580.422 Course Notes: Cable Theory

Additional reading: Koch, chapt 2 and 3.

Cable theory was originally applied to the conduction of potentials in an axon by Hodgkin and Rushton (1946) and was later applied to the dendritic trees of neurons by Rall (1962). The theory itself is much older and was first developed for analyzing underwater telegraph transmission cables. The general problem addressed by cable theory is how potentials spread in a dendritic tree. This is <u>electrotonic</u> conduction and is assumed to occur by a passive process, i.e. without action potentials. A typical neuron has thousands of synaptic inputs spread across its surfaces. Cable theory is concerned with how these inputs propagate to the soma or the axon initial segment, how these inputs interact with one another, and how the placement of an input on a dendritic tree affects its functional importance to the neuron.

Derivation of the cable equation

Previously, we have considered only point neuron models. That is, we have assumed that the neuron is electrically compact, so that it can be represented by a single patch of membrane. The gist of this assumption is that the membrane potential is the same everywhere in the neuron. In real neurons, this assumption is not true. Substantial differences in potential exist along the length of a neuron's processes and the resulting longitudinal currents must be explicitly considered.

Figure 1 shows three stages of abstraction of a neuron's dendritic membrane. Figure 1A shows a sketch of the neuron, with its soma at right and a dendrite which branches twice spreading off to the left. One length of membrane cylinder from a secondary branch is isolated in Fig. 1B. It is assumed that the cylinder is of uniform radius along its length; this turns out to be a good assumption, dendrites change diameter mostly at branch points. The cylinder is divided into three portions of equal length Δx along the x axis, which runs from left to right. Figure 1C shows an electrical cable model for this length of cylinder. Each of the subcylinders labeled #1, #2, and #3 is assumed to be an isopotential patch of membrane. The membrane of each subcylinder is represented by a parallel combination of membrane capacitance $c_m \Delta x$ and an unspecified circuit for the ionic conductances in the membrane, represented by a box. The total current through a membrane patch is $I_m(x)\Delta x$. Note that the membrane current varies with distance x down the cylinder. I_m and c_m are membrane current and capacitance <u>per unit length of cylinder</u> so that multiplying by Δx gives the total current and capacitance in a subcylinder.

The membrane potentials inside the cell $V_i(x)$ and outside the cell $V_e(x)$ are shown at the nodes in Fig. 1C. It is assumed that the potentials also vary with distance down the cylinder, so they are functions of distance x. The membrane potential is $V_i(x)-V_e(x)$ as usual. Because the potentials vary along the length of the cylinder, there will be currents $I_i(x)$ and $I_e(x)$ flowing between the nodes. $I_i(x)$ is the total current flowing down the interior of the cylinder and $I_e(x)$ is the total current flowing parallel to the cylinder in the extracellular space. In a real brain there will be many cylinders from different neurons packed together, so there will be many extracellular currents. $I_e(x)$ is only the portion of the extracullar current associated with the cylinder under study.

