Cable Theory: Questions

- Q1. Input resistance at a node

An experimentalist manages to patch an electrode directly on the point on the dendritic tree where three long dendrites meet, each with distinct properties. At that point she injects a constant current I_{app} into the cell. The electrotonic length constants in each dendrite are $\lambda_1, \lambda_2, \lambda_3$ and the resistances for an electrotonic length's worth of dendrite are $R_{\lambda 1}, R_{\lambda 2}, R_{\lambda 3}$. Use a coordinate system on each dendrite where the point where the dendrites meet is at $x = 0$ and where x increases away from the node.
[Q] What is the general solution to the steady-state cable equation in the dendrites?
[A] This is taken directly from the lecture notes and is of the form

$$v_k(x) = A_k e^{-x/\lambda_k}. \tag{1}$$

[Q] Noting that the voltage cannot jump at any point, write down an equation relating the v_ks at the injection site in terms of the injection-site voltage v_0
[A]

$$v_1(0) = v_2(0) = v_3(0) = v_0 \tag{2}$$

so that $A_k = v_0$.
[Q] Now consider the conservation of current. Let $I_k(0)$ be the current flowing down dendrite k at the point of the node $x = 0$. Write an equation relating these currents.
[A] By current conservation we have

$$I_{app} = I_1(0) + I_2(0) + I_3(0). \tag{3}$$

[Q] Use this result to solve the voltage distribution in each dendrite.
[A] The current is related to the voltage via

$$I_k(0) = -\frac{\lambda_k}{R_{\lambda k}} \left.\frac{\partial v_k}{\partial x}\right|_{x=0} = \frac{v_0}{R_{\lambda k}} \tag{4}$$

So that from the current relation

$$I_{app} = v_0 \left(\frac{1}{R_{\lambda 1}} + \frac{1}{R_{\lambda 2}} + \frac{1}{R_{\lambda 3}} \right). \tag{5}$$

From this v_0 is found as a function of the input current and so the voltage distribution can be written

$$v_k(x_k) = \left(\frac{I_{app}}{\frac{1}{R_{\lambda 1}} + \frac{1}{R_{\lambda 2}} + \frac{1}{R_{\lambda 3}}} \right) e^{-x_k/\lambda_k}. \tag{6}$$

[Q] Show that the input resistance is consistent with the three dendrites acting as resistors in parallel.
[A] The input resistance is given by $v_0 = I_{app} R_{in}$ so that

$$\frac{1}{R_{in}} = \frac{1}{R_{\lambda 1}} + \frac{1}{R_{\lambda 2}} + \frac{1}{R_{\lambda 3}} \tag{7}$$

which is consistent with the formula for resistors in parallel.

• Q2. Voltage-clamp and synaptic current

A common method for measuring synaptic current is to use a technique called *voltage clamp*. In this method the voltage at the point of injection is fixed at some value v_0 by injecting an appropriate current I_{app}. If the voltage is to be constant it means that I_{app} must balance any internal currents at that point and hence I_{app} is equal in magnitude to the internal currents flowing into the injection point. This provides a method for measuring the internal currents in a neuron.

Consider a dendrite of length L closed at each end; $x = 0$ is the point of current injection where the voltage is fixed, and at $x = L$ there is a synapse. The synapse has a reversal potential E_s and an absolute conductance G_s. By application of a drug to the bathing solution containing the neuron, the synapse is kept permanently open; it is a steady-state situation. The voltage at $x = 0$ is clamped to the resting voltage E_L and we measure all voltages from this value $v = V - E_L$.
[Q] Write down the general steady-state solution to the cable equation. How many free constants are there?
[A]

$$v = Ae^{-x/\lambda} + Be^{x/\lambda} \tag{8}$$

There are two free constants.
[Q] Apply the boundary condition at $x = 0$ and write the solution in terms of a hyperbolic trigonometric function.
[A] The condition is $v(x = 0) = 0$ so that $A = -B = \kappa/2$ and so

$$v = \kappa \sinh\left(\frac{x}{\lambda}\right). \tag{9}$$

[Q] What is the voltage at L in terms of the unknown constant?
[A] It is

$$v_L = \kappa \sinh\left(\frac{L}{\lambda}\right). \tag{10}$$

[Q] What is the v-dependent form of the incoming synaptic current into the dendrite at L?
[A] Don't forget voltages are measured from E_L so that

$$I_{syn} = G_s(E_s - E_L - v_L). \tag{11}$$

[Q] Match this to the current in the dendrite at L and fix the last free constant.
[A] The current at L in the dendrite is

$$I_L = -\frac{\kappa}{R_\lambda} \cosh\left(\frac{x}{\lambda}\right). \tag{12}$$

This must balance with the synaptic current $I_L + I_{syn} = 0$ so that

$$\frac{\kappa}{R_\lambda} \cosh\left(\frac{x}{\lambda}\right) = G_s(E_s - E_L - v_L). \tag{13}$$

But we need v_L which is given in terms of A above, so that

$$\frac{\kappa}{R_\lambda} \cosh\left(\frac{x}{\lambda}\right) = G_s\left(E_s - E_L - \kappa \sinh\left(\frac{L}{\lambda}\right)\right) \tag{14}$$

which can be rearranged to give

$$\kappa = \frac{G_s R_\lambda (E_s - E_L)}{\cosh\left(\frac{L}{\lambda}\right) + G_s R_\lambda \sinh\left(\frac{L}{\lambda}\right)}. \tag{15}$$

[Q] Calculate the magnitude of the current that is being injected at $x = 0$ to keep the voltage $v = 0$.
[A] This is given by

$$I_{app} = I_0 = -\frac{\lambda}{R_\lambda}\frac{\partial v}{\partial x}\bigg|_{x=0} = -\frac{G_s(E_s - E_L)}{\cosh\left(\frac{L}{\lambda}\right) + G_s R_\lambda \sinh\left(\frac{L}{\lambda}\right)}. \tag{16}$$

[Q] Under what circumstances does the applied current give an accurate measure of the the current flowing into the synapse?
[A] If L is much less than the electrotonic length λ.

- Q3. Dynamics of Charge Spread on a Long Dendrite

If a charge Q is injected at position $x = 0$ at a time $t = 0$ on an infinitely long dendrite, the voltage distribution is of the form

$$V = E_L + \frac{Ae^{-t/\tau_L}}{\sqrt{4\pi t/\tau_L}}\exp\left(-\frac{x^2}{4\lambda^2 t/\tau_L}\right) \tag{17}$$

[Q] Show that this form satisfies the cable equation for $t > 0$.
[A] This is straightforward differentiation.
We now want to fix the prefactor A (what units does this have?). Charge is related to voltage by $Q = CV$.
[Q] Consider the voltage distribution close to the point of injection just after $t = 0$ and use it to fix the prefactor A in terms of Q, R_λ and τ_L. You will need to know how to calculate the integral of a Gaussian to solve this.
[A] Let C be the capacitance per unit area. Then it must be that

$$Q = \int_{-\infty}^{\infty}(C 2\pi a dx) v(x) \tag{18}$$

We assume that t/τ_L so that the e^{-t/τ_L} factor may be ignored. The form of x in equation (17) is a Gaussian and its integral is

$$\int_{-\infty}^{\infty} v(x)dx = A\lambda \tag{19}$$

So that

$$Q = C2\pi a\lambda A = \tau_L(2\pi a\lambda g_L)A = \frac{\tau_L}{R_\lambda}A \tag{20}$$

and

$$A = \frac{QR_\lambda}{\tau_L}. \tag{21}$$