580.439/639 Homework 7 Solutions

Problem 1

Part a) For the cylinder model:

$$q = \sqrt{1 + s\tau_m} \qquad L = \frac{\Delta x}{\lambda} = \frac{\Delta x}{\sqrt{\dfrac{a}{2G_m R_i}}} \qquad G_\infty = \frac{1}{r_i \lambda} = \pi a^{3/2} \sqrt{\frac{2G_m}{R_i}}$$

where s is the Laplace transform variable in units of Hz. In class, s was dimensionless, because the transform was done in terms of $T = t/\tau_m$ as the time variable. If t had been used, then the result would have been as above. Using t instead of T is appropriate here, because t will be used for the compartmental model. For that model:

$$r_{ij} = \frac{R_i \Delta x}{\pi a^2} \qquad g_{mj} = G_m 2\pi a \Delta x \qquad c_{mj} = C_m 2\pi a \Delta x$$

Part b) In class, it was shown that the cylinder model gives the following:

$$\begin{bmatrix} V_0 \\ I_0 \end{bmatrix} = \begin{bmatrix} \cosh(qL) & \sinh(qL)/G_\infty q \\ G_\infty q \sinh(qL) & \cosh(qL) \end{bmatrix} \begin{bmatrix} V_1 \\ I_1 \end{bmatrix} =$$

$$= \begin{bmatrix} \cosh\left(\sqrt{1+s\tau_m}\, L\right) & \sinh\left(\sqrt{1+s\tau_m}\, L\right) / G_\infty \sqrt{1+s\tau_m} \\ G_\infty \sqrt{1+s\tau_m}\, \sinh\left(\sqrt{1+s\tau_m}\, L\right) & \cosh\left(\sqrt{1+s\tau_m}\, L\right) \end{bmatrix} \begin{bmatrix} V_1 \\ I_1 \end{bmatrix}$$

For the compartmental model, mesh equations can be written as follows:

$$V_0 = I_0 \frac{r_{ij}}{2} + (I_0 - I_1)\, z_{mj}$$
$$V_1 = (I_0 - I_1)\, z_{mj} - I_1 \frac{r_{ij}}{2}$$

where z_{mj} is the parallel combination of g_{mj} and c_{mj}: $z_{mj} = 1/(g_{mj} + s c_{mj}) = 1/g_{mj}\left(1 + s\tau_{mj}\right)$. Again, s is the Laplace transform variable in units of Hz. After some algebra, these can be rearranged in the following form:

$$\begin{bmatrix} V_0 \\ I_0 \end{bmatrix} = \begin{bmatrix} 1 + \dfrac{r_{ij} g_{mj}}{2}(1+s\tau_m) & r_{ij} + \dfrac{r_{ij}^2}{4} g_{mj}(1+s\tau_m) \\ g_{mj}(1+s\tau_m) & 1 + \dfrac{r_{ij} g_{mj}}{2}(1+s\tau_m) \end{bmatrix} \begin{bmatrix} V_1 \\ I_1 \end{bmatrix} \qquad (\dagger)$$

Note that the time constant τ_m is the same in the two models. To see this, note that $\tau_m = C_m/G_m$ in the cylinder model and $\tau_m = c_{mj}/g_{mj} = C_m\, 2\pi a\, \Delta x / (G_m\, 2\pi a\, \Delta x) = C_m/G_m$ in the compartmental model.

Part c) The Taylor series approximations for cosh() and sinh() are

$$\cosh(u) = 1 + \frac{u^2}{2!} + \frac{u^4}{4!} + \cdots$$

$$\sinh(u) = u + \frac{u^3}{3!} + \frac{u^5}{5!} + \cdots$$

Substituting the Taylor series for cosh() and sinh() in the cylinder model and keeping only the first two terms gives

$$\begin{bmatrix} V_0 \\ \\ I_0 \end{bmatrix} \approx \begin{bmatrix} 1 + \frac{q^2L^2}{2!} & \frac{1}{G_\infty q}(qL + \frac{q^3L^3}{3!}) \\ G_\infty L q^2 (1 + \frac{q^2L^2}{3!}) & 1 + \frac{q^2L^2}{2!} \end{bmatrix} \begin{bmatrix} V_1 \\ \\ I_1 \end{bmatrix} \qquad (\dagger\dagger)$$

This approximation depends on the fact that $|q^2L^2| << 1$, which is less restrictive than the assumption that $|qL| << 1$, stated in the problem set.