The internal current $I_i(x)$ flows through resistance $r_i\Delta x$, which is the resistance of the solutions inside the cylinder between the center of one subcylinder and the center of the next. $r_e\Delta x$ is similarly defined as the resistance in the extracellular space between the center of two subcylinders, i.e. as the resistance to the flow of current $I_e(x)$. r_i and r_e are again defined as resistances per unit length of cylinder.
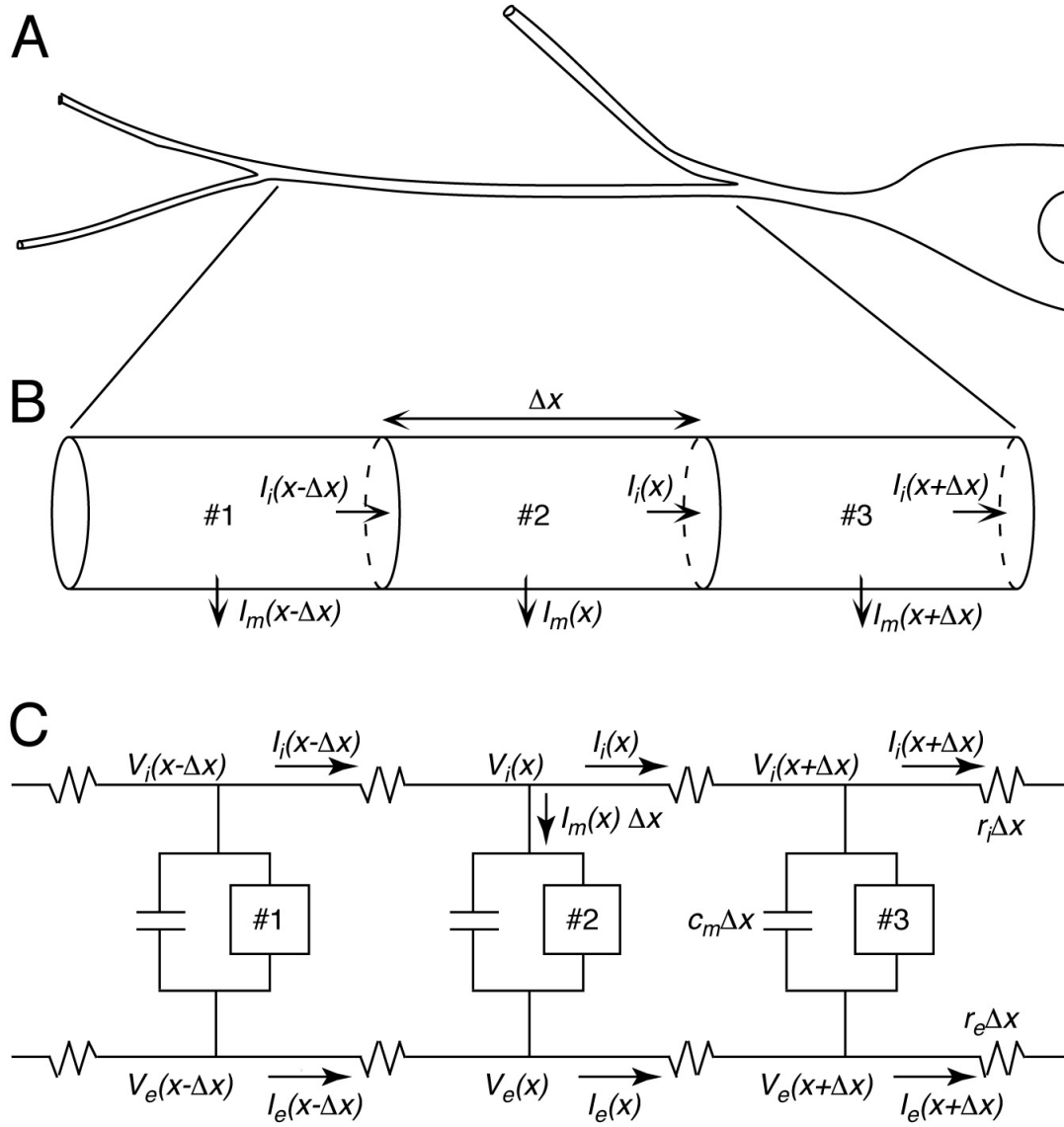
Figure 1. A Sketch of a portion of the dendritic tree of a neuron emerging from the soma at right. B Portion of a secondary dendrite divided into three subcylinders. The axial current I_i and the membrane current I_m are shown next to the arrows. C Discrete electrical model for the three subcylinders. Axial currents flow from one subcylinder to the next through resistances $r_i\Delta x$. Membrane currents flow through a parallel combination of the membrane capacitance $c_m\Delta x$ and membrane ion channels, represented by the boxes. Explicit circuits for the boxes are shown in Fig. 2.

Ohm's law for current flow in the intracellular and extracellular spaces gives:

$$V_i(x) - V_i(x + \Delta x) = I_i(x)\, r_i\, \Delta x \qquad \text{and} \qquad V_e(x) - V_e(x + \Delta x) = I_e(x)\, r_e\, \Delta x \qquad (1)$$

Rearranging and taking the limit as Δx goes to 0,

$$\lim_{\Delta x \to \infty} \frac{V_i(x+\Delta x)-V_i(x)}{\Delta x} = \frac{\partial V_i}{\partial x} = -r_i\, I_i(x) \qquad \text{and} \qquad \frac{\partial V_e}{\partial x} = -r_e\, I_e(x) \tag{2}$$

Conservation of current at the intracellular and extracellular nodes gives

$$I_i(x-\Delta x)-I_i(x)=I_m(x)\,\Delta x \qquad \text{or} \qquad \frac{\partial I_i}{\partial x} = -I_m(x)$$

$$I_e(x-\Delta x)-I_e(x)=-I_m(x)\,\Delta x \qquad \text{or} \qquad \frac{\partial I_e}{\partial x} = I_m(x) \tag{3}$$

Defining the membrane potential as $V = V_i\text{-}V_e$ allows the membrane current I_m to be written as the sum of the ionic current $I_{ion}(x,V,t)$ through the box and the current through the membrane capacitance:

$$I_m(x)\,\Delta x = I_{ion}(x,V,t)\,\Delta x + c_m\,\Delta x\,\frac{\partial V}{\partial t} \tag{4}$$

As for I_m, I_{ion} is ionic current per unit length of membrane cylinder. The ionic current is in general a complex and nonlinear function of membrane potential modeled, for example, by Hodgkin-Huxley type equations.

