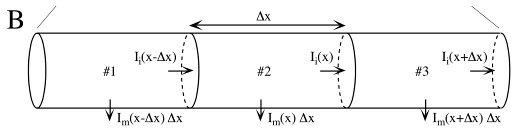
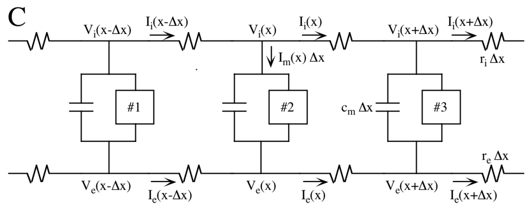
Derive non-linear cable equation





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

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

Rearranging and taking the limit as Δx goes to 0,

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

Conservation of current at the intracellular and extracellular nodes gives

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

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

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

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

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

$$= (r_i + r_e)\, I_m$$

<u>nonlinear cable equation:</u>

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

Derive linear cable equation

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

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

and

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

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

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

Parameters

$$r_i = \frac{R_i}{\pi a^2}$$

$$c_m = 2\pi a C$$

$$g_m = \frac{2\pi a}{R_m}$$

$$r_e = 0, \textit{assumed negligible}$$

$$\lambda = \sqrt{\frac{r_m}{r_e + r_i}} = \sqrt{\frac{r_m}{r_i}} = \sqrt{\frac{R_m a}{2 R_i}}$$

$$\tau_m = R_m C$$

$$G_{\bowtie} = \frac{1}{r_i \lambda}$$

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

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

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

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

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

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

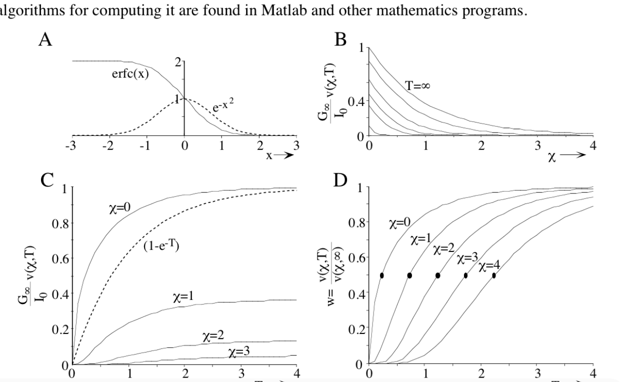
$$= \sqrt{s+1}\,\left[A(s) - B(s)\right] = -\frac{I_0}{s\,G_\infty} \qquad (20)$$

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

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

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

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.



3 points refer to previous plots

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 $T=\infty$, i.e. in the steady state. In the steady state, Eqn. 24 becomes

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

   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 χ=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

$$\text{speed}=2\frac{\lambda}{\tau_m}=\sqrt{\frac{2a}{R_m R_i C^2}} \qquad (27)$$

Rall motorneuron model

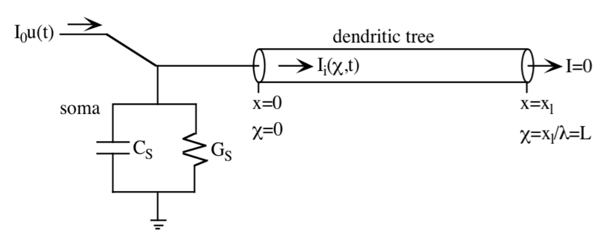


Figure 6. Rall motorneuron model. The soma is represented by the point-model consisting of the somatic capacitance C_S and resting conductance G_S. The dendritic tree is represented by a single membrane equivalent cylinder, which runs from x=0 to $x=x_l$. L is the electrotonic length of the dendritic cable. $I_0u(t)$ is an external current injected into the soma of the cell through a microelectrode.

$$\left.\frac{\partial v}{\partial \chi}\right|_{\chi=L}=0$$

$$I_0\,u(t)=C_S\left.\frac{\partial v}{\partial t}\right|_{\chi=0}+G_S\,v(\chi=0,T)-G_\infty\left.\frac{\partial v}{\partial \chi}\right|_{\chi=0}$$

$$=\frac{C_S}{\tau_m}\left.\frac{\partial v}{\partial T}\right|_{\chi=0}+G_S\,v(\chi=0,T)-G_\infty\left.\frac{\partial v}{\partial \chi}\right|_{\chi=0}$$