1) The terms on the diagonal are the same in (†) and (††) because

$$q^2 = 1 + s\tau_m \quad \text{and} \quad L^2 = \frac{\Delta x^2}{\lambda^2} = \frac{\Delta x^2}{\left(\frac{a}{2G_m R_i}\right)} = \frac{R_i \Delta x}{\pi a^2} 2\pi a G_m \Delta x = r_{ij} g_{mj}$$

2) The terms below the diagonal are also the same because

$$G_\infty L q^2 = \pi a^{3/2} \sqrt{\frac{2G_m}{R_i}} \frac{\Delta x}{\sqrt{\frac{a}{2G_m R_i}}} (1 + s\tau_m) = 2\pi a G_m \Delta x (1 + s\tau_m) = g_{mj}(1 + s\tau_m)$$

Notice that this captures only the first term in the approximation from the cylinder model. The second term can be neglected to the extent that $|q^2L^2| << 1$, as above.

3) For the upper diagonal term, there are two terms in both the cylinder and compartmental models. Proceeding as above, it is straightforward to show that

$$\frac{L}{G_\infty} = r_{ij} \quad \text{and} \quad \frac{q^2L^3}{G_\infty} = r_{ij}^2\, g_{mj}(1 + s\tau_m)$$

That is, the first terms agree exactly, but the second terms have different multipliers, 1/4 for the compartmental model but 1/3! = 1/6 for the cylinder model. Fortunately the second term is small compared to the first since from Eqn. (††)

$$\frac{\text{second term}}{\text{first term}} = \frac{q^3L^3/3!}{qL} = \frac{q^2L^2}{3!} << 1$$

Thus satisfactory agreement between the two models can be expected as long as $|qL|^2 << 1$. Note that this corresponds to choosing $\Delta x/\lambda$ to be small since

$$|qL|^2 = \left|(1+s\tau_m)\left(\frac{\Delta x}{\lambda}\right)^2\right| = \left(\frac{\Delta x}{\lambda}\right)^2 |(1+s\tau_m)|$$

Thus at D.C. (s=0), the condition corresponds to $(\Delta x/\lambda)^2 << 1$ or $\Delta x^2 << \lambda^2$. In other words, the lengths of the cylinders corresponding to each compartment should be short compared to the length constant of the cylinder.

Part d) At frequencies above D.C., the term $|(1+s\tau_m)|$ increases. In the sinusoidal steady state at frequency ω, the increase goes as $(1+\omega^2\tau_m{}^2)^{1/2}$. Thus to attain the condition $|qL|^2 << 1$, Δx^2 should be chosen to be small compared to $\lambda^2/(1+\omega^2\tau_m{}^2)$. As a rule of thumb, dendritic trees are strongly lowpass and frequencies above $1/\tau_m$ are unlikely to be important. Thus choosing $\Delta x^2 << \lambda^2/2$ is likely to be sufficient.

Problem 2

Part a) For a semi-infinite cable the membrane potential in the DC steady state is

$$V(\chi, T \to \infty) = V_0 e^{-\chi} = V_0 e^{-x/\lambda}$$

thus the *MET* from point 0 to χ is

$$MET_{0\chi} = -\ln A_{0\chi} = -\ln \frac{V_0 e^{-\chi}}{V_0} = \chi = \frac{x}{\lambda}$$

which is the electrotonic distance as required.

Part b) The voltage gain A_{PR} can be written in terms of the transfer and input impedances as

$$A_{PR} = \frac{V_R}{V_P} = \frac{K_{PR}I_P}{K_{PP}I_P} = \frac{K_{PR}}{K_{PP}}$$

It was shown in class that $K_{PR} = K_{RP}$. Assume that $K_{PP} > K_{RR}$ when P is further from the soma than R as in the figure in the problem set. Then

$$A_{PR} = \frac{K_{PR}}{K_{PP}} < \frac{K_{RP}}{K_{RR}} = A_{RP}$$

and so $MET_{PR} > MET_{RP}$ as required. This means that potentials spread further away from the soma than they do toward the soma.

