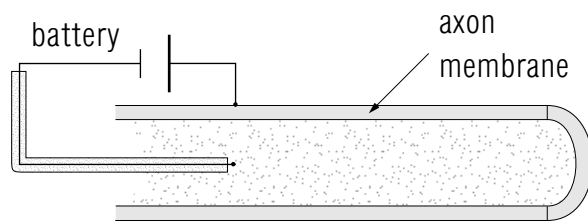


DC CONDUCTION ALONG A NERVE



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by

Mary Blair and Peter Signell
Michigan State University

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Input Skills:

1. State Ohm's law (MISN-0-118).
2. State the two node rules for resistive D. C. circuits (MISN-0-119).

Output Skills (Knowledge):

- K1. Describe the differences between the responses of an axon to stimuli that are below and above the threshold for action potential response.
- K2. Derive the voltage, current, and resistance distributions along a nerve axon due to a voltage applied at one point, where the applied potential is below the threshold for action potential response.

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1. Introduction to Neurons

1a. Neurons Transmit Information. Neurons, or nerve cells, are cells that transmit information in the nervous system. Such transmission is accomplished by the conduction of electrical impulses along the neuron and by the release of chemical messenger packets that carry the information across gaps, called synapses,¹ between neurons. The activity of the neuron is a fascinating topic in biology, medicine, chemistry, and physics.

1b. Neurons Have Three Components. Basically, a nerve cell is composed of three distinct parts:

- (i) dendrites, that collect information from neighboring neurons and from the environment;
- (ii) a cell body, containing the nucleus and other structures necessary for metabolic activity in the cell; and
- (iii) an axon that carries the nerve impulse, called the action potential.

A cross-section view of an axon is shown in Fig. 1.

1c. Above Threshold: the “Action Potential” Response. The normal mode of transmission of the action potential along an axon is essentially independent of the magnitude of the stimulus. For this reason, it is sometimes called an “all or nothing” phenomenon. During the response, the trans-membrane potential of the axon rapidly switches from negative to positive and then recovers, creating a “pulse.” The regenerative action that creates this pulse is due to changes in the permeability of the membrane to various ions. To trigger this response, the stimulus must be above a threshold value.

1d. Below Threshold: A Passive Response. If a stimulus is below the threshold for an action potential response, the permeability of the axon membrane does not change significantly and the axon response

¹“Synapse” is pronounced “sin’ - aps.”

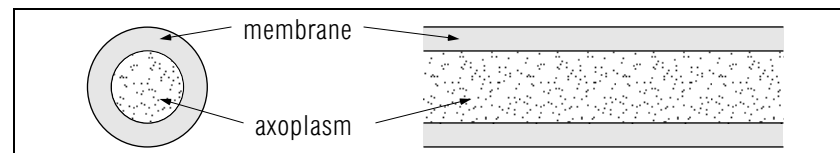


Figure 1. Cross-sectional and longitudinal views of a nerve axon.

is passive. Study of this response is interesting in its own right and it also provides a good basis for understanding the propagation of action potentials.

2. The Passive-Case Circuit

2a. Description of Nerves. Nerve trunks, often called simply “nerves,” will be considered here to be cylindrical and infinite in length, and to consist of a large number of axons of uniform diameter, evenly spaced within a sheath. It is reasonable to suppose that the physical environments of the axons are essentially identical and uniform, so we need only consider a single representative axon. We will only deal here with the sub-threshold passive case, where the stimulus is provided by a battery as in Fig. 2.

2b. Electrical Model for a Nerve Axon. We consider the case where the battery has been connected long enough for a steady state to be established. Then a current continually flows away from the battery, down the axon, and some of it continually leaks “sideways” through the membrane as it goes. Thus the current gradually decreases as it goes. Fig. 3 shows how the axon would look if its parts were discrete instead of continuous. Here R_i is the resistance to longitudinal flow inside the axon, R_o the resistance to longitudinal flow outside, and R_m the resistance of the membrane to “sideways” current leakage. This circuit can be replaced by the equivalent one in Fig. 4a, where we have combined R_o and R_i and

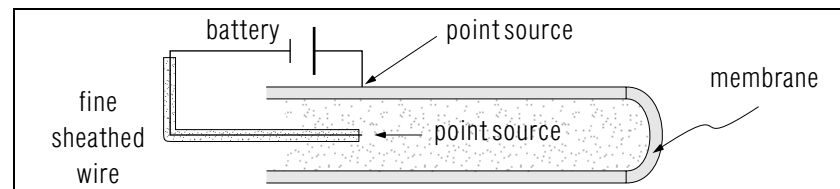


Figure 2. Sub-threshold stimulus of a nerve axon.

