TRANSIENT POTENTIALS IN DENDRITIC SYSTEMS OF ARBITRARY GEOMETRY

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ABSTRACT A simple graphical calculus is developed that generates analytic solutions for membrane potential transforms at any point on the dendritic tree of neurons with arbitrary dendritic geometries, in response to synaptic "current" inputs. Such solutions permit the computation of transients in neurons with arbitrary geometry and may facilitate analysis of the role of dendrites in such cells.

INTRODUCTION

The variety of dendritic patterns found in differing neuronal types (Cajal, 1909) provides a more than adequate motivation to investigate the functional role played by dendritic geometry in neuronal interactions. Rall (1959–1973) has initiated such an investigation, particularly with the discovery (Rall, 1962 *a*) that a class of dendritic geometries exist that may be characterized mathematically by the cylindrical cable equation (Hodgkin and Rushton, 1946). Rall's equivalent cylinder class of dendritic geometries provides that compromise between facts and analytic tractability which is the philosophical goal of the model builder. This simplification has facilitated the analysis of problems such as the functional distribution of excitatory and inhibitory synapses (Rall, 1964), as well as, for example, the functional significance of dendritic spines (Rall and Rinzell, in preparation).

A natural question that arises from Rall's investigations is to what extent are arbitrary dendritic geometries approximated by the equivalent cylinder assumption. To answer this it is necessary to calculate the transients arising in neurons of arbitrary dendritic geometry. Such transients can of course be obtained using numerical methods based on an approximation of the cable equation for spatially inhomogeneous structures by way of compartmental analysis (Rall, 1964, 1967). Numerical calculations of this type are in fact of considerable value for the analysis of arbitrary dendritic structures, especially now that staining techniques for individual neurons have been developed that permit the measurement of dendritic branch lengths and diameters. There remains, however, the problem of determining analytically transients in arbitrary dendritic structures. The existence of such an analytic solution can be expected to lead to new insights concerning the role of dendrites in structures which differ markedly from the equivalent cylinder class, to facilitate the comparison between differing types of neurons, and perhaps to provide a more efficient and economical method than compartmental analysis for the computation of transients. We solve the analytical problem in this paper, and give the exact solution (as a Laplace transform) for the transients arising from synaptic current stimuli at any points on an arbitrary dendritic tree.

The primary mathematical difficulty in such a direct treatment of the problem is that analytic expressions for the transients are enormously complicated. Thus it is necessary to develop a geometric notation in order to express the essential aspects of the formulae. The development of such a notation is the main problem discussed in this paper. In later papers we hope to apply the analysis to some of the problems cited above.

THEORETICAL MEMBRANE POTENTIALS

We list here a number of formulae for the membrane potential, $v(x,t)$, resulting from a current source, in dendritic systems of simple geometry. This will lead us to a discussion of the more general configurations for which a geometric notation is introduced. Specifically, we present solutions for the Laplace transform, $V(x,s)$, of the membrane potential, since only this is available in closed form. The details of the derivation of the solutions are presented in the Appendix. They are based on the well-established cable equation representation of electrotonic potentials (Rall, 1959)

$$\lambda^2(\partial^2 v/\partial x^2) - \tau\frac{\partial v}{\partial t} - v = 0. \tag{1}$$

Note that in Eq. 1, $v(x,t)$ is assumed measured relative to some resting potential v_r. By considering the Laplace transform of the membrane potential, $V(x,s)$,

$$V(x,s) = \int_0^\infty e^{-st}v(x,t)\mathrm{d}t, \tag{2}$$

the solution at any point x along a primary dendritic branch of length L, is traditionally written in the electrical transmission line literature (Weber, 1965), as

$$V(x,s) = \frac{[\sinh\gamma x + k_0\cosh\gamma x]\, Z_L I^*(s)}{(k_0 + k_L)\cosh\gamma L + (1 + k_0 k_L)\sinh\gamma L}, \tag{3}$$

where $I^*(s)$ is the Laplace transform at a current source (synapse) $i(t)$, applied at $x = L$, $k_0 = Z_0/Z_c$, $k_L = Z_L/Z_c$, where $Z_c = R/\gamma$ is the "characteristic impedance" of the primary dendritic branch, Z_0 the terminal impedance of the soma and Z_L that of secondary dendritic branches, and where R is the axial resistance per unit length along the primary dendritic branch, and $\gamma = (\tau s + 1)^{1/2}/\lambda$.

