580.439/639 Homework #8 Solutions

Problem 1

Part a) Ignoring r_e and using the following equations for r_i, c_m, and I_i

$$r_i = \frac{R_i}{\pi a^2} \qquad c_m = C_m 2\pi a \qquad I_i = 2\pi a I_i^*$$

allows Eqn. 1.1 in the problem statement to be rewritten as

$$\frac{\pi a^2}{R_i}\frac{\partial^2 V}{\partial x^2} = 2\pi a\, C_m \frac{\partial V}{\partial t} + 2\pi a\, I_i^* \tag{1.3}$$

where I_i^* is the current *density* in the membrane (current/area) as opposed to I_i which is the current *per unit length of membrane cylinder* and a is the membrane cylinder radius. Dividing Eqn. 1.3 by $2\pi a$ gives an equation in which the axon radius a appears only in one term:

$$\frac{a}{2R_i}\frac{\partial^2 V}{\partial x^2} = C_m \frac{\partial V}{\partial t} + I_i^* \tag{1.4}$$

Part b) If V(x,t) is a propagating constant-waveshape pulse of the form $F(x-\Theta t)$ then the derivatives can be written as follows

$$\frac{\partial V}{\partial x} = \frac{\partial F(x-\Theta t)}{\partial x} = \frac{dF}{du}\frac{\partial u}{\partial x} = \frac{dF}{du}$$

where $u = x-\Theta t$. Similarly

$$\frac{\partial^2 V}{\partial x^2} = \frac{d^2 F}{du^2} \tag{1.5}$$

and by the same argument

$$\frac{\partial V}{\partial t} = \frac{\partial F(x-\Theta t)}{\partial t} = \frac{dF}{du}\frac{\partial u}{\partial t} = -\Theta\frac{dF}{du} \tag{1.6}$$

Now substitution of Eqns 1.5 and 1.6 into 1.4 gives the following ordinary differential equation for the waveshape F:

$$\frac{a}{2R_i}\frac{d^2 F}{du^2} = -C_m\Theta\frac{dF}{du} + I_i^*$$

Part c) The equation for HH variable n(V,t,x) is written below. Notice that x has been added as an independent variable here because n will vary with position down the axon. However, the x-dependence of this equation is via V(x,t), and no additional complexity is added to the equation for dn/dt:

$$\frac{\partial n(x,t)}{\partial t} = \frac{n_\infty(V(x,t)) - n(x,t)}{\tau_n(V(x,t))}$$

Now substituting F(u) for V and n(u) for n(x,t) in the equation above and using the chain rule (Eqn 1.6) again gives

$$\frac{dn(u)}{du} = -\frac{1}{\Theta}\frac{n_\infty(F) - n}{\tau_n(F)}$$

The other two equations, for $\partial m/\partial t$ and $\partial h/\partial t$, can be treated similarly.

Part d) The first part of this problem can be derived by differentiating Eqn. 1.6 to give

$$\frac{\partial^2 V}{\partial t^2} = \Theta^2 \frac{d^2 F}{du^2} \tag{1.7}$$

Comparing Eqns. 1.5 and 1.7 gives the following relationship between $\partial^2 V/\partial x^2$ and $\partial^2 V/\partial t^2$ for the special case of V a propagating wave.

$$\frac{\partial^2 V}{\partial t^2} = \Theta^2 \frac{\partial^2 V}{\partial x^2}$$

So that Eqn. 1.4 can be expressed in terms of time derivatives of V as an ordinary differential equation describing the dynamics of V at a fixed point x

$$\frac{a}{2R_i\Theta^2}\frac{d^2V}{dt^2} = C_m\frac{dV}{dt} + I_i^*$$

Then $K = a/2R_i\Theta^2$. Note that this equation applies to all axons with the same R_i, C_m, and complement of channels (I_i^*), regardless of radius.

Part e) If K is a constant, then propagation velocity Θ is given by

$$\Theta = \sqrt{\frac{a}{2R_i K}}$$

Problem 2

The resistance of a thin shell of inner radius r and outer radius r+dr for current flow in the radial direction is given by

$$dR = \frac{R_{my}\,dr}{2\pi r}$$

where R_{my} is the bulk resistivity of the material and it is assumed that the shell has unit length. Adding up all the shells between radius d/2 and D/2 gives

$$r_m = \int_0^{r_m} dR = \int_{d/2}^{D/2} \frac{R_{my}}{2\pi r}\, dr = \frac{R_{my}}{2\pi} \ln\frac{D}{d}$$