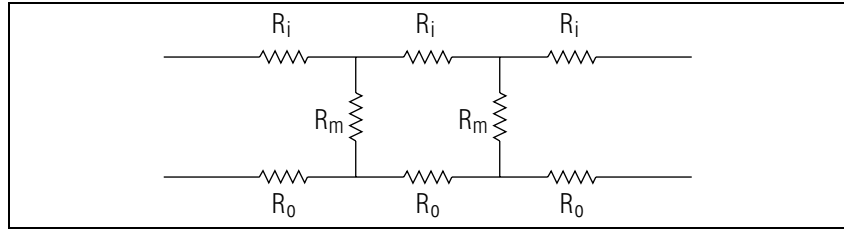


Figure 3. Discrete-element approximation for an axon.

called the sum R_a :

$$R_o + R_i \equiv R_a.$$

In the real axon the material can be considered to be continuous so we can treat the circuit as linear only if we evaluate an infinitesimal length of it as in Fig. 4b. The resistance to longitudinal flow increases with the length of the element, so we define the resistance per unit length along the axon as ρ_a and we write:

$$dR_a = \rho_a dx.$$

The (longitudinal) voltage drop across this resistance is:

$$dV(x) = I(x)dR_a = I(x)\rho_a dx, \quad (1)$$

For leakage across the membrane, the quantity that increases proportionally to the length of the segment is the conductance:² increasing the length of the membrane provides more surface area over which leakage

²Conductance G is defined as the reciprocal of resistance, so Ohm's law, $V = IR$, becomes $I = GV$. The parallel resistance addition law,

$$\frac{1}{R} = \frac{1}{R_1} + \frac{1}{R_2},$$

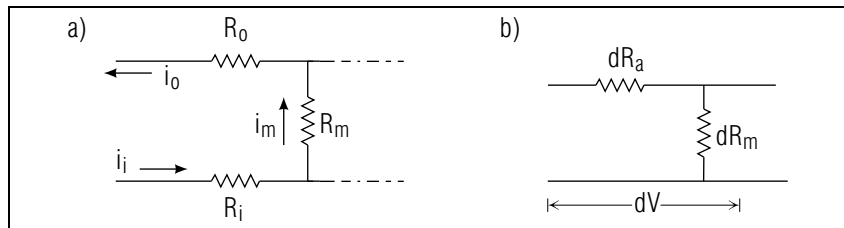


Figure 4. An element from Fig. 3: (a) discrete approximation; (b) continuous axon (infinitesimal element).

can occur. We denote the leakage conductance per unit length of the axon by g_m so the leakage conductance of our element is:

$$dG_m = g_m dx,$$

and the leakage current in our element is:

$$dI(x) = V(x)dG_m = V(x)g_m dx. \quad (2)$$

An easy way to solve the above equations is to write Eq. (1) as a differential equation and then to differentiate it and substitute Eq. (2) into it. This gives:

$$\frac{d^2V(x)}{dx^2} = V(x)g_m\rho_a, \quad (3)$$

for which the solution is:

$$V(x) = Ae^{\gamma x} + Be^{-\gamma x}. \quad (4)$$

Here $\gamma \equiv \sqrt{g_m\rho_a}$ as can be easily seen by substituting Eq. (4) into Eq. (3). The constants A and B must be determined by boundary conditions.

2c. The “Long Axon” Voltage. Since a physical axon is very long compared to its diameter, a commonly used approximation is to assume the axon to be infinitely long, in which case we must have $A = 0$ in Eq. (4) or the potential will be infinite at infinity! Then evaluating Eq. (4) at the position x_0 where the battery potential V_0 is applied, we get:

$$V(x) = V(x_0)e^{-\gamma(x-x_0)}. \quad (5)$$

▷ Verify Eq. (5) by substituting it into Eq. (4) and by evaluating Eq. (5) at infinity and at x_0 . Note that two values must be checked because Eq. (4) is of second order.

By symmetry, the voltage will decay in the same way in each direction from the point of application so we write:

$$V(x) = V(x_0)e^{-\gamma|x-x_0|}.$$

This voltage distribution is shown in Fig. 5.

becomes:

$$G = G_1 + G_2.$$

Conductance is measured in mhos, where a mho is the reciprocal of the ohm. Thus $\text{mho} = \text{ohm}^{-1}$. Resistances add in series because the battery must do more work as the current traverses successive resistances, while conductances add in parallel because the current has various paths through which to travel.