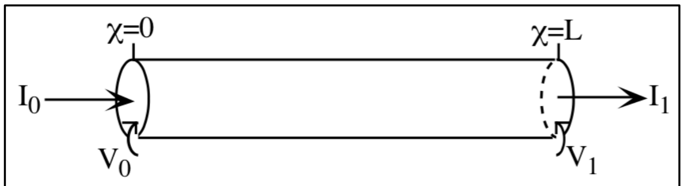


Figure 7. Two-port model for a length of dendritic cylinder

$$v(\chi=0,T)=V_0(T) \quad \text{and} \quad v(\chi=L,T)=V_1(T)$$

$$I_i(\chi=0,T)=I_0(T) \quad \text{and} \quad I_i(\chi=L,T)=I_1(T)$$

There must also be a boundary condition in the time dimension. One of three situations will be considered. In each case, the cable equation is reduced to the ordinary differential equation

$$\frac{d^2\bar{V}}{d\chi^2}=q^2\bar{V} \qquad (31)$$

where q is a variable that depends on the situation considered. The three situations are as follows:

1. D.C. steady state: in this case, all the sources are D.C. values and enough time has elapsed that the membrane potential and all currents in the system are steady, not varying with time. In this case $\partial v/\partial T=0$ in Eqn. 10, q=1, and $\bar{V}=v$ in Eqn. 31.

2. Laplace transform from zero initial conditions: this is the same transform that was applied in Eqns. 15-18. In this case, $q=\sqrt{s+1}$ and $\bar{V}(\chi,s)$ is the Laplace transform of $v(\chi,T)$. The boundary conditions are also Laplace transformed.

3. Fourier transform in the sinusoidal steady state: this is similar to case 2. The sources are all sinusoidal at frequency ω and have been applied to the system long enough that transient components have died away. In this steady state, the membrane potentials and currents are also sinusoidal at frequency ω. Then, $q=\sqrt{1+j\omega}$, where $j=\sqrt{-1}$, and $\bar{V}(\chi,j\omega)$ is the Fourier transform of $v(\chi,T)$. The boundary conditions are also Fourier transformed in this case.

The solution to Eqn. 31 can be written as

$$\bar{V}(\chi,q)=A(q)\sinh(q\chi)+B(q)\cosh(q\chi) \qquad (32)$$

where sinh(x)=[exp(x)-exp(-x)]/2 and cosh(x)=[exp(x)+exp(-x)]/2. It will also be useful to have the axial current $\bar{I}_i(\chi,q)=-G_\infty\,\partial\bar{V}/\partial\chi$ (from Eqn. 14); from Eqn. 32, this is

$$\bar{I}_i(\chi,q)=-G_\infty\,q\left[A(q)\cosh(q\chi)+B(q)\sinh(q\chi)\right] \qquad (33)$$

$$\bar{V}(0,q)=B=\bar{V}_0 \quad \text{and} \quad \bar{I}_i(0,q)=-G_\infty\,q\,A=\bar{I}_0 \qquad (34)$$

A and B are determined by Eqn. 34, resulting in the following solution for membrane potential and axial current in the finite cable.

$$\begin{bmatrix}\bar{V}(\chi,q)\\ \bar{I}_i(\chi,q)\end{bmatrix}=\begin{bmatrix}\cosh(q\chi) & -\sinh(q\chi)/G_\infty q\\ -G_\infty\,q\sinh(q\chi) & \cosh(q\chi)\end{bmatrix}\begin{bmatrix}\bar{V}_0\\ \bar{I}_0\end{bmatrix} \qquad (35)$$

Note that $\bar{V}_1$ and $\bar{I}_1$ are specified in this case by the functions in Eqn. 35 evaluated at $\chi=L$.

