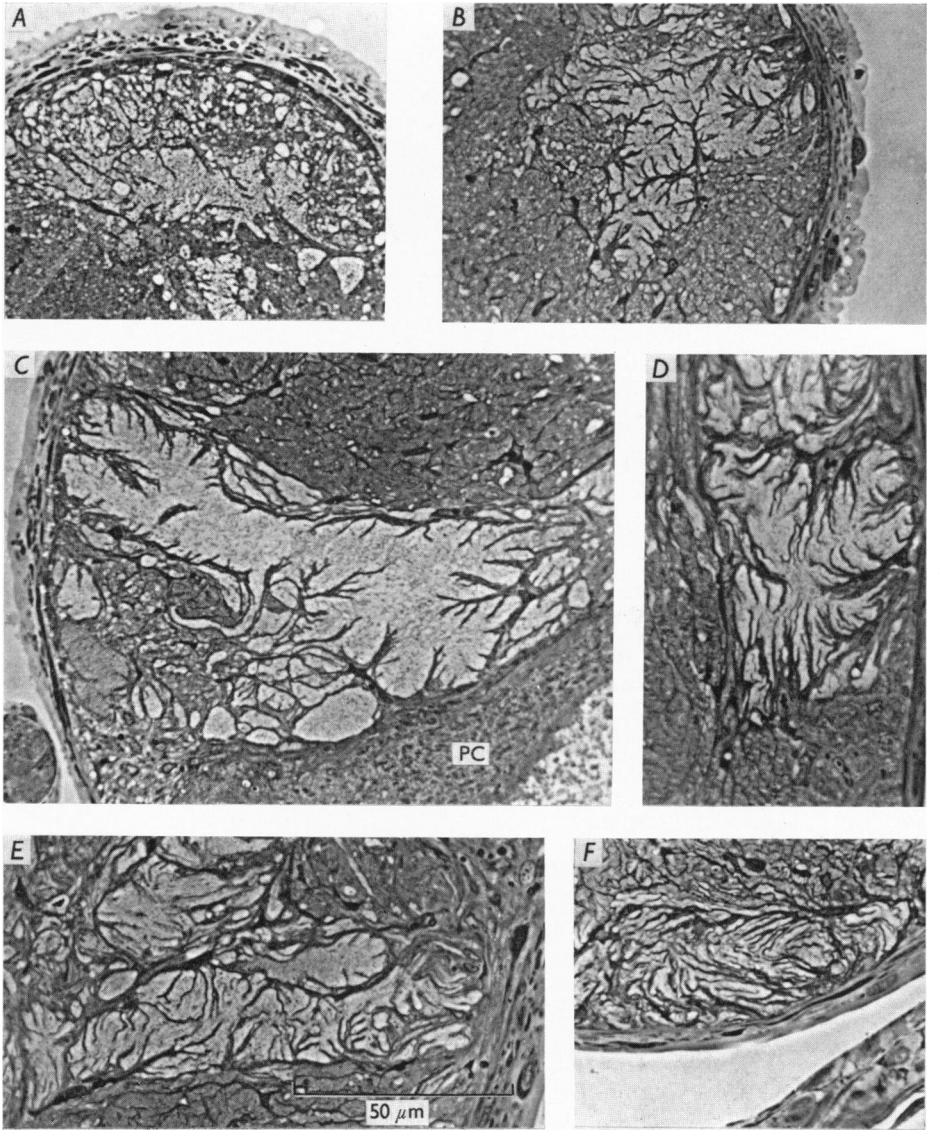
A: $X = 0{\cdot}1$ mm; *B*: $X = 3{\cdot}5$ mm; *C*: $X = 7{\cdot}50$ mm; *D*: $X = 10{\cdot}2$ mm; *E*: $X = 15{\cdot}0$ mm; *F*: $X = 25{\cdot}2$ mm. Note that the magnification is the same for all the photographs. In *C* the cytoplasm of a peripheral cell (PC) is visible. The arrow, in the same photograph, indicates a fine axonal branch (see text for further comments).

PLATE 4

Low power electron micrograph of the G cell axon. This section was cut in a plane approximately perpendicular to the long axis of the axon. Note the numerous and deep indentations of the axon's plasma membrane.


A
200 μm
B
50 μm


A
CS
OGL
GCS
10 μm
B
1 μm


A
B
C
PC
D
E
50 μm
F


25 μm