Part b) The length constant λ is given by

$$\lambda = \sqrt{\frac{r_m}{r_i}} = \sqrt{\frac{R_{my}}{2\pi}\ln\frac{D}{d} \bigg/ \frac{R_i}{\pi(d/2)^2}} = \sqrt{\frac{R_{my}}{8R_i}}\, d\sqrt{\ln\frac{D}{d}}$$

If the outer diameter of the myelin is fixed at D, and the inner diameter d is allowed to vary, the maximum value of λ can be found by differentiating w.r.t. d and setting the derivative equal to 0.

$$\frac{d\lambda}{dd} = \sqrt{\frac{R_{my}}{8R_i}}\left[\sqrt{\ln\frac{D}{d}} - 1\bigg/ 2\sqrt{\ln\frac{D}{d}}\right] = 0$$

which gives

$$\ln\frac{D}{d} = \frac{1}{2} \qquad \Rightarrow \qquad d = 0.61D$$

That this is a maximum can be verified by considering the second derivative.

Part c) The time constant τ_m is given by

$$\tau_m = r_m c_m = \frac{R_{my}}{2\pi}\ln\frac{D}{d}\,\frac{2\pi\kappa\varepsilon_0}{\ln\frac{D}{d}} = (\text{const})$$

That is, the membrane time constant is constant, regardless of axon diameter. As a result the ratio λ/τ_m is proportional to λ and has the same diameter dependence as λ. Thus if λ is maximized by d=0.61D, then λ/τ_m is also maximized by d=0.61D.

Problem 3

Part a) From the usual equations,

$$\tau = R_m C_m = 1.2 \text{ x } 10^4 \ \Omega - \text{cm}^2 \cdot 1.2 \text{ x } 10^{-6} \ \text{fd/cm}^2 = 0.0144 \ \text{s} \ = \ 14.4 \text{ ms}$$

$$\lambda = \sqrt{\frac{R_m\, a}{2\, R_i}} = \sqrt{\frac{1.2 \text{ x } 10^4\ \Omega\text{-cm}^2 \cdot 0.5 \text{ x } 10^{-4}\text{ cm}}{2 \cdot 150\ \Omega\text{-cm}}} = 447\ \mu$$

the electrotonic length is then

$$L = \frac{l}{\lambda} = \frac{10\ \mu}{447\ \mu} = 0.022$$

Part b) The cable equation is, as usual

$$\frac{\partial^2 V}{\partial \chi^2} = \frac{\partial V}{\partial T} + V$$

In the sinusoidal steady state, initial conditions are not needed and the cable equation becomes

$$\frac{\partial^2 \overline{V}}{\partial \chi^2} = (1 + j\omega)\,\overline{V} \tag{3.1}$$

where $\overline{V}$ is the Fourier transform of V and $j\omega\overline{V}$ is the Fourier transform of $\partial V/\partial T$. Recall that ω is related to frequency in Hz (Ω) as $\omega = \Omega/\tau_m$, where τ_m is the membrane time constant.

The boundary conditions suggested by the problem statement are, after Fourier transformation

$$\overline{V}(0,j\omega) = 0 \quad \text{and} \quad G_\infty \left.\frac{\partial \overline{V}}{\partial \chi}\right|_{\chi=L} = \overline{I}_L(j\omega)$$

Note that χ=0 is the soma end of the cilium and χ=L is the transducer-channel end of the cilium. There is no negative sign in the χ=L equation because of the reverse direction of current definition in the problem statement.

Part c) The solution to the cable equation (Eqn. 3.1) is

$$\overline{V}(\chi,j\omega) = A\, e^{\chi\sqrt{j\omega+1}} + Be^{-\chi\sqrt{j\omega+1}}$$

At χ=0,

$$\overline{V}(0,j\omega) = 0 \quad \Rightarrow \quad A + B = 0 \quad \Rightarrow \quad A = -B$$

so that $\overline{V}(\chi,j\omega) = A\sinh\left[\chi\sqrt{j\omega+1}\right]$. At $\chi = L$,

$$G_\infty \left.\frac{\partial \overline{V}}{\partial \chi}\right|_{\chi=L} = G_\infty A\sqrt{j\omega+1}\cosh\left[L\sqrt{j\omega+1}\right] = \overline{I}_L(j\omega)$$

