NOTES TO THE PRECEDING PAPER: LENGTH-TO-LENGTH TRANSMISSION AS THE BASIS OF CONDUCTION

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1. MISTAKES AND CORRECTIONS

After the publication of the preceding paper (1), I found a mistake in eq. (2) and another in deriving eq. (3) from (2), to my great sorrow. The eq. (2) as an approximate expression of $P_x$ should have been

$$ P_x = \int_0^x Ve^{-x/k'} \, dx, \quad \alpha : \text{ const.} \tag{1} $$

The basic idea was $dP_x = Ve^{-x/k'} \, dx$, in other words, that the potential contributed to the point $X$ (the point $y=0$, fig. 1 of the preceding paper) by a small active region $dx$ at $x$, is proportional to $dx$. $\alpha$ is the proportionality factor which was dropped in the original treatment, by mistake.

Now,

$$ P_x = \int_0^x Ve^{-x/k'} \, dx = V\alpha k'(1 - e^{-x/k'}). \tag{2} $$

For $x = \infty$; $P_x = V\alpha k'$.

In actuality, the transverse current at $X$ will increase gradually with $x$ to attain a certain definite value in the end, as long as the active membrane resistance is not zero. In proportion to this, $P_x$ will increase and attain almost $V$ itself at $x = \infty$ in case the active membrane resistance is very small as compared to the resting. Hence,

$$ V\alpha k' = V, \quad \alpha k' = 1. $$

Consequently,

$$ P_x = V(1 - e^{-x/k'}). \tag{3} $$

Next, from

$$ P_y = P_x e^{-y/k} = V(1 - e^{-x/k'}) e^{-y/k} = S, $$

we have as before

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\[ y = k \log \frac{V}{S} (1 - e^{x/k'}) , \]

or, assuming \( k' \approx \frac{k}{5} \approx 1 \text{ mm} \approx \text{const.} \) and denoting \( \frac{V}{S} \) by S.F. (safety factor),

\[ y = k \log (\text{S.F.})(1 - e^{-x}), \quad y, k, x \text{ in mm}. \quad (4) \]

This is nothing but the eq. (4) in the original paper.

Thus, the mistake could be corrected without affecting the final result of calculation.

2. LENGTH CONSTANT, \( k' \), OF ACTIVE MEMBRANE

In the original paper, the concept of "length constant" was extended to the active membrane, to have an idea about the current distribution in the active region itself. This was one of the essential points of the theory, and in fact it played a very important role throughout the treatise.

The value \( k' \approx 1 \text{ mm} \) for the squid giant axon was obtained from 1) \( k \approx 5 \text{ mm} \) and 2) \( k/k' = \sqrt{r_m/r'_m} \approx \frac{\sqrt{40}}{6} \), where \( k \) is the length constant of resting membrane, and \( r_m \) and \( r'_m \) the resting and active membrane resistances, respectively, of unit length of fibre. The relation \( k/k' \approx 6 \) was derived from admitting \( k' = \sqrt{r_m/r'_m} \) (\( r_i, r_e \) : internal and external resistance respectively per unit length of fibre), to be combined with \( k = \sqrt{r_m/r'_m} \), although, strictly, it was not without question to apply this simplified formula to active nerve, where the membrane resistance is very low. Therefore, the estimate \( k' \approx 1 \text{ mm} \) may not be very accurate, but it will serve well for approximation.

3. THE VALUE OF "\( L \)" OF MYELINATED FIBRES

In chapter VI of the preceding paper (1), I evaluated the specific length, \( L \), of the nodal membrane, required to be excited for initiation of impulse. The evaluation was based upon 1) \( k \approx 5 \text{ mm} \) and 2) \( AB \) (fig. 15 in the preceding paper) \( \approx 1,000 \text{ msce.} \) The former was borrowed from Rushton (2) for approximation, and the latter was a supposition considered possible from Tasaki's experience (3) that \( AB \) (fig. 15) varied widely from several tens to several hundreds msce. The result was \( L \approx 5 \mu \), a value about ten times larger than the nodal breadth, which is said to be 0.5 \( \mu \) or less (4). It was supposed that in thoroughly physiological conditions (undissected, circulated etc.), \( L \) might be much smaller and occupy just a fraction of a nodal breadth.

In the preceding paper, stress was laid on the existence and significance of \( L \), and not very much on the value. For this reason just Rushton's data \( k \approx 5 \text{ mm} \) was employed throughout for the sake of orientation. Another reason was that the data was just of the order of values of \( k \) obtained on several kinds of unmyelinated fibres (5). But still the obtained value, \( L = 5 \mu \), was too large to
be pushed in a single nodal breadth.

