Instructions

1. **Staple** this cover sheet to your exam and solutions and return it to Yuri Dabaghian in DH 2006 by 12 am on Thursday, October 19.

2. Print your name on the line below

3. (5) Indicate your compliance with the honor system by writing out in full and signing the traditional pledge, “*On my honor, I have neither given nor received any unauthorized aid on this exam,*” on the lines below

4. Do any five problems out the proposed seven.

5. Work each part in great detail.
Problem 1 Consider the passive isopotential cell, where the potential, \( v = V - V_{Cl} \), is governed by

\[
\tau v'(t) + v(t) = f(t), \quad v(0) = 0, \tag{1}
\]
for \( \tau = C_m/g_{Cl} \) and \( f(t) = I_{stim}(t)/(AC_m) \).

(1a) Use the identity

\[
\frac{d}{dt}(v(t)e^{t/\tau}) = (v'(t) + \frac{1}{\tau}v(t))e^{t/\tau} \tag{2}
\]

to show

\[
v(t) = \frac{1}{\tau} \int_0^t e^{(s-t)/\tau} f(s) ds. \tag{3}
\]

(1b) Suppose the cell is driven by the impulse \( I_{stim}(t) = I_0 \delta(t - t_1) \), where \( \delta \) denotes the Dirac-delta function. Compute \( v_{\text{max}} = \max_t v(t) \). At what time does the potential attain its maximum value?

(1c) Since the passive cell cannot model the action potential, we often assume the cell spikes when its potential reaches a threshold \( v_{th} \). Using the same stimulus as in (b), determine the threshold current \( I_\theta = \min (I_0) \) such that \( v_{\text{max}} \geq v_{th} \). When \( I_0 \geq I_\theta \), at what time will the cell spike?

(1d) Assume the cell receives a delta-impulse every \( t \) ms, i.e.,

\[
I_{stim}(t) = I_0 \sum_{k=1}^{\infty} \delta(t - k\Delta t). \tag{4}
\]

Determine the threshold potential \( I_\theta \) as a function of the input frequency \( \omega = 1/\Delta t \). Sketch a plot of this function.

Hint: Evaluate \( v(t_n) \) and use the geometric series:

\[
\sum_{k=0}^{\infty} x^k = \frac{1}{1-x} \tag{5}
\]

for \( |x| < 1 \).

Problem 2 Consider the isopotential cell with the active \( h \)-current:

\[
C_m V'(t) = -g_{Cl}(V(t) - V_{Cl}) - g_h q^2(t)(V(t) - V_h) + I_{stim}(t) \tag{6}
\]
\[
\tau_q q'(t) = q_{\infty}(V) - q(t) \tag{7}
\]

(2a) What equation must the resting potential, \( V_r \), satisfy?
(2b) Assume that for some small \( \epsilon \), \( I_{stim}(t) = \epsilon \tilde{I}(t) \), \( V(t) = V_r + \epsilon \tilde{V}(t) + O(\epsilon^2) \), and \( q(t) = q_\infty(V_r) + \epsilon \tilde{q}(t) + O(\epsilon^2) \). Expand each function, \( q_\infty(V) \) and \( \tau_q(V) \), as a Taylor series about \( V_r \). Then, derive the quasi-active equations describing the linear perturbations from rest.

(2c) Construct the quasi-active system

\[
y'(t) = By(t) + f(t),
\]

where \( y = [\tilde{q} \tilde{V}]^\top \) ("\( \top \)" means "transposed"). Identify each element of \( B \) and \( f \).

**Problem 3** Consider the simplified cable with three compartments, where \( v_s \) is the soma potential, \( v_p \) is the potential for the proximal compartment, and \( v_d \) is the potential for the distal compartment. Let \( C \) be the membrane capacitance, \( G \) be the membrane conductance, and \( R \) be the axial resistance.