A second useful solution begins with an alternative way of writing the solutions to the cable equation, Eqn. 31:

$$\bar{V}(\chi,q)=A(q)\sinh[q(L-\chi)]+B(q)\cosh[q(L-\chi)]$$
$$\bar{I}_i(\chi,q)=G_\infty q\left\{A(q)\cosh[q(L-\chi)]+B(q)\sinh[q(L-\chi)]\right\} \qquad (36)$$

In this case, applying the boundary conditions at $\chi=L$, i.e. $\bar{V}_1$ and $\bar{I}_1$ gives

$$\begin{bmatrix}\bar{V}(\chi,q)\\ \bar{I}_i(\chi,q)\end{bmatrix}=\begin{bmatrix}\cosh[q(L-\chi)] & \sinh[q(L-\chi)]/G_\infty q\\ G_\infty\,q\sinh[q(L-\chi)] & \cosh[q(L-\chi)]\end{bmatrix}\begin{bmatrix}\bar{V}_1\\ \bar{I}_1\end{bmatrix} \qquad (37)$$

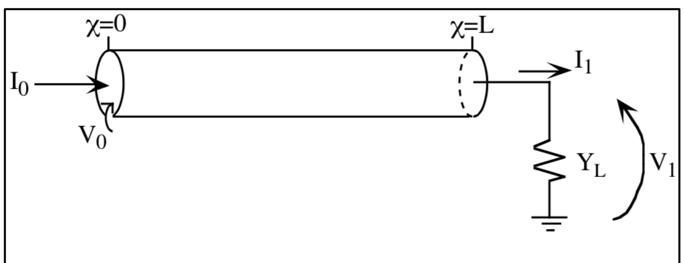


Figure 8. Finite cable loaded with an admittance Y_L at one end and voltage clamped at the other.

$$\begin{bmatrix}\bar{V}(\chi,q)\\ \bar{I}_i(\chi,q)\end{bmatrix} = \begin{bmatrix}\cosh[q(L-\chi)] & \sinh[q(L-\chi)]/G_\infty q\\ G_\infty q\sinh[q(L-\chi)] & \cosh[q(L-\chi)]\end{bmatrix}\begin{bmatrix}\bar{V}_1\\ Y_L\bar{V}_1\end{bmatrix} \tag{38}$$

The constraint that $\bar{V}(\chi=0,q)=\bar{V}_0$ can be applied to solve for $\bar{V}_1$, the one unknown in Eqn. 38. Using the voltage equation in Eqn. 38 gives

$$\bar{V}_0 = \bar{V}(\chi=0,q) = \bar{V}_1\left(\cosh qL + \frac{Y_L}{G_\infty q}\sinh qL\right) \tag{39}$$

Using Eqn. 39 to eliminate $\bar{V}_1$ in Eqn. 38 gives the membrane potential in this finite cylinder as

$$\bar{V}(\chi,q) = \bar{V}_0\,\frac{\cosh[q(L-\chi)] + \dfrac{Y_L}{G_\infty q}\sinh[q(L-\chi)]}{\cosh qL + \dfrac{Y_L}{G_\infty q}\sinh qL} \tag{40}$$

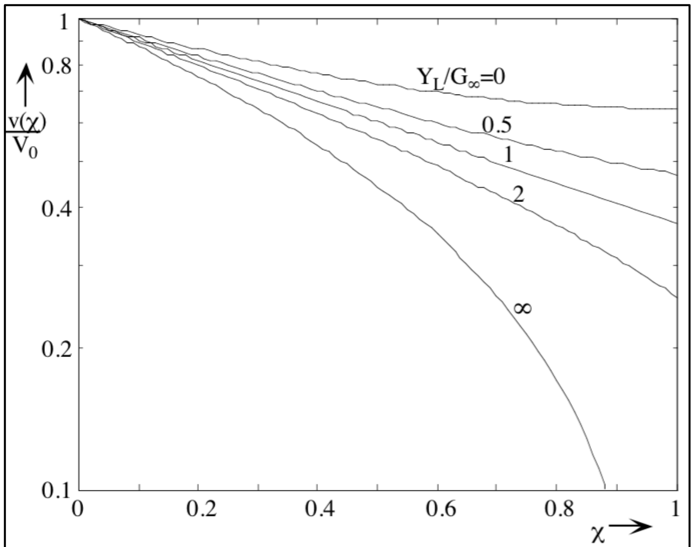
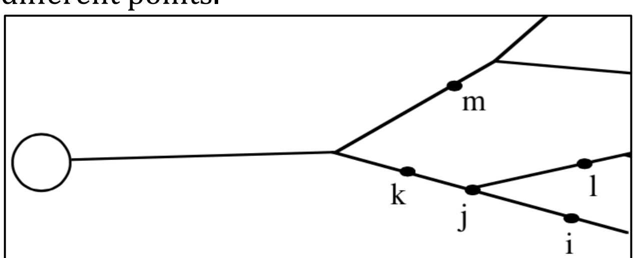


Figure 9 Decay of potential in a finite cylinder of electrotonic length 1 for the D.C. steady state case. Cylinder is voltage clamped at one end and terminated by a load admittance Y_L at the other (Fig. 8). Parameters on the curves are load admittance values relative to G_∞.

