

## CABLE THEORY

In this module we will derive the cable equation for cables of constant radius. The steady-state and time-dependent properties of this equation will then be analysed. The Rall ball-and-stick model of a soma coupled to a dendrite will then be introduced.

*Mathematical Physiology*, Keener and Sneyd. Chapter 8 p249-265. Springer.

*Theoretical Neuroscience*, Dayan and Abbott. Chapter 6 p203-220. MIT Press

*Spiking Neuron Models*, Gerstner and Kistler. Chapter 2 p53-67. Cambridge University Press

*Methods in Neuronal Modelling*, Koch and Segev. Chapter 2 p27-p92. MIT Press

### • THE CURRENT-VOLTAGE RELATION IN A CABLE

Consider a short slice of dendrite that can be modelled as a cylindrical cable of radius  $a$  and length  $\Delta$ . The voltages are  $V(x)$  and  $V(x + \Delta)$  at the left and right ends of the segment, respectively. The current flowing through the segment is  $I$ . From Ohms law we have:

$$V(x + \Delta) - V(x) = -IR \quad (1)$$

where the minus sign is because current flows down the potential gradient and  $R$  is the resistance of the short segment. On physical grounds it can be expected that the resistance is inversely proportional to the area, proportional to the length and also to some constant that has units of  $\Omega\text{m}$  which we will call  $r_a$  - the axial resistance:

$$R = \frac{\Delta r_a}{\pi a^2}. \quad (2)$$

Inserting this into equation (1) and re-arranging for  $I$  gives

$$I = -\frac{\pi a^2}{r_a} \frac{V(x + \Delta) - V(x)}{\Delta} \quad \text{so in the limit } \Delta \rightarrow 0 \text{ we get } I(x) = -\frac{\pi a^2}{r_a} \frac{\partial V}{\partial x}. \quad (3)$$

### • DERIVATION OF THE CABLE EQUATION

We now consider a section of cable which has leak channels, and where effects of the membrane capacitance are also accounted for. At position  $x$  of the cable, the current flowing in along the cable is  $I(x)$  and at position  $x + \Delta$  the current flowing out is  $I(x + \Delta)$ . If  $C$  and  $g_L$  are the capacitance and conductance per unit area, we get:

$$I_C = 2\pi a \Delta C \frac{dV}{dt} \quad \text{and} \quad I_L = 2\pi a \Delta g_L (V - E_L). \quad (4)$$

The total sum of currents must be zero, so

$$I_C + I_L = I(x) - I(x + \Delta). \quad (5)$$

On inserting the forms for the current and dividing through by the surface area of the short cylinder we have

$$C \frac{\partial V}{\partial t} = g_L (E_L - V) - \frac{1}{2\pi a} \frac{I(x + \Delta) - I(x)}{\Delta} \quad (6)$$

which on the limit of  $\Delta \rightarrow 0$  yields

$$C \frac{\partial V}{\partial t} = g_L (E_L - V) - \frac{1}{2\pi a} \frac{\partial I}{\partial x}. \quad (7)$$

If a current  $I_{app}$  were to be injected at  $x_0$  then by conservation of current:

$$I(x_0 + \epsilon) - I(x_0 - \epsilon) = I_{app}. \quad (8)$$

We now consider the equation for the voltage in a region of cable for which there is no injected current. Substituting in the axial current (3) and dividing by  $g_L$  gives

$$\tau_L \frac{\partial V}{\partial t} = E_L - V + \lambda^2 \frac{\partial^2 V}{\partial x^2} \quad (9)$$

where we have identified a constant  $\lambda$  with units of length that satisfies

$$\lambda^2 = \frac{a}{2r_a g_L}. \quad (10)$$

The electrotonic length  $\lambda$  is an important quantity; it measures the extent to which voltage is attenuated in cable structures. The current voltage relation (3) can also be written in terms of this quantity:

$$I = -(2\pi a \lambda g_L) \left( \lambda \frac{\partial V}{\partial x} \right) = -\frac{\lambda}{R_\lambda} \frac{\partial V}{\partial x} \quad (11)$$

where a resistance  $R_\lambda = 1/(2\pi a \lambda g_L)$  has been identified. This is the leak resistance of a section of cable  $\lambda$  long. It can be verified that it is also equivalent to the total axial resistance for a cable of length  $\lambda$ .

