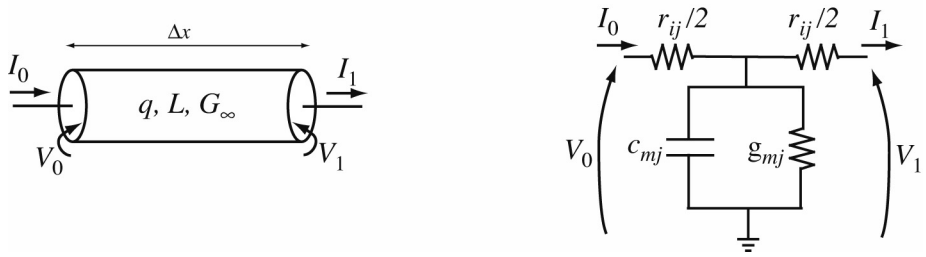
580.439/639 Homework #7

Two problems are due November 17, 2014

Problem 1

In considering branching linear cable structures, the two models sketched below are used.



The model at left (the *cylinder* model) is used in the exact theoretical calculations in which transfer impedances and similar quantities are computed and the model at right (the *compartmental* model) is used in practical computations in which the dendritic tree is represented by a series of discrete compartments, one for each Δx length of cable; the subscript j in the model at right refers to the j^{th} compartment. The compartmental version is usually used in modeling real neurons, because it is possible to make g_{mj} non-linear, i.e. to add HH voltage (and Ca^{++})-dependent conductances to it. Ideally, these two models should give identical two-port descriptions for the linear model, i.e. it should not be possible to tell them apart, given access to only I_0, I_1, V_0, and V_1.

Part a) Write equations that express the parameters of the two models above in terms of the same fundamental set of constants: G_m, C_m, R_i, a, and Δx (the conductance of a unit area of membrane, the capacitance of a unit area of membrane, the resistivity of cytoplasm, the radius of the cylinder, and the length of the cylinder, respectively). For this problem, $q = \sqrt{1+s}$, for non-dimensionalized time $T=t/\tau_m$. The answer to the question requires that it be expressed in terms of dimensional time t.

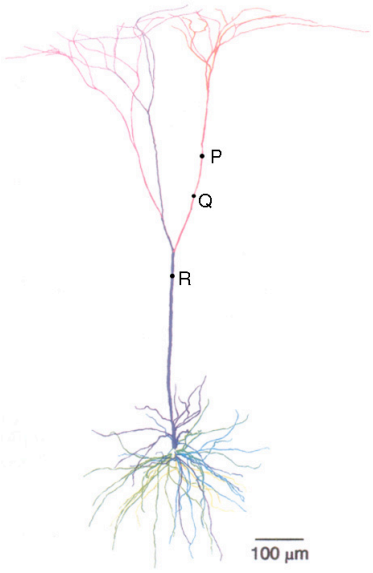
Part b) Write two matrix equations of the form sketched at right, which express the relationship of the two-port parameters in terms of the parameters of the two models above. Express both in terms of the Laplace transform variable s and make sure you use the same units for s (Hertz). In other words, substitute for q in the cylinder model. These will look very different, in that one is expressed in terms of cosh() and sinh() and the other in terms of polynomials.

$$\begin{vmatrix} V_0 \\ I_0 \end{vmatrix} = \mathbf{M} \begin{vmatrix} V_1 \\ I_1 \end{vmatrix}$$

Part c) The two models are the same in the limit as $|qL|^2 \ll 1$. Using Taylor series approximations for cosh() and sinh(), rewrite the cylinder model for the case of small qL. Compare the two matrix equations term by term and show that they are the same for small qL. State the condition that guarantees that $|qL|^2 \ll 1$ in a compartmental model (in terms of cylinder lengths, etc.).

Part d) From part c), it is clear that if you chose Δx to be small enough, the compartmental model is a good approximation to the cylinder model. Suppose you want the compartmental model to be accurate not only at D.C. (q=1) but also up to some frequency ω_0. Does this mean that Δx should be shorter or longer than is needed in a D.C.-only model? How does the length Δx vary with ω_0?