Eq. 3 is a simple enough structure until it is necessary to specify the terminal impedances Z_0 and Z_L. For the case of branching systems we show that a geometric

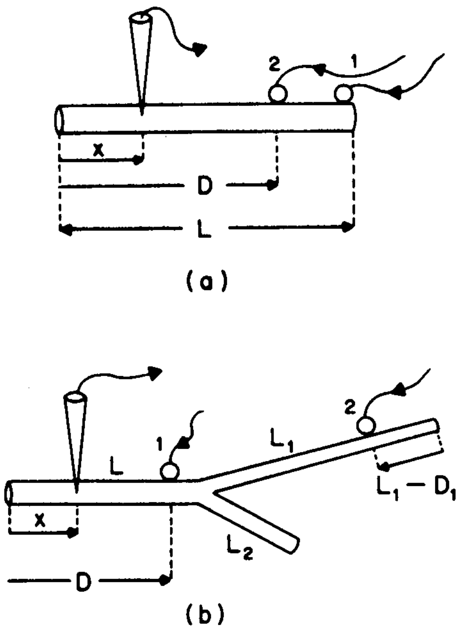


FIGURE 1 (*a*) Unbranched dendritic tree of length L showing a recording electrode at x, and current pulse inputs at a distance D and L from the origin, respectively. (*b*) Branched dendritic tree showing a recording electrode and a current input on the primary branch, and a current input on a secondary branch.

representation of this equation is far more useful. We begin by considering some special cases of Eq. 3 emphasizing how the geometrical notation is, in some basic sense, natural. To keep things as uncluttered as possible we assume that all peripheral branches satisfy a zero potential boundary condition. Since our potentials are assumed relative to v_r this corresponds to the "killed end" solutions of Rall (1959). The modifications required to include the more realistic situation, a "sealed end," or $\partial v/\partial x = 0$ at a boundary, are discussed at the end of the section. The cases we consider here are illustrated in Fig. 1.

(*a*) In the simplest cylindrical membrane system of length L with current source transform, $I^*(s)$, (e.g., synaptic current source) at any point D along the membrane axis, an intracellular electrode at $x(x < D)$ records a potential whose transform, $V(x,s)$, is shown in the Appendix (Eq. 47) to be,

$$V(x,s) = \frac{Z_c \sinh\gamma x \cdot \sinh\gamma(L - D) \cdot I^*(s)}{\sinh\gamma L}. \tag{4}$$

(*b*) In the simplest branching situation, a Y-branched membrane system, primary branch of length L and peripheral branches of length L_1 and L_2 with a current source transform at some point D along the peripheral branch L_1, an intracellular electrode at a distance x along the primary branch records a potential whose transform, $V(s,x)$

is derived in the Appendix (Eq. 63) to be,

$$V(x,s) = \frac{Z_c Z_{c_1} Z_{c_2} \sinh\gamma x \sinh\gamma_2 L_2 \sinh\gamma_1 (L_1 - D) I^*(s)}{\begin{bmatrix} Z_c Z_{c_1} \sinh\gamma L \sinh\gamma_1 L_1 \cosh\gamma_2 L_2 \\ + Z_c Z_{c_2} \sinh\gamma L \cosh\gamma_1 L_1 \sinh\gamma_2 L_2 \\ + Z_{c_1} Z_{c_2} \cosh\gamma L \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \end{bmatrix}}. \qquad (5)$$

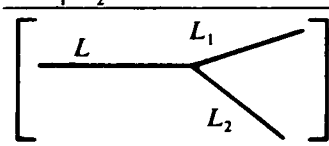
A GEOMETRIC CALCULUS

The initial insight into simplifying an analytic approach to branching systems comes with the realization that Eqs. 4 and 5 have the same structure when viewed from a geometric vantage point. Firstly, the numerators in both can be viewed as a factorization of a graph. This is revealed by considering Fig. 1. By deleting that portion of the dendritic membrane system along the direct path from the recording electrode to the synapse, only the remaining lengths, x and $(L - D)$ in the case of Eq. 4; x, $L_1 - D$, L_2 in the case of Eq. 5, contribute to the numerator. This is proved as a general theorem in the Appendix. Secondly the denominator in both Eqs. 4 and 5, from a geometric view, represents the total structure of the original dendritic system under consideration. That is, in the trivial case of Eq. 4 the denominator is a function of the length L and in the branching case, Eq. 5, the denominator is a function of the lengths L, L_1, and L_2. Furthermore, in Eq. 5 a cyclical symmetry is evident. Upon interchanging L, L_1, and L_2 the denominator remains invariant. This fundamental invariance suggests a geometric representation, a triad of lengths L, L_1, and L_2 for the denominator in Eq. 5, and, of course, representing the denominator in Eq. 4 by a straight line segment of length, L. Thus we propose that Eqs. 4 and 5 may be represented (respectively) as

$$V(x,s) = \frac{[\underline{\;x\;}][\underline{\;L - D\;}]}{[\underline{\;L\;}]} I^*(s) \qquad (6)$$

and

$$V(x,s) = \frac{Z_c Z_{c_1} Z_{c_2} [\underline{\;x\;}][\underline{\;L_1 - D\;}][\underline{\;L_2\;}] I^*(s)}{\left[\qquad \right]}. \qquad (7)$$