To summarise, the equations that govern the electrical characteristics of a cable are: (8) if there is injected current; equation (9) in the bulk, away from any points of injection; equation (11) for relating voltage to current, as boundary conditions are sometimes on the current; and finally it can be noted that to prevent infinite currents there must be no jumps in the voltage  $V$  anywhere (though abrupt changes in the gradient are allowed, at the point of current injection).

• STEADY CURRENT INJECTION ON AN INFINITE CABLE

We now consider a section of cable that is infinitely long, with an applied current  $I_{app}$  being injected constantly at  $x = 0$ . Imagine that the cable is horizontal, so we may say that everything to the left of the point of injection is labelled by a 1 and everything to the right by a 2. We also measure the voltage from the baseline:  $v = V - E_L$ . In the steady state the general solution of (9) is

$$v = A e^{\pm x/\lambda}. \quad (12)$$

So, if the voltage is to remain finite when  $|x| \rightarrow \infty$  the solutions to the left and right of the point of current injection are

$$v_1(x) = A_1 e^{x/\lambda} \quad \text{and} \quad v_2(x) = A_2 e^{-x/\lambda} \quad (13)$$

and because there can be no voltage jump at  $x = 0$  it must be that  $A_1 = A_2$  and we will call this quantity  $v_0$ . We now write down the conservation-of-current equation where  $I_1$  is the current just before the point of injection and  $I_2$  just after.

$$I_1 + I_{app} = I_2 \quad \text{so that} \quad -\frac{v_0}{R_\lambda} + I_{app} = \frac{v_0}{R_\lambda} \quad (14)$$

where the form for the current in terms of a voltage derivative has been used and the solutions (13) substituted. On solving for  $v_0$  we get

$$v_0 = \frac{I_{app} R_\lambda}{2} \quad \text{giving the full solution} \quad V(x) = E_L + \frac{I_{app} R_\lambda}{2} e^{-|x|/\lambda}. \quad (15)$$

It can be noted that the input resistance, defined by the voltage at the point of current injection divided by the current injected, is  $R_{in} = R_\lambda/2$  which is consistent with the two branches behaving as parallel resistors to ground with resistance  $R_\lambda$  each:

$$\frac{1}{R_{in}} = \frac{1}{R_\lambda} + \frac{1}{R_\lambda}. \quad (16)$$

It can be noted that the injecting electrode has an effect that decays with a length constant  $\lambda$  and so any experimental measurements probe only a distance  $\lambda$  from the recording electrode.

• BOUNDARY EFFECTS

There are two kinds of boundary that can be considered. The first is a short-circuit where the end of the cable is open to the extracellular media (for example if the dendrite was cut) so that at this point the absolute voltage is grounded  $V = 0\text{mV}$ . If such a cut boundary is located at the LHS of a semi-infinite cable, the boundary conditions require that the voltage distribution looks like

$$V = E_L (1 - e^{-x/\lambda}). \quad (17)$$

This is not a case which is important for the usual function of neurons. A second more relevant case is a closed end of a dendrite. In this case it is the current at the boundary that is zero  $I = 0$  (assuming negligible effects from channels sitting on the cylinder end). This requires that

$$I = -\frac{\lambda}{R_\lambda} \frac{\partial V}{\partial x} = 0 \quad \text{which is a gradient condition on } V \text{ so } \frac{\partial V}{\partial x} = 0. \quad (18)$$

We will now examine the consequences of this condition.

