

Massachusetts Institute of Technology
Department of Electrical Engineering and Computer Science,
Department of Mechanical Engineering, Department of Biological Engineering,
Harvard-MIT Division of Health Sciences and Technology
2.791J/2.794J/6.021J/6.521J/20.370J/20.470J/HST.541J
Quantitative Physiology: Cells and Tissues

Homework Assignment #8

Issued: November 16, 2006

Due: November 30, 2006

Exercise 1. Does the time constant of a cylindrical cell depend on its dimensions? Does the space constant of a cylindrical cell depend on its dimensions?

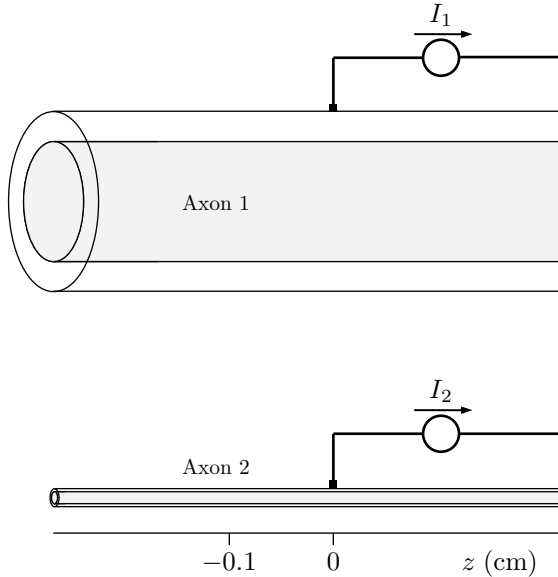
Exercise 2. The space constant decreases as the specific membrane conductance is increased. Give a *physical* explanation for this result.

Exercise 3. What are the distinctions among the conductance variables G_m , \mathcal{G}_m , and g_m ?

Exercise 4. A squid axon is placed in a large volume of sea water so that you may assume that $r_o \ll r_i$. The following data are given: resistivity (specific resistance) of squid axoplasm, $\rho_i = 30 \Omega \cdot \text{cm}$; diameter of axon is $500 \mu\text{m}$; space constant, $\lambda_C = 6 \text{ mm}$; thickness of membrane $d = 50 \text{ \AA}$; capacitance per unit area of membrane $C_m = 1 \mu\text{F}/\text{cm}^2$.

- a) Find the conductance of the axon per unit length, g_m .
- b) Find the conductance of the axon per unit area, G_m .
- c) Find λ_C for unmyelinated axons whose membranes have specific properties (i.e., G_m and ρ_i) that are identical to those of the squid axon but whose diameter are: 1 mm; 0.1 mm; 0.01 mm; 0.001 mm.
- d) Find τ_M for the squid axon and for the same axons considered in part (c).