The factor Z_c Z_{c_1} Z_{c_2} in Eq. 7 arises because the appropriate deletion has gone through a bifurcation point. It will be shown that for each deleted bifurcation point,

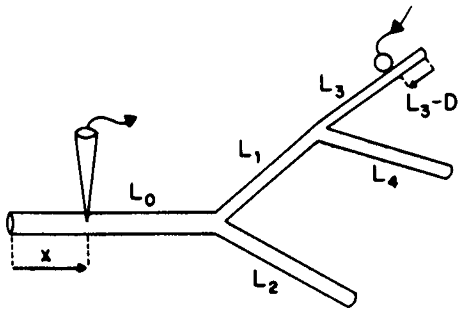
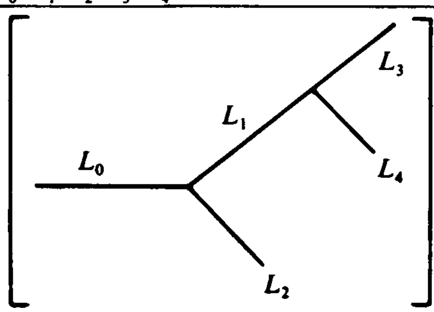


FIGURE 2 Branched dendritic tree showing a recording electrode on the primary branch, and a current input on a tertiary branch.

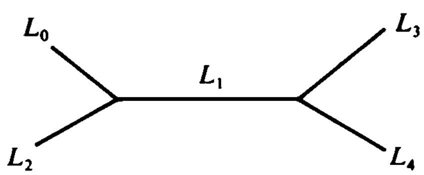
corresponding to the junction of branches of lengths L_i, L_j, L_k, a factor $Z_{c_i} Z_{c_j} Z_{c_k}$ appears in the numerator of $V(x,s)$.

The simplicity and utility of these ideas becomes apparent by considering the next level of complexity, a dendritic system with five branches, as shown in Fig. 2. Applying the deletion rule to obtain the factors for the numerator, the foregoing suggests that the membrane potential transform may be written immediately as

$$V(x,s) = \frac{Z_{c_0} Z_{c_1}^2 Z_{c_2} Z_{c_3} Z_{c_4} [\underline{x}][\underline{L_3 - D}][\underline{L_2}][\underline{L_4}] I^*(s)}{\left[\quad\right]} . \qquad (8)$$

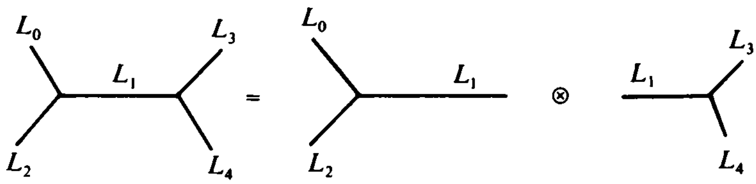


Since we have agreed that a line segment of length L_i in the numerator of Eq. 8 corresponds to a factor $Z_{c_i} \sinh \gamma_i L_i$, the remaining difficulty is how to translate the diagram for the denominator into the appropriate array of hyperbolic sines and cosines. By re-drawing the figure for the denominator in Eq. 8 the symmetries may be made more apparent, i.e.,



(9)

It is clear that the structure of diagram 9 remains invariant if branches L_0 and L_2 are interchanged with the branches L_3 and L_4 and, according to our hypothesis, this must be the case in the corresponding analytic formula as well. This then suggests another factorization which utilizes the inherent symmetry. Although not immediately obvious, the appropriate decomposition may be written as



(10)

where the operator ⊗ represents multiplication in the ordinary sense when the corresponding analytic formulae are substituted except for terms involving L_1 for which the following "parity" rule applies:

$$\begin{aligned}\sinh\gamma_1 L_1 \sinh\gamma_1 L_1 &=> \sinh\gamma_1 L_1\\ \cosh\gamma_1 L_1 \cosh\gamma_1 L_1 &=> \sinh\gamma_1 L_1\\ \sinh\gamma_1 L_1 \cosh\gamma_1 L_1 &=> \cosh\gamma_1 L_1.\end{aligned}$$

The validity of this factorization for the general situation is shown in the Appendix.