(3a) Write the governing equations for \( v_s, v_p, \) and \( v_d \), where \( v_s(0) = v_p(0) = v_d(0) = 0 \). Show that if \( v \equiv [v_s \ v_p \ v_d]^\top \), then \( v \) can be written as

\[
v'(t) = Bv(t) + f(t).
\]

Write the matrix \( B \) and driving term \( f \).

(3b) Assume \( Bq_n = z_n q_n \) with orthonormal eigenvectors:

\[
q_i^\top q_j = \begin{cases} 
1, & \text{if } i = j \\
0 & \text{otherwise.}
\end{cases}
\]

Let

\[
f(t) = \sum_{i=1}^{3} c_i(t) q_i
\]

3
\[ v(t) = \sum_{i=1} a_i(t)q_i. \]  

Write the soma potential \( v_s \) in terms of the eigenvalues and eigenvectors of \( B \). You may find Equation (1) from Problem 1 helpful in solving for the coefficients \( a_i \).

(3c) Let \( R = C = G = 1 \). Then \( B \) has the orthonormal eigenvectors

\[
q_1 = \frac{1}{\sqrt{3}} \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix}, \quad q_2 = \frac{1}{\sqrt{2}} \begin{bmatrix} -1 \\ 0 \\ 1 \end{bmatrix}, \quad q_3 = \frac{1}{\sqrt{6}} \begin{bmatrix} -1 \\ 2 \\ -1 \end{bmatrix} \]  

(13)

Compute the corresponding eigenvalues. Is the resting potential stable?

(3d) Assume the stimulus is constant, \( I_{stim}(t) = I_0 \). Solve for the steady-state soma potential,

\[
\lim_{t \to \infty} v_s(t) \]  

(14)
in terms of \( I_0 \).

(3e) Assume the proximal compartment receives the stimulus \( I_{stim} = I_0 \) instead of the distal compartment. What is the new steady-state potential at the soma?

Problem 4. Together, we shall study, by hand, the passive sealed fiber undergoing a known distributed current stimulus, \( I \). That is,

\[
\frac{a}{2R^2} v_{xx} = C_m v_t + G_m v + I(x,t), \quad 0 < x < l \]  

(15)

\[
v_x(0,t) = v_x(l,t) = 0, \quad v(x,0) = 0. \]  

(16)

We will solve this at first for a general \( I \) and then finish up with a particular case.

(4a) We shall expand everything in terms of the solutions to

\[-q''(x) = zq(x), \quad q'(0) = q'(l) = 0. \]  

(17)

Solve for the eigenpairs \( \{q_n, z_n\}_{n=0}^\infty \) of (2) and normalize the eigenfunctions in order that \( \int_0^l q_n^2(x) \, dx = 1 \).

(4b) Now write

\[
v(x,t) = \sum_{n=0}^\infty q_n(x)T_n(t)I(x,t) = \sum_{n=0}^\infty q_n(x)i_n(t) \]  

(18)
and plug these into (1) and derive a sequence of ordinary differential equations (and initial conditions) for the unknown \( T_n \) in terms of the known \( i_n \).

(4c) Solve these ordinary differential equations.

(4d) Explicitly compute each \( i_n \) in the case that \( I(x,t) = t \exp(-t) \cos(\pi x/l) \). What are the corresponding \( T_n \)? And finally, what is \( v \)?

**Problem 5.** If the stimulus above was a conductance change, rather than a direct current stimulus we would instead be faced with

\[
\frac{a}{2R_2} v_{xx} = C_m v_t + G_m v + G(x,t)(v - E), \quad 0 < x < l
\]

\[
v_x(0,t) = v_x(l,t) = 0
\]

\[
v(x,0) = 0.
\]  

(19)

you might think of \( G \) as some effective synaptic conductance and \( E \) as the (constant) synaptic reversal potential. As our eigentechnique of problem 1 does not directly apply we turn to a strictly numerical attack.

(5a) Equipartition the fiber into \( N \) equipotential compartments and show how (3) becomes a system of \( N \) ordinary differential equations for the \( N \) compartment potentials. Write this in matrix terms.

(5b) Setup both forward and backward Euler time discretizations of this system of ordinary differential equations.