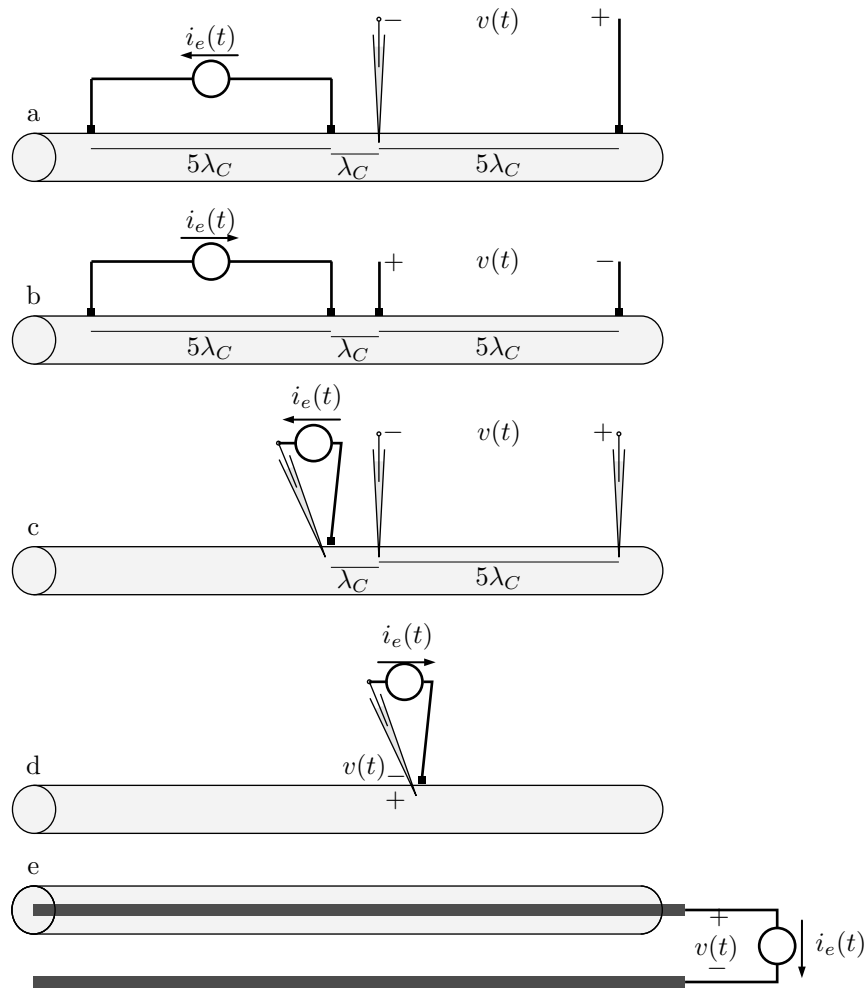
Problem 1. Constant currents I_1 and I_2 are applied to the exteriors of Axons 1 and 2, respectively, and the resulting time-independent changes in membrane potential are $v_{m1}(z)$ and $v_{m2}(z)$, respectively. I_1 and I_2 are adjusted so that $v_{m1}(0) = v_{m2}(0) = 10$ mV. This change in potential is sufficiently small so that the membrane voltage-current characteristic may be assumed to be linear. You may also assume that $r_o \ll r_i$ for both axons and that r_o is the same for both axons. The geometries and parameters for Axons 1 and 2 are given below, where a is the axon radius, ρ_i is the cytoplasmic resistivity, and G_m is the specific membrane conductance.



Axon #	a (μm)	ρ_i ($\Omega \cdot \text{cm}$)	G_m (S/cm^2)
1	100	100	5×10^{-3}
2	10	100	$(1/8) \times 10^{-3}$

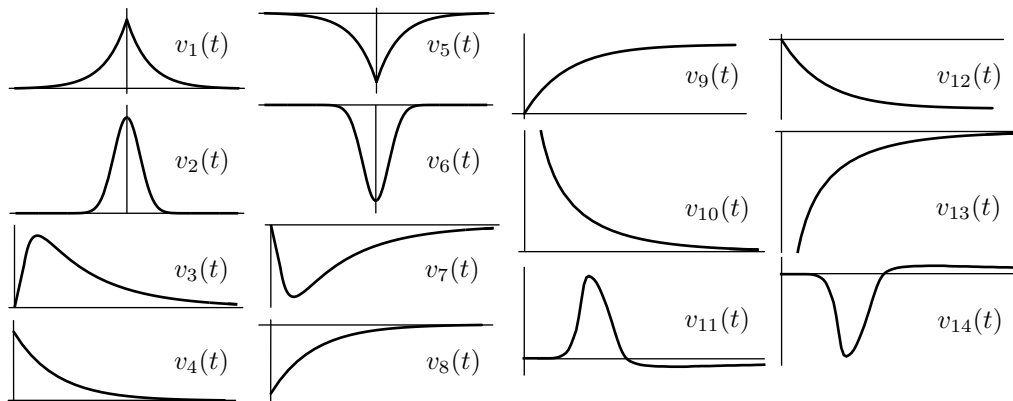
- Let $v_{m1}(-0.1)$ and $v_{m2}(-0.1)$ be the membrane potential changes at $z = -0.1$ cm for the two axons. Determine the value of the ratio $A = v_{m1}(-0.1)/v_{m2}(-0.1)$.
- Determine the value of the ratio $B = I_1/I_2$.