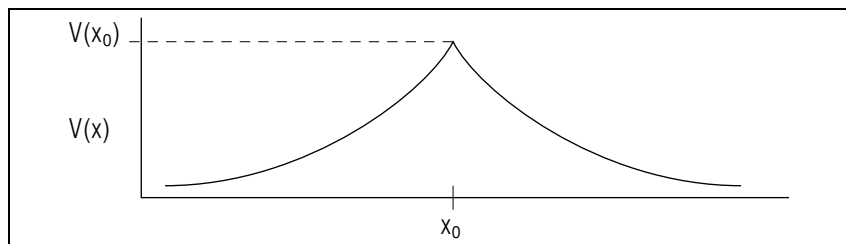


Figure 5. The voltage along the passive axon.

2d. The “Long Axon” Current. We now put the solution for the potential, Eq. (5), into dI/dx from Eq. (2) and we get:

$$I(x) = I(x_0)e^{-\gamma(x-x_0)}, \quad (6)$$

where $I(x_0) = V(x_0)\sqrt{g_m/\rho_a}$. Thus both the potential and the current fall off exponentially as one moves away from the source point and this fall off is due, of course, to the leakage of current through the membrane.

▷ Show that the voltage and current fall to $1/e$ in 0.8 mm, using typical values of $\rho_a = 1.27 \times 10^{10}$ ohms/m and $g_m = 1.25 \times 10^{-4}$ mhos/m = 1.25×10^{-4} ohms $^{-1}$ /m.

2e. The “Long Axon” Resistance. Given the voltage across the nerve and the current through it at any point, the quotient of the two gives the resistance produced by the axon beyond that point. Dividing Eq. (5) by Eq. (6) we get, for the resistance beyond point x :

$$R(x) = \sqrt{\rho_a/g_m}. \quad (7)$$

Note that the resistance is independent of x , meaning the resistance of the axon beyond any point x is independent of what point you pick as x .

▷ Show that the electrical resistance of a “long axon” is 10 Megohms ($1.0 \times 10^7 \Omega$). Data are in Sect. 2d.

Acknowledgments

This presentation is based one by Russell K. Hobbie in *The American Journal of Physics* **41**, 1176 (1973). Preparation of this module was supported in part by the National Science Foundation, Division of Science Education Development and Research, through Grant #SED 74-20088 to Michigan State University.

A. Resistance Ladder Derivation

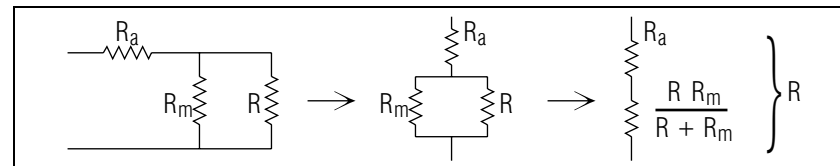


Figure 6. The circuit equivalent to that of Fig. 4 for an infinite resistance ladder.

A very interesting alternative derivation treats the nerve as a resistance ladder (the name coming from the appearance of Fig. 3). The derivation begins by noting that the element in Fig. 4 is part of a resistance ladder that is considered to be infinitely long. In that case, the resistance of the part of the ladder to the right in the figure is the same, whether the element is included or not (the ladder is “the same”). Of course the ladder is not really infinitely long but the potential and current die off as one goes away from the points of interest, so distant parts of the ladder have no influence. Thus we get the equivalent circuit shown in Fig. 6, for which the resistance is:

$$\begin{aligned} R &= \rho_a dx + \left(g_m dx + \frac{1}{R} \right)^{-1} = \rho_a dx + \frac{R}{Rg_m dx + 1} \\ &= \rho_a dx + R(1 - Rg_m dx) = \rho_a dx + R - R^2 g_m dx. \end{aligned}$$

where we have used the fact that $(1 + \epsilon)^{-1} \approx (1 - \epsilon)$ for ϵ being any small quantity and where the approximation improves as ϵ becomes smaller (dx is infinitesimally small).

Finally, the last equation above is solved for R to get:

$$R = \sqrt{\frac{\rho_a}{g_m}},$$

which agrees with Eq. (7).

MODEL EXAM

conductance of axon membrane: 1.25×10^{-4} mhos/m
resistance of axoplasm + “outside” material: 1.27×10^{10} ohms/m

1. See Output Skills K1-K2 in this module’s *ID Sheet*. One or both of these skills may be on the actual exam.

Brief Answers:

1. See this module’s *text*.