The following are the three rules for determining relationships between currents injected at different points.



Rule 1: voltage transfer ratio This situation has already been analyzed. It is diagrammed in Fig. 8. What is desired is the voltage gain from V_0 to V_1 in the presence of a load admittance Y_L. From Eqn. 39,

$$A_{01} = \frac{\bar{V}_1}{\bar{V}_0} = \frac{1}{\cosh qL + \dfrac{Y_L}{G_\infty q}\sinh qL} \tag{40}$$

The gain A_{01} is transformed in the same way as the voltages and currents. That is, if the situation is the D.C. steady state, then A_{01} is the D.C. voltage ratio, a real number; if the cable equation has been Laplace transformed from 0 initial conditions, then A_{01} is the complex transfer gain, a function of s.

This rule expresses the spread of voltage in the tree. For example, in Fig. 10, if $\bar{V}_i$ is known, then $\bar{V}_j$, $\bar{V}_k$, etc.can be computed by application of Eqn. 40 (assuming that Y_L can be computed, the method for doing this is described below) either once or several times. Note that care must be taken to follow the direction of signal flow. If there is a source (voltage clamp or current injection) at point i then the voltage gains A_{ij}, A_{jk}, and A_{jl} are meaningful because they follow the causal direction of signal flow, whereas A_{ji} is not, because it applies when a source at point j is producing a voltage at point i.

Rule 2: input admittance This rule also applies to the situation in Fig. 8, except the goal is to compute the input admittance $Y_{in} = \bar{I}_0/\bar{V}_0$ at one end of a cylinder loaded with admittance Y_L at the other end. The calculation is done directly from Eqn. 38, evaluated at χ=0:

$$\begin{bmatrix}\bar{V}_0\\ \bar{I}_0\end{bmatrix} = \begin{bmatrix}\bar{V}(0,q)\\ \bar{I}_i(0,q)\end{bmatrix} = \begin{bmatrix}\cosh qL & \sinh qL/G_\infty q\\ G_\infty q\sinh qL & \cosh qL\end{bmatrix}\begin{bmatrix}\bar{V}_1\\ Y_L\bar{V}_1\end{bmatrix} \tag{41}$$

The input admittance is then the ratio of the two equations in Eqn. 41:

$$Y_{in} = \frac{\bar{I}_0}{\bar{V}_0} = G_\infty q\,\frac{\sinh qL + \dfrac{Y_L}{G_\infty q}\cosh qL}{\cosh qL + \dfrac{Y_L}{G_\infty q}\sinh qL} = G_\infty q\,\frac{\tanh qL + \dfrac{Y_L}{G_\infty q}}{1 + \dfrac{Y_L}{G_\infty q}\tanh qL} \tag{42}$$

A special case of importance is when Y_L=0, which is usually assumed at the end of a dendritic tree. In this case,

$$Y_{in} = G_\infty q\tanh qL \tag{43}$$

The second rule allows computation of the input admittance of any point on a dendritic tree. The computation is done constructively, as illustrated in Fig. 11. Consider the problem of

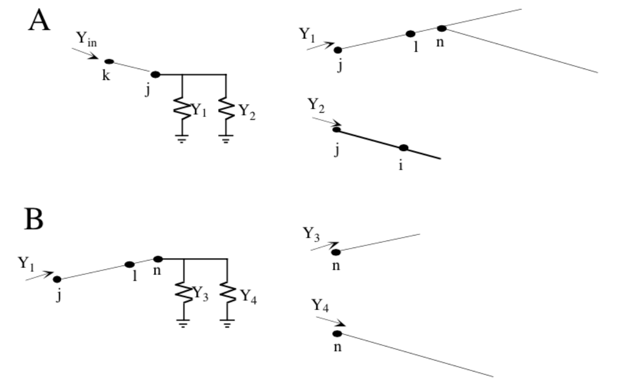


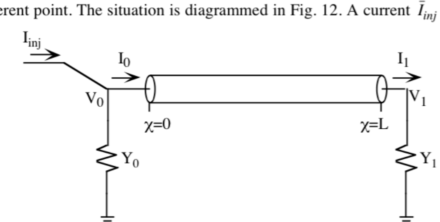
Figure 11 Illustrates the decomposition of the dendritic tree of Figure 10 in order to compute the input admittance at point k, looking out toward the end of the tree. A First segment of the tree, from k to j, terminated by input admittances of the two branches connected to j, shown at right. B Second segment, computing Y_1, the input admittance at j looking out the branch toward l and n.