Problem 2. A large unmyelinated axon is immersed in oil, and five different arrangements of electrodes for delivering current stimuli and for measuring potential responses are attached to the axon as shown below.

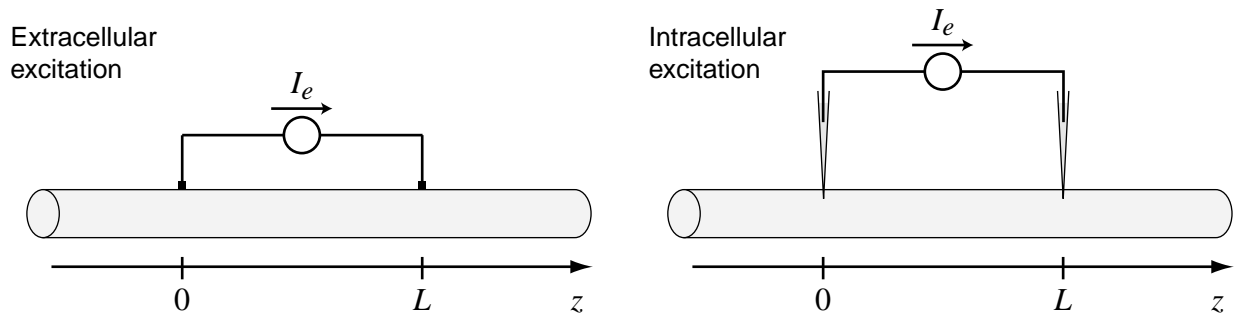


The stimulus current, a brief positive pulse at $t = 0$, is the same for each arrangement of electrodes. Assume that the duration of the pulse is much shorter than the membrane time constant of the cell, and that the cell's membrane can be modeled as a linear cable. The space constant of the cell is λ_C . In arrangement d, the potential is recorded and the current is delivered at the same longitudinal position. Assume that the electrodes have infinitesimal spatial extent in parts a-d and have length much larger than λ_C in part e.

For each of the different arrangements (parts a-e in the figure) determine which of the following waveforms for $v(t)$ represents the deviation of the measured potential from its resting value. For each waveform, the horizontal axis corresponds to $v(t) = 0$, and the vertical axis to $t = 0$. If no waveform applies, answer *None*. Explain the basis of your choice in each case.



Problem 3. A large invertebrate axon is immersed in oil and stimulated with a constant current $I_e > 0$. The current is delivered using a pair of electrodes that are either extracellular or intracellular, as illustrated in the following figure.

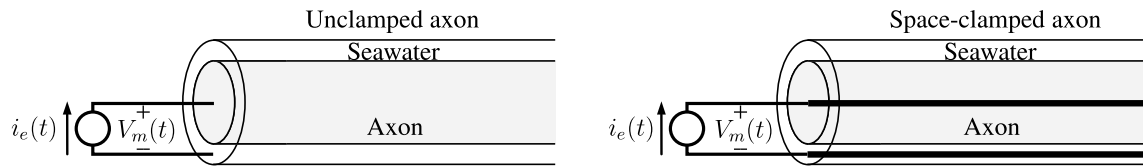


The current I_e is sufficiently small that the cell behaves as a linear cable. The specific resistances of the internal and external conductors are $100 \text{ k}\Omega/\text{cm}$ and $10 \text{ k}\Omega/\text{cm}$, respectively. The specific conductance and capacitance of the membrane are $10 \text{ mS}/\text{cm}$ and $0.1 \text{ }\mu\text{F}/\text{cm}$, respectively. The membrane potential is allowed to come to steady state. [Remember: V_m is positive when the inside of the cell is positive with respect to the outside of the cell. Also, the reference direction for the longitudinal currents is in the $+z$ direction.]