Differentiating and subtracting Eqns. 2 and substituting Eqns. 3 allows the following relationship between membrane potential and membrane current to be written:

$$\frac{\partial^2 V}{\partial x^2} = \frac{\partial^2 (V_i - V_e)}{\partial x^2}$$

$$= -r_i \frac{\partial I_i}{\partial x} + r_e \frac{\partial I_e}{\partial x}$$

$$= (r_i + r_e) I_m \tag{5}$$

Substituting Eqn. 4 gives the <u>nonlinear cable equation</u>:

$$\frac{1}{r_i + r_e} \frac{\partial^2 V}{\partial x^2} = c_m \frac{\partial V}{\partial t} + I_{ion} \tag{6}$$

Equation 6 models the distribution of membrane potential in a membrane cylinder. The right hand side is the usual equation used for a point neuron model, and expresses the fact that the total membrane current at a point is the sum of the currents through the membrane capacitance and the ion channels. The left hand side is the current injected into the point by the rest of the system, i.e. the current which spreads from adjacent points on the cylinder. The ionic current I_{ion} can be modeled by the usual Hodgkin-Huxley equations.

Equation 6 is linear, but the model for I_{ion} is not, if a full Hodgkin-Huxley model is used. It is useful to consider a simplified, completely linear, version of the cable equation. This is accomplished by using an approximate linear model for I_{ion}. Figure 2 shows circuit diagrams for the membrane model, i.e. for the contents of the boxes in Fig. 1. At left is the full model with sodium,

potassium, and leakage conductances. In a real neuron, there could be additional parallel battery-resistor combinations for calcium conductances and for multiple kinds of sodium and potassium conductances. In the circuit at right, the battery-resistor pairs have been combined into a single equivalent battery and resistor representing the resting potential E_{rest} and the resting membrane conductance g_m. The single battery-resistor circuit at right is a Thévenin equivalent. See Question 2 for the relationship between the two circuits.
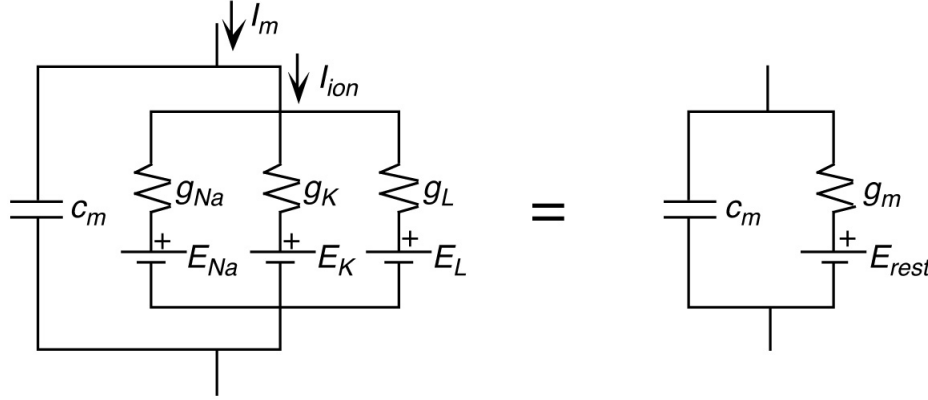

Figure 2 Circuits for the membrane patch. At left is a full Hodgkin-Huxley model, in which g_{Na} and g_K are nonlinear conductances. At right, the resistor-battery circuits have all been combined into a single Thévenin equivalent. In the linear cable model, g_m is assumed to be a constant, linear, conductance

The resistors in the circuit at left in Fig. 2 are non-linear and the membrane conductance g_m in the circuit at right is also non-linear, in the absence of further assumptions. To derive a linear cable equation, it will be assumed that g_m is a constant, linear resistance equal to the resting conductance of the membrane. This is an approximation which is valid only to the extent that membrane potential excursions are small enough not to induce significant gating of the voltage-dependent channels in the real membrane circuit. Given recent evidence, it is clear that dendritic trees contain significant densities of voltage-gated channels and that these channels participate in the responses to synaptic activation. Nevertheless, there are many insights into the functioning of dendritic trees that can only be gained from analysis of the linear cable model.