computing the input admittance, looking out toward the end of the dendrites, at point k on the dendritic tree of Fig. 10. As shown in Fig. 11A, this is the input admittance of the cable from k to j terminated by the parallel combination of admittances Y_1 and Y_2. These are the input admittances of the two branches at j, shown at right in Fig. 11A. Admittance Y_2 can be computed immediately from Eqn. 43, because it is the input admittance of a single cable terminated at the end of the tree. Admittance Y_1 requires another decomposition, shown in Fig. 11B. At point n there are two branches, with input admittances Y_3 and Y_4. Both of these can be computed immediately from Eqn. 43. Once Y_3 and Y_4 are computed, Y_1 can be computed from Eqn. 42 using Y_3+Y_4 as the load admittance for the cable shown in the left part of Fig. 11B. Now the input admittance at k can be computed from Y_1 and Y_2 using Eqn. 42 and the cable in the left part of Fig. 11A.

Note that the input admittance at a point on the tree can be computed using this rule, by summing the input admittances looking away from the point in the two directions, toward and away from the soma.

Rule 3: transfer impedance The third rule allows calculation of the potential produced at a point by current injected at a different point. The situation is diagrammed in Fig. 12. A current $\bar{I}_{inj}$

Figure 12 Cable terminated at both ends by admittances and driven at one end by an injected current.



is injected at one end of a cylinder and a potential $\bar{V}_1$ is produced at the other end. The relationship between these two can be computed by starting with Eqn. 35, evaluated at χ=L. With the constraints provided by the load impedance at the right end and the current injection at the left end, the equation gives

$$\begin{bmatrix}\bar{V}_1\\ Y_1\bar{V}_1\end{bmatrix} = \begin{bmatrix}\cosh(qL) & -\sinh(qL)/G_\infty q\\ -G_\infty q\sinh(qL) & \cosh(qL)\end{bmatrix}\begin{bmatrix}(\bar{I}_{inj}-\bar{I}_0)/Y_0\\ \bar{I}_0\end{bmatrix} \tag{44}$$

If $\bar{I}_0$ is eliminated between the two equations in Eqn. 44, that leaves an equation relating $\bar{I}_{inj}$ and $\bar{V}_1$. The transfer impedance K_{01} is the ratio of these two quantities and is given by

$$K_{01} = \frac{\bar{V}_1}{\bar{I}_{inj}} = \frac{1}{(Y_0+Y_1)\cosh qL + \left(\dfrac{Y_0Y_1}{G_\infty q} + G_\infty q\right)\sinh qL} \tag{45}$$

The combination of transfer impedance and voltage transfer ratio can be used to compute transfer impedances between any two points in a dendritic tree. For example, for the tree in Fig. 10, if a current is injected at point i, the voltages at various other points on the tree will be given by Equations 46. Note how the branch points are handled. The transfer impedance K_{ij} cannot extend across a branch point, so the transfer impedance and voltage gain must be applied sequentially from branch point to branch point.

$$\bar{V}_j = K_{ij}\,\bar{I}_{inj} \qquad \bar{V}_k = K_{ij}\,A_{jk}\,\bar{I}_{inj}$$
$$\bar{V}_l = K_{ij}\,A_{jl}\,\bar{I}_{inj} \qquad \bar{V}_n = K_{ij}\,A_{jl}\,A_{ln}\,\bar{I}_{inj} \tag{46}$$

These relationships use Rules 1 and 3 explicitly; they also require Rule 2, however, in order to compute the admittances necessary to the use of Rules 1 and 3.

Symmetry: $K_{ij} = K_{ji}$

Positivity: $K_{ij} \le K_{ii}$ and $K_{ij} \le K_{jj}$ (for D.C. steady state (q=1 and all quantities real) only. The quantities K_{ii} and K_{jj} are the input impedances (resistances in the D.C. steady state) of the dendritic tree at points i and j.

