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 $I_{\text{app}}$ 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

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

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

[A]

$$v_1(0) = v_2(0) = v_3(0) = v_0 \quad (2)$$

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

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

[Q] Use this result to solve the voltage distribution in each dendrite.

[A] The current is related to the voltage via

$$I_k(0) = -\frac{\lambda_k}{R_{\lambda_k}} \frac{\partial v_k}{\partial x} \bigg|_{x=0} = \frac{v_0}{R_{\lambda_k}}. \quad (4)$$

So that from the current relation

$$I_{\text{app}} = v_0 \left( \frac{1}{R_{\lambda_1}} + \frac{1}{R_{\lambda_2}} + \frac{1}{R_{\lambda_3}} \right). \quad (5)$$

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

$$v_k(x_k) = \left( \frac{I_{\text{app}}}{\frac{1}{R_{\lambda_1}} + \frac{1}{R_{\lambda_2}} + \frac{1}{R_{\lambda_3}}} \right) e^{-x_k/\lambda_k}. \quad (6)$$

[Q] Show that the input resistance is consistent with the three dendrites acting as resistors in parallel.

[A] The input resistance is given by $v_0 = I_{\text{app}}R_{\text{in}}$ so that

$$\frac{1}{R_{\text{in}}} = \frac{1}{R_{\lambda_1}} + \frac{1}{R_{\lambda_2}} + \frac{1}{R_{\lambda_3}} \quad (7)$$

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] 

$$ v = A e^{-x/\lambda} + B e^{x/\lambda} \quad (8) $$

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

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

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

[A] It is

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

[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

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

[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

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

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

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

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

$$ \frac{\kappa}{R_\lambda} \cosh \left( \frac{x}{\lambda} \right) = G_s \left( E_s - E_L - \kappa \sinh \left( \frac{L}{\lambda} \right) \right) \quad (14) $$
which can be rearranged to give
\[ \kappa = \frac{G_s R_\lambda (E_s - E_L)}{\cosh \left( \frac{L}{\lambda} \right) + G_s R_\lambda \sinh \left( \frac{L}{\lambda} \right)} \]  

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

(Q) Under what circumstances does the applied current give an accurate measure of the current flowing into the synapse?

[A] If \( L \) is much less than the electrotonic length \( \lambda \).

● 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
\[ V = E_L + \frac{A e^{-t/\tau_L}}{\sqrt{4\pi t/\tau_L}} \exp \left( -\frac{x^2}{4\lambda^2 t/\tau_L} \right) \]  

(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 \( Q, R_\lambda \) and \( \tau_L \). 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
\[ Q = \int_{-\infty}^{\infty} C 2\pi a dx v(x) \]  

We assume that \( t/\tau_L \) so that the \( e^{-t/\tau_L} \) factor may be ignored. The form of \( x \) in equation (17) is a Gaussian and its integral is
\[ \int_{-\infty}^{\infty} v(x) dx = A \lambda \]

So that
\[ Q = C 2\pi a \lambda A = \tau_L (2\pi a \lambda g_L) A = \frac{\tau_L A}{R_\lambda} \]

and
\[ A = \frac{QR_\lambda}{\tau_L} \]