If g_m is a linear resistance, then $I_{ion}=g_m(V-E_{rest})$. Substituting this in Eqn. 6 and changing the membrane potential variable to $v=V-E_{rest}$, gives the <u>linear cable equation</u>.

$$\frac{1}{r_i + r_e} \frac{\partial^2 v}{\partial x^2} = c_m \frac{\partial v}{\partial t} + g_m v = c_m \frac{\partial v}{\partial t} + \frac{1}{r_m} v \tag{7}$$

where use has been made of the fact that, because E_{rest} is a constant

$$\partial^2 V / \partial x^2 = \partial^2 (V - E_{rest}) / \partial x^2 = \partial^2 v / \partial x^2$$

and

$$\partial V / \partial t = \partial (V - E_{rest}) / \partial t = \partial v / \partial t$$

$$\tag{8}$$

Equation 7 can be rewritten in a non-dimensional form by multiplying both sides by membrane resistance r_m

$$\frac{r_m}{r_i + r_e} \frac{\partial^2 v}{\partial x^2} = r_m c_m \frac{\partial v}{\partial t} + v \qquad \text{or} \qquad \lambda^2 \frac{\partial^2 v}{\partial x^2} = \tau_m \frac{\partial v}{\partial t} + v \tag{9}$$

Two new constants are defined here, the <u>length constant</u> λ and the <u>membrane time constant</u> τ_m. These names will be justified in terms of the solutions derived in later sections. Now define new <u>dimensionless distance and time variables</u> χ and T as $\chi = x/\lambda$ and $T = t/\tau_m$. Finally, the linear cable equation can be written in terms of the dimensionless variables as

$$\frac{\partial^2 v}{\partial \chi^2} = \frac{\partial v}{\partial T} + v \tag{10}$$

which follows from the chain rule for derivatives. Equation 10 is the form in which the cable equation will be used for most of the rest of the discussion.

Question 1. Show that $\partial V_e^2 / \partial x^2 = -r_e I_m$. Under appropriate conditions, this equation can be used to infer membrane current density I_m from extracellular potential measurements V_e only. What anatomical features of the system are necessary to allow this calculation? Hint: the equation is one-dimensional; under what conditions is the extracellular potential near a group of neurons likely to vary along one axis only? Describe how the calculation would be done.

Question 2. Show that, for the circuits in Fig. 2:

$$E_{rest} = \frac{g_{Na}E_{Na} + g_K E_K + g_L E_L}{g_{Na} + g_K + g_L} \qquad \text{and} \qquad g_m = g_{Na} + g_K + g_L \tag{11}$$

Question 3. Consider the case in which the membrane consists only of a leakage channel and a Hodgkin-Huxley type delayed rectifier potassium channel (left side of Fig. 3). This nonlinear circuit can be approximated by the linear circuit at right in Fig. 3; the approximation is accurate if membrane potential excursions from the resting potential are small. Derive a linear cable equation for this small-signal equivalent model for the membrane patch. Note that it will not be possible to write this as a single equation in the form of Eqn. 7; instead two linear differential equations will be required. However if the system is Laplace or Fourier transformed, then a single equation of the form $d^2\bar{V}/dx^2 = A\bar{V}$ can be derived. A is a complex scalar function of the Fourier or Laplace transform variable and $\bar{V}$ is the Fourier or Laplace transformed membrane potential. Derive an expression for A in terms of the parameters of the linear circuit in Fig. 3.

Figure 3 At left is a circuit patch model for a membrane containing only a leakage channel g_L and a Hodgkin-Huxley type delayed rectifier channel g_K. At right is a linear approximation of the nonlinear circuit.
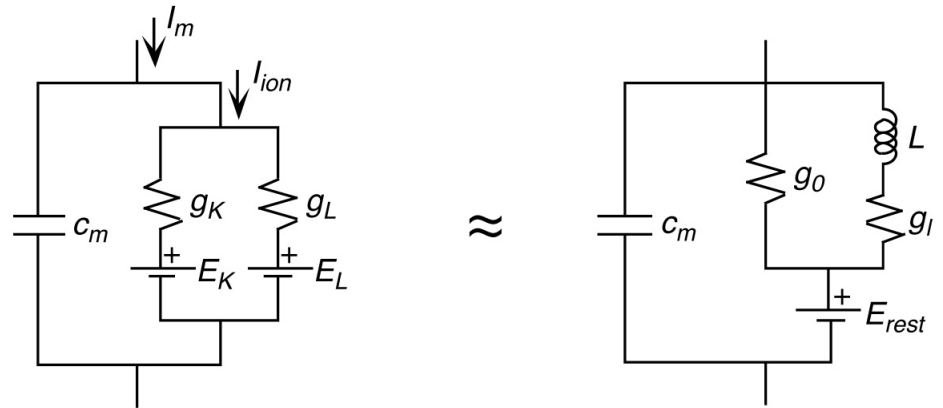
Cable equation parameters