Transitivity: $K_{ij} = K_{il}\,K_{lj}/K_{ll}$ True for points i, l, and j on a path without loops and point l in between i and j.

Equivalent cylinder theorem. Consider an arbitrarily branching structure like the tree shown in Fig. 15. Three conditions can be stated:

1. The cumulative electrotonic lengths from soma to the tip of the dendritic tree is the same by all direct paths. That is, for the example in Fig. 15

$$L_{total} = L_{11} + L_{21} + L_{31} = L_{11} + L_{21} + L_{32} = \cdots = L_{11} + L_{22} + L_{34} \tag{47}$$

2. At every branch point, there is an impedance match in the sense that the sum of the G_∞s of the child branches equals the G_∞ of the parent branch. For example

$$G_{\infty 11} = G_{\infty 21} + G_{\infty 22} \quad \text{and} \quad G_{\infty 21} = G_{\infty 31} + G_{\infty 32} \quad \text{etc.} \tag{48}$$

Note that this is usually stated as the 3/2 power law: at every branch point

$$a_{parent}^{3/2} = \sum_{\substack{\text{all child}\\ \text{branches } j}} a_j^{3/2} \tag{49}$$

3. The termination condition is the same at all dendritic tips, in the sense that $Y_{ij} / qG_{\infty ij}$ is the same for all terminal branches.

If these conditions are true, then the dendritic tree is equivalent to a cylinder with the electrotonic length L_{total}, a G_∞ value equal to $G_{\infty 11}$, and terminated by an admittance which is the sum of the admittances terminating the original tree. The equivalence holds in the following ways:

1. If the soma is voltage (or current) clamped, then $v(\chi)$ is the same in the original tree and the equivalent cylinder. Note that this rule applies to voltage measured in terms of electrotonic distance χ, not physical distance x.

2. The input admittance of the original tree is the same as that of the equivalent cylinder.

3. If current I_{inj} is injected into one branch at an electrotonic length L_I from the soma in the original tree, then the potential distribution is the same in the original tree and cylinder for the ultimate parent branch only. For example, if current were injected into branch *21* or *33* in the tree in Fig. 15, then the potential would be the same in the *11* branch and in the first L_{11} of the equivalent cylinder.

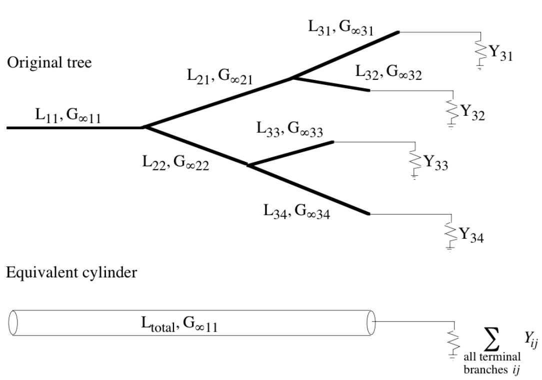


Figure 15 Top shows the branching structure of a dendritic tree with arbitrary termination admittances. Bottom shows the equivalent cylinder for this tree. L is electrotonic length equal to physical length divided by length constant. G is the infinite cylinder input conductance, Eqn. 13. Y is the admittance terminating each dendritic branch.

All following notes about cable theory are extra, taken from the solutions to homework 6 and 7.

$$\frac{1}{r_i + r_e}\frac{\partial^2 V}{\partial x^2} = i_m(x,t,V) = \text{membrane current/unit length of cylinder}$$

$$\frac{1}{r_i + r_e}\frac{\partial^2 \bar{V}}{\partial x^2} = \bar{i_m}(x, j\,\omega, V)$$

and

$$\bar{i_m}(x, j\,\omega, V) = \frac{1}{z_m}\bar{V}$$

where the bars indicate that the variables have been Fourier transformed.

$$\frac{1}{r_i + r_e}\frac{\partial^2 \bar{V}}{\partial x^2} \approx \frac{1}{r_i}\frac{\partial^2 \bar{V}}{\partial x^2} = \frac{1}{z_m}\bar{V} \quad \text{or} \quad \frac{z_m}{r_i}\frac{\partial^2 \bar{V}}{\partial x^2} - \bar{V} = 0$$