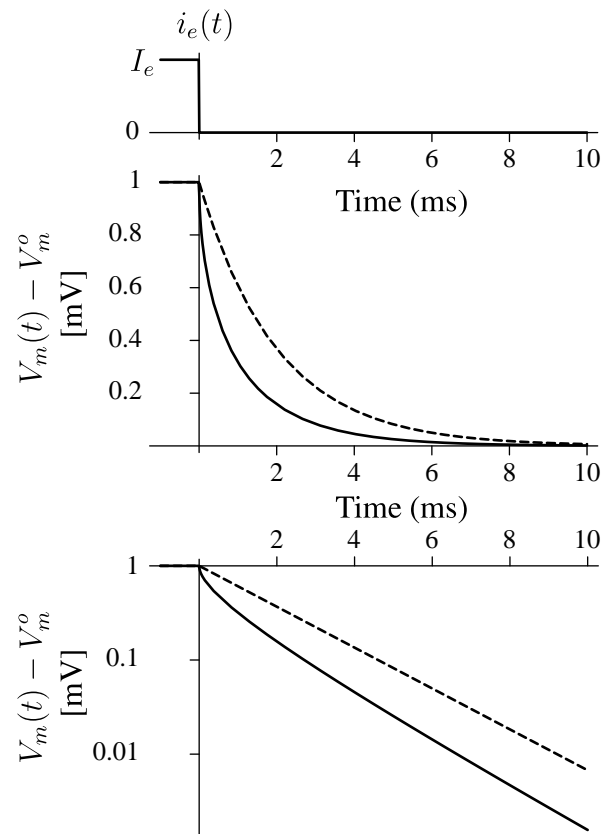
Determine if the following statements are true or false.

- a) The intracellular potential at $z = L$ is greater than the intracellular potential at $z = 0$.
 - a1) True or False for extracellular excitation?
 - a2) True or False for intracellular excitation?
- b) The extracellular potential at $z = L$ is greater than the extracellular potential at $z = 0$.
 - b1) True or False for extracellular excitation?
 - b2) True or False for intracellular excitation?
- c) The external longitudinal current $I_o(z)$ is equal to 0 for $z < 0$.
 - c1) True or False for extracellular excitation?
 - c2) True or False for intracellular excitation?
- d) The membrane potential at $z = L$, $V_m(L)$, is greater than the membrane potential at $z = 0$, $V_m(0)$.
 - d1) True or False for extracellular excitation?
 - d2) True or False for intracellular excitation?
- e) The internal longitudinal current at a point just to the right of the rightmost electrode, i.e., $I_i(L^+)$, is less than zero.
 - e1) True or False for extracellular excitation?
 - e2) True or False for intracellular excitation?

Problem 4. Electrical responses for an unmyelinated axon are measured in two configurations — unclamped and space clamped — as shown in the following figure.



The stimulus current and voltage responses are shown in the following figure.



The current stimulus has an amplitude I_e for $t < 0$ and an amplitude of 0 for $t \geq 0$. Each of the voltage responses are shown twice: with a linear ordinate (middle panel) and on a logarithmic scale (lower panel). For each configuration, I_e is adjusted so that the membrane potential exceeds the resting potential by 1 mV for $t < 0$. This potential change is so small that the voltage-current characteristic of an incremental portion of the axon membrane can be considered to be represented as a constant conductance and a capacitance in parallel.

Part a. Which trace, solid or dashed, corresponds to the response of the space clamped axon? Briefly explain.

Part b. Determine the membrane time constant, τ_M , when the axon is space-clamped. Briefly explain.

Part c. Determine the membrane time constant, τ_M , when the axon is unclamped. Briefly explain.

Problem 5. An axon of radius a is placed in a bath of sea water. The conduction velocity of the action potential in sea water is ν . The axon space constant is λ_C and the membrane time constant is τ_M . The sea water surrounding the axon is replaced by a solution that consists of 78% sea water and 22% distilled water by volume. It is assumed that: (1) the axon is cylindrical in both solutions; (2) the change in length of the axon is negligible; (3) the volume of the axon is assumed equal to that of the intracellular water; (4) the quantity of intracellular ions remains constant; (5) the replacement does not affect the electrical characteristics of a unit area of membrane; (6) the extracellular resistance per unit length is negligible (i.e., $r_o \ll r_i$). For each of the following, explain your reasoning and determine:

- a) the conduction velocity of the action potential in the diluted sea water in terms of ν ;
- b) the axon space constant in the diluted sea water in terms of λ_C ;
- c) the membrane time constant in the diluted sea water in terms of τ_M .