Problem 2



Electrotonic length is a measure of the distance that disturbances spread in dendritic trees. In the simplest case, it is defined as $L=x/\lambda$, physical distance x divided by length constant λ. This has a direct interpretation for single cables, like the distance between P and Q in the neuron drawn at right. But when there is branching, as between Q and R, the usefulness of x/λ is limited by the effects of branching, which drains signals and therefore reduces signal propagation. As a result, the attenuation between two points like P and R larger than expected from the simple electrotonic length. Zador and colleagues (*J Neurosci* 15:1669 (1995)) suggested a different distance measure, the *MET* where

$$MET_{PR} = -\ln A_{PR} = -\ln \frac{V_R}{V_P} \ ,$$

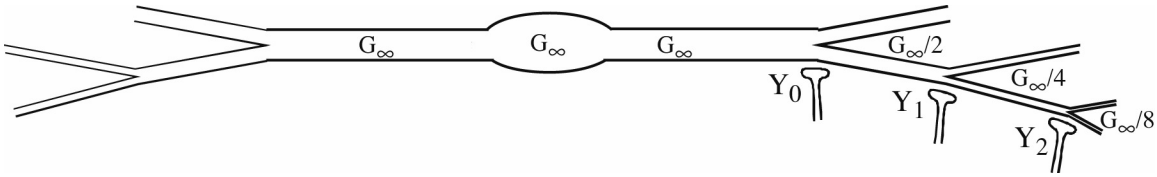
where A_{PR} is the voltage gain defined as the potential at R given a source at P. Note that $MET>0$ because $V_R<V_P$ for a source at P. For the following, use the DC steady state for simplicity.

Part a) Show that the MET_{ab} is the same as the electrotonic length x_{ab}/λ for a semi-infinite cable.

Part b) Show that the MET_{PR} is asymmetric, meaning that $MET_{PR} \neq MET_{RP}$. In particular, show that the $MET_{RP} < MET_{PR}$ if R is further from the soma than P, as in the figure above. (HINT: $K_{PR} = K_{RP}$ and assume that $K_{PP}>K_{RR}$ for P further from the soma along a dendrite, as in the example discussed in class).

Problem 3

Consider the bipolar cell sketched below. The dendritic branching is such that the equivalent cylinder theorem holds everywhere, including at the soma; that is, the soma is just part of the cable formed by the primary dendrites, all of which have the same properties. Only part of the tree is shown; assume that the branching is fully symmetric, as required by the equivalent cylinder theorem. Recently, it has been shown that the EPSP produced at the site of a synapse grows larger as the synapse moves further out on the dendritic tree. In the example below, the EPSP produced at the synapse furthest to the right (Y_2) would be the largest.



Part a) Explain qualitatively why this result should be so. Assume that the conductances of all the synapses are the same. (Remember, we're talking about the EPSP produced at the synaptic site, not the EPSP in the soma produced by that synapse.)

Part b) To analyze this situation, assume the synapses each inject a current I_0, so that the problem is linear. Then the EPSP at the synaptic site is given by I_0 K_{ii}, where K_{ii} is the input impedance of the dendritic tree at the site of the synapse. Work out values for K_{ii} at the three synapses shown above <u>for the D.C. steady state</u> (q=1). The synapses are assumed to sit right at the branch points, as drawn. Assume that each distal branch of the tree is terminated by its characteristic impedance $Y_L = qG_\infty/2^n$, where n is the number of branch points (note this is different from the usual assumption Y_L=0; this is done to make the solution simpler). This means that the distal branches appear to be infinitely long. The result will be messy. To simplify it further, assume that $\tanh(L) = 0.2$ for L the electrotonic distance between successive branch points.

Part c) How is the result changed if the synapse is assumed to change a synaptic conductance instead of injecting a current (assuming that only one synapse is activated at a time)? Give a qualitative answer here.