The parameters of the cable model are defined in this section. Various electrical parameters of neural cables are introduced and defined. For all the following, a is the <u>radius of the membrane cylinder</u>.

r_i = resistance of the solution inside a unit length of membrane cylinder to axial current flow I_i, with units like Ω/cm.

$= R_i / \pi a^2$ where R_i is the <u>resistivity of the solution</u>, defined as the resistance from one face to the opposite face for a cube of solution of unit dimensions. Typically R_i is 60-200 Ω·cm for neural cytoplasm. r_i is equal to the resistance of a unit length of cylinder of cross sectional area πa^2.

c_m = capacitance of the membrane of a unit length of membrane cylinder, with units like µFd/cm.

$= 2\pi a C$ where C is the <u>capacitance of a unit area of membrane</u>. For neurons, $C \approx 1$ µFd/cm². c_m is the capacitance of a unit length of cylinder with radius a, which therefore has surface area $2\pi a$.

$g_m = 1/r_m$ = conductance of the membrane of a unit length of membrane cylinder, with units like S/cm. Note that the resistance of a unit length, r_m has units Ω·cm.

$= 2\pi a / R_m$ where R_m is the <u>resistance of a unit area of membrane</u>. For neurons, R_m is generally in the range $10^4 - 10^5$ Ω·cm². It would be more intuitive to express R_m as a conductance with units S/cm² by analogy to C. However, in virtually all publications, this constant is given in terms of resistance. g_m or $1/r_m$ is the conductance of a unit length of cylinder with surface area $2\pi a$.

r_e = resistance to longitudinal flow of current in the extracellular space, with units like Ω/cm. This constant is not defined in terms of the parameters of the membrane cylinder. Instead, it is assumed to be negligible compared to the other impedances in the circuit and ignored, i.e. $r_e = 0$.

Given the parameters defined above, the length constant and membrane time constants can be specified in terms of more fundamental parameters. These are given below along with a new constant G_∞ which is the input conductance of an semi-infinite cylinder. The properties of G_∞ will be derived in a later section.

λ = length constant, with units cm. From Eqn. 9,

$$= \sqrt{\frac{r_m}{r_e + r_i}} \approx \sqrt{\frac{r_m}{r_i}} = \sqrt{\frac{R_m \, a}{2 \, R_i}} \tag{12}$$

where the assumption $r_e \ll r_i$ has been used to eliminate r_e from the equation. Note that λ varies as the square root of cylinder radius a.

τ_m = membrane time constant. Also from Eqn. 9,
$= r_m c_m = R_m C$

Note that τ_m does not depend on cylinder radius.

Later the following additional parameter will be useful:

G_∞ = input conductance of a semi-infinite cylinder at its end.

$$= \frac{1}{r_i \lambda} = \sqrt{\frac{2}{R_i R_m}} \pi a^{3/2} \tag{13}$$

The dependence of G_∞ on the 3/2 power of cylinder radius will be important in considering the equivalent cylinder theorem in a later section.

Solutions for a semi-infinite cylinder

The basic properties of electrotonic conduction can be seen by considering a simple case, a semi-infinite cylinder driven with a step of current at its end. The cylinder is shown in Fig. 4 . The step of current is injected at the end of the cylinder ($x=\chi=0$) and we want to know the time course of membrane potential in the cylinder at various positions $V(x,t)$.
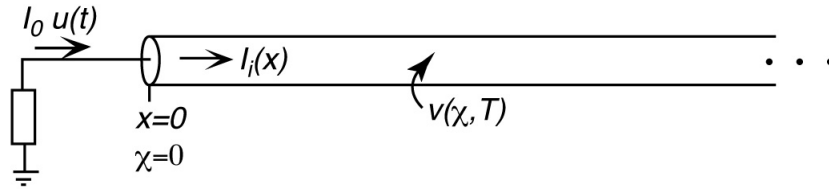

Figure 4. Semi-infinite cable driven by a step current at its end.