Thus

$$A = \frac{\overline{I}_L(j\omega)}{G_\infty\sqrt{j\omega+1}\cosh\left[L\sqrt{j\omega+1}\right]}$$

and the voltage in the cilium is given by

$$\bar{V}(\chi, j\omega) = \frac{\bar{I}_L(j\omega)}{G_\infty \sqrt{j\omega+1}} \frac{\sinh\left[\chi\sqrt{j\omega+1}\right]}{\cosh\left[L\sqrt{j\omega+1}\right]}$$

The axial current in the cilium is given by (where the direction of the current arrow is reversed, as in the problem statement)

$$\bar{I}_i(\chi, j\omega) = G_\infty \frac{\partial\bar{V}}{\partial\chi} = \bar{I}_L(j\omega) \frac{\cosh\left[\chi\sqrt{j\omega+1}\right]}{\cosh\left[L\sqrt{j\omega+1}\right]}$$

and at $\chi = 0$, the somatic end of the cilium

$$\bar{I}_0(j\omega) = \bar{I}_i(0, j\omega) = \frac{\bar{I}_L(j\omega)}{\cosh\left[L\sqrt{j\omega+1}\right]} \tag{3.2}$$

Note that Eqn. 3.2 can be derived easily by starting with the transformed two-port model of the finite cable derived in class:

$$\begin{bmatrix} \bar{V}_0 \\ -\bar{I}_0 \end{bmatrix} = \begin{bmatrix} \cosh(qL) & \sinh(qL)/G_\infty q \\ G_\infty q \sinh(qL) & \cosh(qL) \end{bmatrix} \begin{bmatrix} \bar{V}_L \\ -\bar{I}_L \end{bmatrix} \tag{3.3}$$

where the transform variable $q = \sqrt{j\omega+1}$ and the voltage and current variables have been Fourier transformed. The negative signs on the currents $\bar{I}_0$ and $\bar{I}_I$ are necessary because of the convention used for current directions in this problem. From the boundary conditions, $\bar{V}_0 = 0$, so the first equation in Eqn. 3.3 is

$$0 = \bar{V}_L \cosh(qL) - \frac{\bar{I}_L}{G_\infty q} \sinh(qL) \tag{3.4}$$

The second equation in Eqn. 3.3 expresses the relationship between $\bar{I}_0$ and $\bar{I}_I$, in term of $\bar{V}_I$. Using Eqn. 3.4 to eliminate $\bar{V}_I$ gives

$$-\bar{I}_0 = G_\infty q \sinh(qL)\, \bar{V}_L - \cosh(qL)\, \bar{I}_L$$

$$\bar{I}_0 = -G_\infty q \sinh(qL) \frac{\sinh(qL)\, \bar{I}_L}{G_\infty q \cosh(qL)} + \cosh(qL)\, \bar{I}_L$$

$$= \frac{-\sinh^2(qL) + \cosh^2(qL)}{\cosh(qL)} \bar{I}_L$$

$$= \frac{1}{\cosh(qL)} \bar{I}_L$$

which is the same result as Eqn. 3.2. Use has been made of the identity

$$\cosh^2(qL) - \sinh^2(qL) = 1$$

At D.C. (ω= 0 Hz), the transfer current gain is essentially 1,

$$\frac{1}{\cosh\left[0.022\ \sqrt{j0 + 1}\right]} = \frac{1}{\cosh\left[0.022)\right]} = 0.9998$$

The gain at 1 kHz is given by

$$\left.\frac{1}{\cosh\left[L\sqrt{j\omega+1}\right]}\right|_{\omega/\tau_m=2\pi\cdot 10^3} = \frac{1}{\cosh\left[0.022\ \sqrt{j2\pi \text{ x } 10^3\ 0.0144 +1}\right]}$$

$$= \frac{1}{\cosh\left[0.022\ \sqrt{j90.48 +1}\right]}$$

$$= \frac{1}{\cosh\left[0.022\ \sqrt{90.48\ e^{j\,0.4965\pi}}\right]}$$

choosing only the first-quadrant root gives (the third quadrant root gives the same final answer)

$$= \frac{1}{\cosh\left[0.022 \cdot 9.512\ e^{j\,0.2482\pi}\right]}$$

$$= \frac{1}{\cosh\left[0.15 + j\ 0.15\right]}$$

Using the fact that cosh[a+jb] = cosh(a) cos(b) + j sinh(a) sin(b),

$$= \frac{1}{1.00 + j\ 0.023} = 1.00 - j\ 0.023 = 1\ \cdot e^{-j\,0.0073\pi}$$

so that the electrotonic properties of the cilium produce essentially no attenuation or phase shift of the current I_L at 1 KHz.

The gain is 0.5 at 95 kHz (this is a good problem for Mathematica).