• SEMI-INFINITE CABLE WITH A CLOSED BOUNDARY

We will now derive the distribution for a semi-infinite cable  $x \geq 0$  with a closed boundary at  $x = 0$  and a steady current injection at  $x = x_0$ . The solution below  $x_0$  we will call  $v_1$  and above  $v_2$ , where the voltage is measured from the baseline  $E_L$ . Hence

$$v_1 = Ae^{(x-x_0)/\lambda} + Be^{-(x-x_0)/\lambda} \quad \text{and} \quad v_2 = Ce^{-(x-x_0)/\lambda}. \quad (19)$$

At the closed boundary at  $x = 0$  no current flows so

$$Ae^{-2x_0/\lambda} = B. \quad (20)$$

At the point of current injection the voltage does not jump and the total currents must add up to zero, where  $I_1$  is the current just to the left of the point of injection and  $I_2$  the current just to the right

$$A + B = C \quad \text{and} \quad I_1 + I_{app} = I_2 \quad \text{so that} \quad A - B + C = I_{app}R_\lambda \quad (21)$$

The three equations in (20) and (21) can be solved to give

$$A = \frac{I_{app}R_\lambda}{2}, \quad B = \frac{I_{app}R_\lambda}{2}e^{-2x_0/\lambda} \quad \text{and} \quad C = \frac{I_{app}R_\lambda}{2} (1 + e^{-2x_0/\lambda}). \quad (22)$$

On insertion into the solution, and using modulus signs to write equations  $v_1$  and  $v_2$  together, we have

$$v = \frac{I_{app}R_\lambda}{2}e^{-|x-x_0|/\lambda} + \frac{I_{app}R_\lambda}{2}e^{-|x+x_0|/\lambda}. \quad (23)$$

This solution is similar to the case of the infinite cable, except that there appears to be also an effect of an identical strength input at  $x = -x_0$ , which of course is past the end of the cable. This is the mirror image of the voltage distribution coming from the true point of injection reflected in the closed boundary at  $x = 0$ . It is an example of the *method of images* that can be used to solve linear equations with closed (reflecting) boundaries, once the solution on the infinite line is known. The physical interpretation is that the current “reflects” from the closed boundary.

• FINITE CABLE WITH ONE CLOSED BOUNDARY

We now consider a finite cable of length  $L$  with a closed boundary at  $L$  and a voltage  $v_0$  due to a current input  $I_{app}$  at  $x = 0$ . The general solution is the double exponential

$$v = Ae^{x/\lambda} + Be^{-x/\lambda} \quad (24)$$

with the boundary conditions

$$A + B = v_0 \quad \text{at } x = 0 \quad \text{and} \quad Ae^{2L/\lambda} = B \quad \text{at } x = L \text{ from the } I_L = 0 \text{ condition.} \quad (25)$$

On solving for  $A$  and  $B$  we get

$$v = \frac{v_0}{e^{L/\lambda} + e^{-L/\lambda}} \left( e^{(x-L)/\lambda} + e^{(L-x)/\lambda} \right) = v_0 \frac{\cosh\left(\frac{L-x}{\lambda}\right)}{\cosh\left(\frac{L}{\lambda}\right)}. \quad (26)$$

This can be related to the current input at  $x = 0$  and the input resistance at  $x = 0$  for the closed length of cable  $R_0 = v_0/I_{app}$ .

$$I_0 = \frac{v_0}{R_\lambda} \tanh\left(\frac{L}{\lambda}\right) \quad \text{so that} \quad R_0 = R_\lambda \coth\left(\frac{L}{\lambda}\right). \quad (27)$$

We will refer to the input resistance of this structure as  $R_C$  and the conductance as  $G_C = 1/R_C$ .

• THE RALL SOMA AND DENDRITE MODEL

We now consider a model neuron made from a isopotential soma  $V_s$  attached to a single dendritic cylinder with a spatially dependent voltage  $V_d(x)$  with the end at  $x = 0$  attached to the soma and the end at  $x = L$  closed. An experimentalist is injecting an applied current  $I_{app}$  at the soma to measure the total input resistance of the combined structure:

$$\tau_L \frac{\partial V_s}{\partial t} = E_L - V_s + (I_{app} - I_0) R_s \quad \text{soma} \quad (28)$$

$$\tau_L \frac{\partial V_d}{\partial t} = E_L - V_d + \lambda^2 \frac{\partial^2 V_d}{\partial x^2} \quad \text{dendrite} \quad (29)$$

where by continuity  $V_s = V_d(0) = V_0$  and where  $I_0$  is the current flowing from the soma into the dendrite,

$$I_0 = -\frac{\lambda}{R_\lambda} \frac{\partial V_d}{\partial x}. \quad (30)$$

As before we measure all voltages from  $E_L$ . In the steady state the somatic voltage obeys

$$v_s = v_0 = (I_{app} - I_0) R_s \quad (31)$$

and the current  $I_0$  flowing into a closed cylinder was given in equation (27) in terms of  $v_0$ . Inserting this current into equation (31) gives

$$v_0 \left( 1 + \frac{R_s}{R_\lambda} \tanh \left( \frac{L}{\lambda} \right) \right) = I_{app} R_s. \quad (32)$$