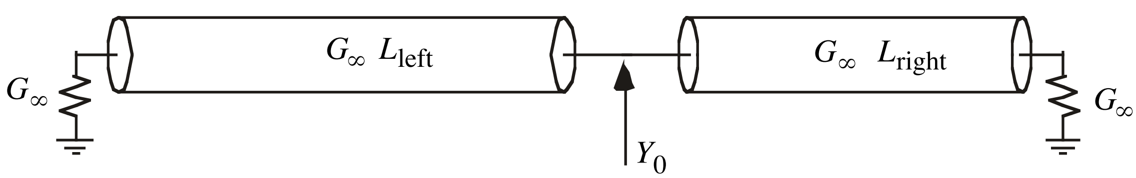
Problem 3

Part a) As the synapse moves away from the soma, the dendritic branches are smaller in diameter. All other things being equal, that means a higher input impedance, so a given current will produce a larger EPSP. The situation is slightly more complex because synapses produce conductance changes. In class, the membrane potential change produced by a synapse was derived as

$$V = E\frac{g_{syn}/Y_{in}}{1+g_{syn}/Y_{in}} \qquad (*)$$

where g_{syn} is the synaptic conductance, Y_{in} is the input admittance of the dendritic branch, and E is the synaptic reversal potential. This equation is only strictly true in the D.C. steady state or for some condition in which g_{syn} is constant in time, in which case Y_{in} is a conductance. In this condition, as Y_{in} decreases (further out in the dendritic tree) V increases. Ultimately, when $g_{syn}/Y_{in} >> 1$, saturation occurs and no further increases are observed.

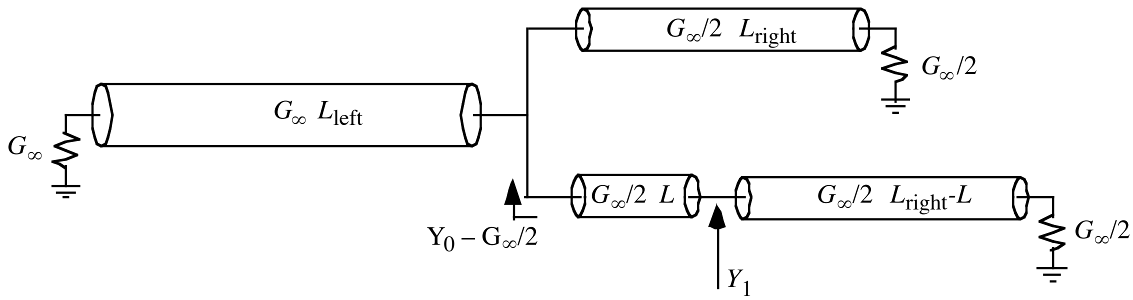
Part b) This part will be done assuming q=1, i.e. D.C. steady state. The task is to compute Y_{in} at the branch points of the dendritic tree, where the synapses are located. Because the cell can be reduced to an equivalent cylinder, the input admittance Y_0 (see the sketch in the problem set for the definition of Y_0) can be computed as the parallel combination of the input admittances of two cylinders:



The cylinders are the equivalent cylinders for the part of the tree to the left of Y_0 and for the part of the tree to the right of Y_0. Both cylinders have the G_∞ of the parent part of the original tree, terminated by conductance G_∞, as shown (the sum of the terminating conductances at the 2^n terminal branches). Using the input admittance rule defined in class,

$$Y_0 = G_\infty\frac{\frac{G_\infty}{G_\infty}+\tanh(L_{left})}{1+\frac{G_\infty}{G_\infty}\tanh(L_{left})} + G_\infty\frac{\frac{G_\infty}{G_\infty}+\tanh(L_{right})}{1+\frac{G_\infty}{G_\infty}\tanh(L_{right})} = 2G_\infty$$

At Y_1, the structure is slightly more complex:



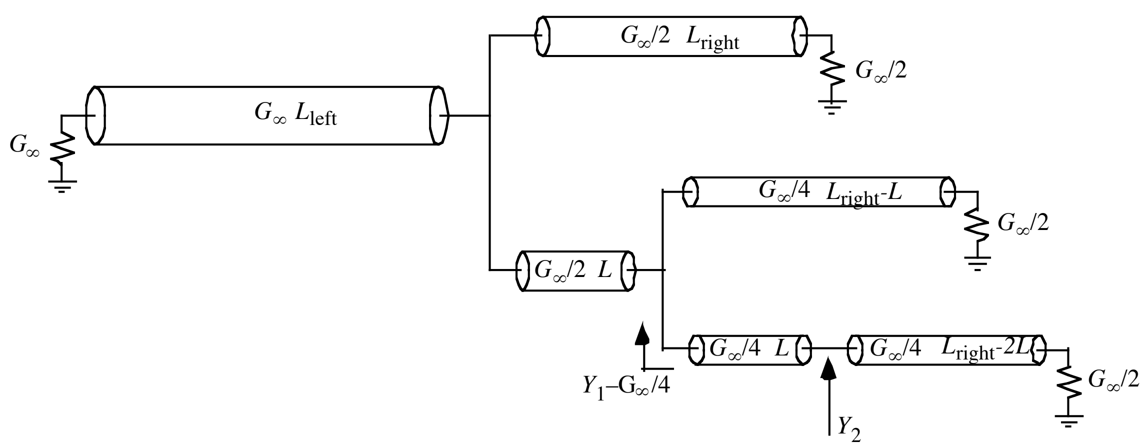
Now the right-hand cylinder has been broken into two parallel cylinders, with $G_\infty/2$ and length L_{right}. The lower one has been split into the cylinder between Y_0 and Y_1 and the rest. Now Y_1 is the sum of the input conductance of the L-length cylinder looking leftward and the remainder cylinder looking right (which is $G_\infty/2$). This can also be expressed as $Y_0–G_\infty/2$ Again using the conductance rule:

$$Y_1 = \frac{G_\infty}{2}\frac{\frac{Y_0 - G_\infty/2}{G_\infty/2} + \tanh(L)}{1+\frac{Y_0 - G_\infty/2}{G_\infty/2}\tanh(L)} + \frac{G_\infty}{2} = \frac{G_\infty}{2}\frac{\frac{3G_\infty/2}{G_\infty/2} + \tanh(L)}{1+\frac{3G_\infty/2}{G_\infty/2}\tanh(L)} + \frac{G_\infty}{2} = \frac{G_\infty}{2}\left[\frac{3+0.2}{1+3\cdot 0.2}+1\right]$$

$$= \frac{3G_\infty}{2}$$

where Y_0-$G_\infty/2$ is the load admittance seen by the length-L cylinder at its left end, equal to the input admittance Y_0 at that point, minus the contribution from the length-L cylinder itself. Alternatively, this is G_∞ from the length-L_{lewft} main cylinder plus $G_\infty/2$ for the upper branch of the length L_{right} cylinder.

Proceeding similarly for Y_2



$$Y_2 = \frac{G_\infty}{4}\frac{\dfrac{Y_1 - G_\infty/4}{G_\infty/4} + \tanh(L)}{1+\dfrac{Y_1 - G_\infty/4}{G_\infty/4}\tanh(L)} + \frac{G_\infty}{4} = \frac{G_\infty}{4}\frac{5+0.2}{1+5\cdot 0.2} + \frac{G_\infty}{4}$$
$$= 0.9 \cdot G_\infty$$

This algorithm can be continued and generalized using induction. At the next branch point, for example, Y_3=0.48G_∞.

So, at the first four branch points, the input conductances are 2, 1.5, 0.9, and 0.5 times G_∞. Clearly K_{ii} is increasing with branching, so the injection of fixed current will lead to larger EPSPs.

Part c) If the synapses are modeled correctly, as conductance changes, then Eqn. (*) should be used. This equation is a monotonic function of g_{syn}/Y_{in}, so the same qualitative effect will be seen, but the saturation of Eqn. (*) when $g_{syn}>Y_{in}$ will limit the extent of the rise distally.