The problem to be solved is the cable equation, Eqn. 10, with suitable boundary conditions. The cable equation needs one boundary condition in the time domain and two in the spatial domain. For almost all cable theory problems, the appropriate time boundary condition is a zero initial condition, i.e. $v(\chi,T=0) = 0$. One spatial boundary condition for this case is that the axial current in the cable must equal the external current injected. Using Eqn. 2 and assuming that $r_e=0$ so that V_e can be ignored, the boundary condition can be written in terms of membrane potential as

$$I_0 u(T) = I_i(\chi = 0, T)$$

$$= -\frac{1}{r_i} \frac{\partial v}{\partial x}\bigg|_{x=0} = -\frac{1}{r_i \lambda} \frac{\partial v}{\partial \chi}\bigg|_{\chi=0} = -G_\infty \frac{\partial v}{\partial \chi}\bigg|_{\chi=0} \tag{14}$$

Note that v, the membrane potential relative to rest, has been substituted for V, the absolute membrane potential, as justified by Eqn. 8. Eqn. 14 provides one boundary condition in space. For this problem, a second boundary condition cannot be given, but the condition that the membrane potential must remain finite over the whole cable (a regularity condition) will suffice as a second constraint.

The problem to be solved is as follows:

$$\frac{\partial^2 v}{\partial \chi^2} = \frac{\partial v}{\partial T} + v$$

$$v(\chi, T = 0) = 0 \tag{15}$$

$$\left.\frac{\partial v}{\partial \chi}\right|_{\chi=0} = -\frac{I_0}{G_\infty} u(t) \quad \text{and} \quad v(\chi, T) < \infty \text{ for all } \chi, T$$

A convenient way to solve problems of this kind is to Laplace transform the variables over the time domain. The Laplace transform of a time function $v(t)$ is defined as follows:

$$\bar{V}(s) = \mathbf{L}[v(t)] = \int_0^\infty v(t) e^{-st} \, dt \tag{16}$$

where $\bar{V}(s)$ is the transformed function and s is the transform variable. Laplace transforms are useful because of the following property:

$$\mathbf{L}[dv/dt] = s\bar{V} - v(t = 0) \tag{17}$$

With this property, differential equations are reduced to algebraic equations, which often simplifies solving the equations.

Transforming the cable equation problem of Eqn. 15 along with its boundary coundtions gives

$$\frac{\partial^2 \bar{V}}{\partial \chi^2} = (s+1)\bar{V}$$

$$\left.\frac{\partial \bar{V}}{\partial \chi}\right|_{\chi=0} = -\frac{I_0}{sG_\infty} \quad \text{and} \quad v(\chi, T) < \infty \text{ for all } \chi, T \tag{18}$$

The membrane potential variable $v(\chi, T)$ has been replaced with the transformed variable $\bar{V}(\chi, s)$. Because Laplace transformation and differentiation are both linear operations, the Laplace transformation does not affect the derivatives with respect to χ in Eqn. 18. The time derivative has been replaced with a multiplication by s as in Eqn. 17 and the zero initial condition has been used as part of that operation. The spatial boundary condition at 0 was transformed, using the fact that $\mathbf{L}[u(t)] = 1/s$. The spatial regularity condition of finite v cannot be transformed directly, but will be used below.

Equation 18 is now an ordinary differential equation whose solution takes the form

$$\bar{V}(\chi, s) = A(s) e^{\sqrt{s+1}\chi} + B(s) e^{-\sqrt{s+1}\chi} \tag{19}$$

where $A(s)$ and $B(s)$ are to be determined from the boundary conditions. Using the boundary condition at 0,

$$\left.\frac{\partial \bar{V}}{\partial \chi}\right|_{\chi=0} = \left[\sqrt{s+1}\, A(s)\, e^{\sqrt{s+1}\,\chi} - \sqrt{s+1}\, B(s)\, e^{-\sqrt{s+1}\,\chi}\right]\Big|_{\chi=0}$$

$$= \sqrt{s+1}\left[A(s) - B(s)\right] = -\frac{I_0}{sG_\infty} \tag{20}$$

The additional condition needed to uniquely specify A and B is the regularity condition. From experience with exponential solutions like Eqn. 19, it seems likely that either A or B should be zero so that as $\chi \to \infty$, the membrane potential remains finite. However, the solution in Eqn. 19 is in terms of the Laplace transform and it is not clear how to directly apply this condition. To apply the regularity condition, assume that $B(s)=0$; in that case Eqns. 19 and 20 give the following solution:

$$\bar{V}(\chi,s) = -\frac{I_0}{G_\infty}\frac{e^{\sqrt{s+1}\,\chi}}{s\sqrt{s+1}} \tag{21}$$