So the input resistance  $R_{in} = v_0/I_{app}$  of the entire neuronal structure is

$$R_{in} = \frac{R_s}{1 + \frac{R_s}{R_\lambda} \tanh \left( \frac{L}{\lambda} \right)}. \quad (33)$$

This is consistent with the somatic and dendritic resistance being in parallel

$$\frac{1}{R_{in}} = \frac{1}{R_s} + \frac{1}{R_C}. \quad (34)$$

where  $R_C$  is the cylinder input resistance given in equation (27).

• CONDUCTANCE OF COMPLEX DENDRITIC STRUCTURES

Dendritic structures do not contain closed loops and hence their total conductance can be calculated by starting at the ends of the dendritic branches and adding up the conductances as they join together towards the soma. For example, imagine two closed dendrites (at the end of part of the dendritic tree) that join to a third parent dendrite. The conductance at the end of the parent dendrite (where it joins the two end dendrites) is

$$G_E = G_{C1} + G_{C2}. \quad (35)$$

We will consider that this is at  $x = L$  of the parent cylinder. The conductance into this cylinder is  $G_0$ . If we can calculate the input conductance as a function of the conductance at the end, then this process could be continued recursively until the conductance of the whole structure is calculated.

To do this we consider a cylinder for which: at  $x = 0$  we have  $v = v_0$ ,  $G_0$ : and at  $x = L$  we have  $G_E$ . The general solution is most conveniently written

$$v = A \cosh \left( \frac{L-x}{\lambda} \right) + B \sinh \left( \frac{L-x}{\lambda} \right) \quad (36)$$

at  $v(L) = v_L$  so  $A = v_L$  and the current flowing at  $L$  is  $I_L$ , so after differentiating we get  $B = R_\lambda I_L = v_L G_E / G_\lambda$ . The full solution is therefore

$$v = v_L \left( \cosh \left( \frac{L-x}{\lambda} \right) + \frac{G_E}{G_\lambda} \sinh \left( \frac{L-x}{\lambda} \right) \right). \quad (37)$$

To calculate the input conductance we need  $G_0 = I_0/v_0$  and so the current at  $x = 0$  must be calculated. This takes the form

$$I_0 = v_L G_\lambda \left( \sinh \left( \frac{L}{\lambda} \right) + \frac{G_E}{G_\lambda} \cosh \left( \frac{L}{\lambda} \right) \right) \quad (38)$$

and so

$$G_0 = \frac{I_0}{v_0} = \frac{G_E + G_\lambda \tanh \left( \frac{L}{\lambda} \right)}{1 + \frac{G_E}{G_\lambda} \tanh \left( \frac{L}{\lambda} \right)}. \quad (39)$$

This can be used to calculate the input conductance for the entire dendritic tree, and can be applied even when each dendrite has a different  $\lambda$  and  $R_\lambda$ .

• DYNAMICS IN PASSIVE STRUCTURES

Again we measure voltage from the resting potential  $E_L$ . The cable equation is

$$\tau_L \frac{\partial v}{\partial t} = -v + \lambda^2 \frac{\partial^2 v}{\partial x^2}. \quad (40)$$

It is convenient to introduce  $\phi$  where  $v = \phi e^{-t/\tau_L}$ . On insertion into the cable equation we get

$$\tau_L \frac{\partial \phi}{\partial t} = \lambda^2 \frac{\partial^2 \phi}{\partial x^2} \quad (41)$$

which is in the familiar form of the diffusion equation. The general solution can be found using a variable-separable method

$$\phi = T(t)X(x) \quad \text{so that} \quad \frac{\tau_L}{T} \frac{\partial T}{\partial t} = \frac{\lambda^2}{X} \frac{\partial^2 X}{\partial x^2} = -k^2 \quad (42)$$

where the form  $-k^2$  is chosen so that the modes will decay in time

$$T_k = e^{-k^2 t / \tau_L} \quad \text{and} \quad X_k = e^{\pm i k x / \lambda}. \quad (43)$$

