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A NOTE ON CONDUCTION VELOCITY

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Martin (1954) has shown that the conduction velocity of a frog's sartorius muscle is not altered by changing the length of the muscle. He points out that this result is consistent with the assumption that stretching straightens out folds in a membrane of constant total area. A quantitative basis for this argument is provided by the expression which Offner, Weinberg & Young (1940) derived for the propagation of a discontinuous change of e.m.f. in a cable-like system. Since the properties assumed by Offner *et al.* do not correspond at all closely to those in an actual nerve or muscle, it is natural to wonder whether more realistic assumptions would give the same answer. The purpose of this note is to show that the result derived from the equation of Offner *et al.* is extremely general, since it turns out to be a consequence of assuming that conduction is brought about by local circuits in a continuous cable-like structure. Myelinated fibres, in which conduction is saltatory, are excluded from the analysis.

For a uniform fibre with internal resistance per unit length r_i the longitudinal current inside the fibre, i_i, is $-\frac{1}{r_i}\frac{\partial v_i}{\partial x}$, where x is distance along the fibre and v_i is the potential of the inside. If the fibre is immersed in a large volume of conducting fluid the outside of the fibre is practically equipotential and the potential of the inside may be equated to the potential difference across the membrane without sensible error. From these relations, and from the fact that the membrane current per unit length, i_m, is necessarily equal to $-\frac{\partial i_i}{\partial x}$, it follows that

$$i_m = \frac{1}{r_i}\frac{\partial^2 v_m}{\partial x^2}, \tag{1}$$

where i_m is the current crossing the membrane per unit length of fibre (outward current here taken as positive) and v_m is the potential difference across the membrane (defined here in the sense internal potential minus external potential).

Equation (1) has been used or implied by many authors from Hermann and

Cremer to the present day; references to the earlier literature are given by Katz (1939).

The current density (I_m) through any patch of membrane which is sufficiently small to be regarded as flat is given by

$$I_m = \frac{1}{sr_i}\frac{\partial^2 v_m}{\partial x^2}, \tag{2}$$

where s is the area of membrane per unit length of fibre. Provided that the fibre is capable of conducting an action potential at constant velocity, θ, it follows that during steady propagation

$$I_m = \frac{1}{sr_i\theta^2}\frac{\partial^2 v_m}{\partial t^2}. \tag{3}$$

No membrane properties are assumed in deriving equation (1) and the only reservation which must be made is that equations (1)–(3) will not be accurate unless the wave-length of the action potential is large compared to the radius of the fibre. This condition is satisfied by striated muscle and by most other electrically excitable tissues. It is now assumed that conduction is brought about by local circuits, or to be more precise, that the only way in which one region of membrane influences the potential difference across another region is by supplying or withdrawing current. This means that the time course of v_m (or I_m) is determinate if the time course of I_m (or v_m) is known. Hence if $I_m = G(t)$ then $v_m = F(t)$, where $F(t)$ and $G(t)$ are single valued functions. In general the relation between $F(t)$ and $G(t)$ is extremely complicated and there will be no simple connexion between them. However, if the membrane is capable of conducting an action potential at constant velocity, it is necessary that one pair of these functions should be linked by equation (4):

$$I_m = \frac{1}{k}\frac{\partial^2 v_m}{\partial t^2}, \tag{4}$$

where k is a constant. Unless this were true it would be impossible to satisfy equation (3), and conduction at constant velocity would be impossible. The important point about the relation is that k depends only on the local properties of the membrane; it does not vary when conduction velocity is altered by factors which change the current distribution in the fibre without affecting the membrane. In the present case stretching is assumed to straighten the membrane but not to alter the properties of any patch which is sufficiently small to be regarded as flat.

On comparing equations (3) and (4) we have

$$\theta = \sqrt{\frac{k}{sr_i}}, \tag{5}$$

or

$$\theta = \sqrt{\frac{kX}{sR_i}}, \tag{6}$$

where X is the cross-sectional area of the fibre and R_i is the specific resistance of the protoplasm. The total volume, V, in a fibre of length L is

$$V=XL, \tag{7}$$

and the total surface area, A, is $A=sL$. (8)

Hence

$$\theta=\sqrt{\frac{kV}{R_i A}}. \tag{9}$$

This does not contain L explicitly; V (the volume) plainly cannot alter on stretching and the same is true of A since we are considering a folded membrane of constant total area.

Dimensional arguments of this type lead to two other results which have been mentioned elsewhere (Rushton, 1951; Rosenblueth, Wiener, Pitts & Garcia Ramos, 1948; Hodgkin, 1947). In the first place it is clear from equation (9) that if one is comparing unmyelinated fibres of different size, but with membranes and axoplasm of identical specific properties, the velocity in a large volume should vary as the square root of the diameter. In practice, this relation is unlikely to be exactly obeyed since it is improbable that the membranes and axoplasm will be identical in fibres of different size. The relation is, however, of value in defining the purely dimensional effect of a change in diameter.

The third result is relevant to the experiments in which fibres are transferred from a large volume of conducting fluid to a small one in which the external resistance per unit length, r_e, is comparable to that of the axis cylinder. In the former case equation (3) applies, in the latter, the term r_i must be replaced by (r_i+r_e). Since the membrane properties are not altered by changing the volume of external fluid it follows that the velocity should be proportional to $(r_i+r_e)^{-\frac{1}{2}}$. The experimental results obtained with the axons of *Carcinus* and *Loligo* agree well with this prediction (Hodgkin, 1939, 1947; Katz, 1947).

SUMMARY

The following theoretical predictions can be made for continuous fibres in which conduction is brought about by local electric circuits.

1. The velocity in a fibre with a folded membrane should be independent of the length of the fibre provided that the total area of membrane remains constant and that stretch does not alter the local electric properties of the membrane.
2. When measured in a large volume, the conduction velocity of fibres with identical membranes and axoplasm should vary as the square root of the fibre diameter.
3. When measured in small volumes, the conduction velocity of a fibre should be inversely proportional to the square root of the sum of the external and internal resistances per unit length.

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