Later, it was noticed that a satisfactory result can be obtained, if we employ recent data on myelinated fibres for calculating the length constant, \( k \). According to a table composed by Stämpfli (6),

\[
\begin{align*}
    r_m &\text{ (membrane resistance)} = 80 \text{ Megohm (for a node)}, \\
    r_i &\text{ (internal resistance)} = 28 \text{ Megohm (for an internode)} \\
    &\text{ = 140 Megohm (for 1 cm.)}.
\end{align*}
\]

Taking into consideration that nodal breadth \( \approx 0.5 \mu \) (4), and admitting the validity of the eq. \( k \approx \frac{r_m}{\sqrt{r_i}} \), we have

\[
k \approx \frac{r_m}{\sqrt{r_i}} \text{ (for 1 mm.)} \approx \frac{80}{2 \times 10^8} \sqrt{\frac{1}{14}} \approx \frac{1}{2 \times 10} \approx 0.05 \text{ (mm.)}
\]

Combining this value with Tasaki's experiment (3), and taking \( AB \) (fig. 15) \( \approx 1,000 \text{ msec.} \) as before, we have (see p. 153 of the preceding paper)

\[
L \approx k \times 0.001 \text{ (mm.)} \approx 0.05 \mu.
\]

Even if we take \( AB = 100 \text{ msec.} \), still we have

\[
L \approx 0.05 \text{ (mm.)} \times 0.01 \approx 0.5 \mu.
\]

Very probably, \( L \) may lie in the range 0.05-0.5 \( \mu \), occupying a fraction of a nodal breadth.

If so, a fractional excitation of a node in spatial sense may not be impossible in the usual node-to-node stimulation, provided that the stimulus intensity is finely controlled, and thus a local response may occur as a local event of all-or-nothing inside \( L \).

The above evaluation started from the presumption that \( L \) exists in the nodal membrane, too. Whether it is really the case or not, can be a quite different matter, as stated in the preceding paper. But it is note-worthy that theoretically, too, the eq. (4) gives \( L \approx 1 \mu \) for S.F. = 10, \( k = 0.05 \text{ mm.} \) and \( k' = \frac{1}{5} \cdot k \) = 0.01 mm. It may be smaller because the safety factor may be larger, as seen in the following paragraph. The existence of \( L \) in the nodal membrane appears thus to be highly probable.

4. SAFETY FACTOR

It is certain that the safety factor defined by \( \frac{V}{S} \) in the preceding paper should be somewhat larger than that for a propagated impulse measured by the usual method of stimulation. But it is not directly measurable, at least unless some special method of uniform stimulation for a small length of fibre shorter than \( L \) is invented, because \( S \) is the potential set up at the membrane by the action potential, and expressed in terms of the peak voltage as reduced to a level, which is just sufficient to activate the membrane locally. However, a
rough estimation in the case of myelinated fibres can be carried out in the following way:

As quoted above (6),

\[ r_m (\text{nodal membrane resistance}) \approx 80 \times 10^6 \text{ ohm}, \]
\[ r_i (\text{internodal axial resistance}) \approx 30 \times 10^6 \text{ ohm}. \]

The membrane potential, \( V_m \), set up by the action potential, \( V \), will be

\[ V_m \approx \frac{80}{110} V \approx \frac{2}{3} V. \]

Hence, expressing the safety factor for propagation by \( F \), and assuming the current to be uniform, we have

\[ V \times \frac{2}{3} \times \frac{1}{F} \approx S, \]
\[ \frac{V}{S} \approx F \times \frac{3}{2} \approx F \times 1.5. \]

Strictly speaking, the current cannot be uniform; consequently, the actual value of \( S \) will be smaller than that estimated above, and the safety factor \( \frac{V}{S} \) will be the larger.

5. MYELINATED AND UNMYELINATED FIBRES

As described above, the length constant of the nodal membrane is estimated to be of the order of 1/100 of that of unmyelinated fibres. This indicates, if viewed from the present theory, that the conduction velocity must be very much smaller, though not to the same extent, in the nodal membrane itself. However, this deficient feature will hardly be a serious matter, because the node is so narrow as 0.5 \( \mu \) and moreover there is the nodal construction for speeding. Important thing will be that a whole node can get excited promptly. A positive reason for the small resistance and the narrow nodal gap is found here. Another difference between the two kinds of fibres may be that in unmyelinated fibres the safety factor for propagation will be larger than in myelinated fibres, because there is no risk of transmission as from node to node. But, in spite of these functional differences, the reason why there are two kinds of fibres, is still vague.

6. MISPRINTS IN THE PRECEDING PAPER (1)

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REFERENCES


Addendum: According to Tosaki’s new measurements, \( r_m \) for a node is 41 Megohm (Am. J. Physiol., 181: 639, 1955), that is, just about half of the value above cited. If this is adopted, then

1) \( k \) and \( L \) of the nodal membrane should be \( \frac{1}{\sqrt{2}} \)-times smaller than evaluated above.

2) \( \frac{V}{S} \approx F \times \frac{70}{40} \approx F \times 1.8. \)