The general solution can be written

$$\phi = \sum_k e^{-k^2 t / \tau_L} \phi_k \quad \text{where} \quad \phi_k = A_k e^{i k x / \lambda} + B_k e^{-i k x / \lambda} \quad (44)$$

where the sum over  $k$  could be an integral if the spectrum is continuous. We now consider the solution of this equation for a closed cable, to examine transients, and for an infinite cable, to examine the velocity of the signal in a passive structure.

• TRANSIENTS IN A CLOSED STRUCTURE

Consider a cable of length  $L$  that is closed on both ends and with some initial distribution of voltage at time  $t = 0$ . The closure requires that the gradient is zero at  $x = 0$  so that  $A_k = B_k$  and at the other boundary, the zero gradient condition is

$$1 = e^{i 2 L k / \lambda} \quad \text{so that} \quad k = \pi n \frac{\lambda}{L}. \quad \text{where } n = 0, 1, 2, \dots \quad (45)$$

Hence the full general solution for this case is

$$v = \sum_{n=0}^{\infty} a_n \cos\left(\frac{\pi n x}{L}\right) e^{-\frac{t}{\tau_L} \left(1 + \left(\frac{\pi n \lambda}{L}\right)^2\right)}. \quad (46)$$

where the  $a_n$  constants depend on the form of the initial voltage. The transient time constants are

$$\tau_n = \frac{\tau_L}{\left(1 + \left(\frac{\pi n \lambda}{L}\right)^2\right)}. \quad (47)$$

The  $n = 0$  mode decays slowest with a time constant  $\tau_L$  and with a spatial form that is a constant along the cable. Hence, it can be said that the transients  $\tau_n$  with  $n > 1$  act to equilibrate the

voltage throughout the neuron, whereas the zero-order mode with  $\tau_0 = \tau_L$  governs the charge leaving the entire structure.

Together with the second mode, the late-time voltage takes the form

$$v(x, t) \simeq a_0 e^{-t/\tau_L} + a_1 e^{-t/\tau_1} \cos\left(\frac{\pi x}{L}\right). \quad (48)$$

The two time constants  $\tau_L$  and  $\tau_1$  can be measured experimentally and can then be used to yield an effective  $\lambda/L$ .

• SIGNAL VELOCITY IN A LONG PASSIVE DENDRITE

The solution of the cable equation on an infinite dendrite, due to an initial brief injection of charge  $Q$  can be written

$$v(x, t) = \frac{QR\lambda}{\tau_L} e^{-t/\tau_L} \frac{\exp\left(-\frac{x^2}{4\lambda^2 t/\tau_L}\right)}{\sqrt{4\pi t/\tau_L}}. \quad (49)$$

We now follow *Dayan and Abbott* and consider the time when the voltage at a distance  $x$  reaches its maximum value, before decaying to zero. This can be found by taking the derivative of (49) with respect to time, and setting this to zero. This yields the equation

$$0 = -\frac{v}{\tau_L} - \frac{v}{2t} + \frac{vx^2}{4\lambda^2 t^2/\tau} \quad (50)$$

which results in a quadratic equation for  $t$ . Taking the positive root of this equation gives

$$\frac{t}{\tau_L} = \frac{1}{4} \left( -1 + \sqrt{1 + 4\frac{x^2}{\lambda^2}} \right). \quad (51)$$

For  $x \gg \lambda$  the relation is  $t/\tau_L \simeq x/2\lambda$  which corresponds to a velocity

$$\frac{dx}{dt} \simeq \frac{2\lambda}{\tau_L}. \quad (52)$$

Typically  $\lambda \sim 100\mu\text{m}$  and  $\tau_L = 20\text{ms}$ . This yields a velocity that is of the order of  $1\text{cm/s}$  which is very slow (given the size of a human, for example). Moreover, the signal is very strongly attenuated, by virtue of the exponential decay in time. Hence, passive cables described by equation (40) cannot be used for signalling over long distances.