The regularity condition must hold in all conditions, including in the steady state as $T \to \infty$. This so-called final value can be computed from a theorem of Laplace transforms:

$$\lim_{t\to\infty} v(t) = \lim_{s\to 0} s\bar{V}(s) \tag{22}$$

Applying the final value theorem to Eqn. 21 gives $v(\chi, T \to \infty) = -I_0\, e^\chi / G_\infty$. Clearly this function does not remain finite as χ goes to infinity. Thus we must conclude that $A(s)=0$ and the solution for the Laplace transform of membrane potential is

$$\bar{V}(\chi,s) = \frac{I_0}{G_\infty}\frac{e^{-\sqrt{s+1}\,\chi}}{s\sqrt{s+1}} \tag{23}$$

Verify for yourself that the transform in Eqn. 23 leads to proper behavior as $T \to \infty$. The membrane potential function can now be obtained by inverting the Laplace transform in Eqn. 23. The method for accomplishing this is described in Jack et al. (1975, chapter 3) and in Hodgkin and Rushton (1946). The solution is as follows:

$$v(\chi,T) = \frac{I_0}{2G_\infty}\left\{ e^{-\chi}\, \mathrm{erfc}\left[\frac{\chi}{2\sqrt{T}} - \sqrt{T}\right] - e^\chi\, \mathrm{erfc}\left[\frac{\chi}{2\sqrt{T}} + \sqrt{T}\right]\right\} \tag{24}$$

The function erfc(x) is the complementary error function, defined as

$$erfc(x) = 1 - \frac{2}{\sqrt{\pi}}\int_0^x e^{-\xi^2}\, d\xi \tag{25}$$

Figure 5A shows plots of exp($-x^2$) and erfc(x) for reference; erfc is a standard function and algorithms for computing it are found in Matlab and other mathematics programs.
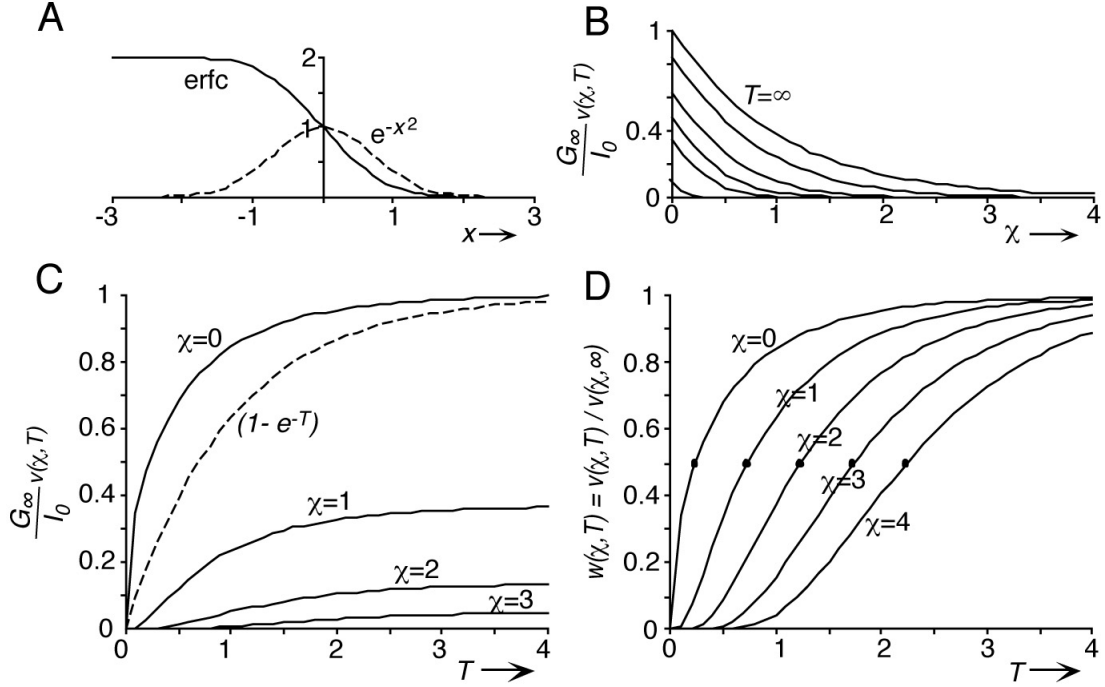
Figure 5. A. Plots of exp($-x^2$) and erfc(x). B. Plot of the distribution of the membrane potential along the cylinder (Eqn. 24) at 6 times: T=0.01, 0.1, 0.2, 0.4, 1.0, and ∞. Membrane potential is normalized by its steady state value at χ=0, I_0/G_∞. C. Plot of the time course of membrane potential at four locations along the cylinder, normalized as in B. For comparison, an exponential rise is also plotted. D. Same as C except membrane potential is normalized by its steady state value.

Several important properties of the solutions to the cable equation can be seen from plots of Eqn. 24 in Fig. 5.

1. Figure 5C shows plots of the growth of membrane potential in response to the step current injection; each curve shows potential growth at a different position along the cylinder, as labeled. Note that at χ=0 the potential grows to a steady value relatively quickly. The growth is faster than exponential, as seen by the comparison with the function (1-exp(-T)), which is plotted for comparison. As the point moves away from the end of the cable (larger χ), the growth of potential is delayed and the steady state value of potential is smaller. The difference in growth rate can be seen in Fig. 5D where the same plots are shown, except normalized by their maximum value. Note that the membrane time constant τ_m sets the time scale of the response, in that the abscissae of Figs. 5C and 5D are scaled in units of τ_m.

   Figure 5C illustrates the basic features of electrotonic conduction: as the potential spreads from the site of a disturbance (in this case the current injection at the end of the cable), the amplitude of the potential gets smaller and its time course is extended. In this case, the rise of the potential is delayed and its rise is slower.

2. Figure 5B shows the potential spread along the cylinder at various times following the onset of the current at T=0. The most illuminating case is for T=∞, i.e. in the steady state. In the steady state, Eqn. 24 becomes

$$v(\chi, T \to \infty) = \frac{I_0}{G_\infty} e^{-\chi} = \frac{I_0}{G_\infty} e^{-x/\lambda} \tag{26}$$

This equation illustrates the meaning of the space constant λ. The decay of potential is exponential along the cylinder, so that potential decays by 1/e for every distance λ. Thus the space constant is a measure of how far a disturbance spreads away from the point of current injection.

Equation 26 also allows the meaning of the parameter G_∞ to be understood. Note that at $\chi=0$, $v(T=\infty)=I_0/G_\infty$. Thus the resistance looking into the end of the semi-infinite cylinder in the steady state, for application of D.C. current, is $1/G_\infty$. This is the basis for the statement made earlier that G_∞ is the input conductance of a semi-infinite cable.

3. A measure of the speed of electrotonic spread can be gotten from the points marked by black circles in Fig. 5D. These circles mark the times at which the potential is half its steady state value, for different values of χ. If the χ values are plotted against the half-times, the result is a straight line with slope $2\lambda/\tau_m$ (Jack et al., 1975). This value can be though of as the speed of spread of electrotonic disturbances. Of course, it is not a true propagation speed, in the sense of the action potential propagation speed, because there is no fixed waveshape that is propagating, i.e. this is not a true wave. Nevertheless, this speed provides a way to calculate the time delays expected in electrotonic conduction. Note that it varies as the square root of the cylinder radius, since

$$\text{speed} = 2\frac{\lambda}{\tau_m} = \sqrt{\frac{2\,a}{R_m R_i C^2}} \tag{27}$$

Question 4 Suppose that the current injected into the semi-infinite cable in Fig. 4 is an impulse, $Q_0\delta(t)$. Solve for the potential distribution in the cable as a function of time and χ. The following Laplace transform pair will be helpful:

$$\frac{e^{-x\sqrt{s}}}{\sqrt{s}} \leftrightarrow \frac{e^{-x^2/4t}}{\sqrt{\pi t}}$$

It will also be helpful to know the frequency shift property: $\mathbf{L}\left[e^{-at}f(t)\right] = \bar{F}(s+a)$. This was one model that was considered for neurons in early papers. The idea was that the dendritic tree is very long, so it could be approximated as infinite, and the soma was unimportant. Show that the membrane time constant τ_m can be determined from a plot of $\ln\left[\sqrt{t}\,v(0,t)\right]$ versus t.

References

Hodgkin, A.L. and Rushton, W.A.H. The electrical constants of a crustacean nerve fibre. *Proc. Roy. Soc.* B-133, 444-79 (1946).

Johnston, D. and Wu, S.M. Foundations of Cellular Neurophysiology. MIT Press, Cambridge (1995).

C. Koch *Biophysics of Computation* (Oxford Press) (especially chapters 2 and 3).

Koch, C. and Segev, I. *Methods in Neuronal Modeling from Ions to Networks* (2nd Ed.). MIT Press, Cambridge (1998).

Rall, W. Theory and physiological properties of dendrites. *Ann. N.Y. Acad. Sci.* 96:1071-1092 (1962).