Sealed Ends

Having discussed the derivation of formulae assuming the killed end boundary condition we now indicate the procedure for the sealed end condition, where the first spatial derivative of the membrane potential vanishes at the terminal ends. In the Appendix we show that the equations corresponding to the situations represented by Eqs. 4 and 5 are, respectively,

$$V(x,s) = \frac{Z_c \cosh\gamma x \cdot \cosh\gamma(L - D) \cdot I^*(s)}{\sinh\gamma L}, \tag{12}$$

and

$$V(x,s) = \frac{Z_c Z_{c_1} Z_{c_2} \cosh\gamma x \cosh\gamma_2 L_2 \cosh\gamma_1 (L_1 - D) \cdot I^*(s)}{\begin{bmatrix} Z_c Z_{c_1} \cosh\gamma L \cosh\gamma_1 L_1 \sinh\gamma_2 L_2 \\ + Z_c Z_{c_2} \cosh\gamma L \sinh\gamma_2 L_2 \cosh\gamma_2 L_2 \\ + Z_{c_1} Z_{c_2} \sinh\gamma L \cosh\gamma_2 L_2 \cosh\gamma_2 L_2 \end{bmatrix}}. \tag{13}$$

Note that the structure of Eqs. 12 and 13 is identical to that in Eqs. 4 and 7. This must be so since the situations differ only in their boundary conditions. Analytically, the difference between the two sets of equations, killed and sealed end conditions, appears to be a kind of interchange of sinh's and cosh's. We formalize this interchange of sinh's and cosh's by defining a graph operation called conjugacy which is denoted by an asterisk. (Note that this does not relate in any way to the asterisk in $I^*(s)$.) That is if,

$$[\overset{L}{\text{—}}] = Z_c \sinh\gamma L, \tag{14}$$

then, the conjugate of Eq. 14 is,

$$[\overset{L}{\text{—}}]^* = Z_c \cosh\gamma L. \tag{15}$$

Clearly a natural result of this definition is that

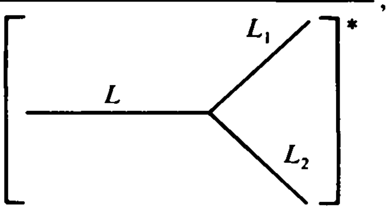
$$[\overset{L}{\text{—}}]^{**} = Z_c \sinh\gamma L, \tag{16}$$

so that Eqs. 12 and 13 may be represented as

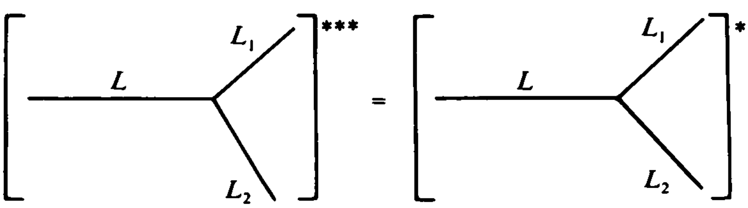
$$V(x,s) = \frac{[\overset{x}{\text{—}}]^* [\overset{L\,-\,D}{\text{———}}]^* I^*(s)}{[\overset{L}{\text{—}}]^{**}} \tag{17}$$

and

$$V(x,s) = \frac{Z_c Z_{c_1} Z_{c_2} [\overset{x}{\text{—}}]^* [\overset{L_2}{\text{—}}]^* [\overset{L_1\,-\,D}{\text{———}}]^* I^*(s)}{[\,\text{graph}\,]^*}, \tag{18}$$



respectively. But again it is a trivial result of the definition of conjugacy that



(19)

so that it appears that sealed end solutions follow from killed end solutions simply by conjugating the graphs an appropriate number of times corresponding to the number of terminal ends which have switched from killed to sealed. For example returning to the simple unbranched system, a cable of length L, assume the end $x = 0$ is killed and the end $x = L$ is sealed. The foregoing suggests that

$$V(x,s) = \frac{[\overset{x}{\text{—}}]\,[\overset{L\,-\,D}{\text{——}}]^{*}\, I^{*}(s)}{[\overset{L}{\text{—}}]^{*}}, \tag{20}$$

or in terms of sinh's and cosh's,

$$V(x,s) = \frac{Z_c \sinh\gamma x \cdot \cosh\gamma(L - D) I^{*}(s)}{\cosh\gamma L}. \tag{21}$$

Referring to Eq. 21 of the Appendix this is indeed the solution. This last example is a hybrid situation, the proximal ($x = 0$) end killed and the peripheral end ($x = L$) sealed. This case is uncommon in our model computer studies. However when it occurs the conjugacy rule must be specified in more detail. The rule generalizes such that if branch i has a boundary condition $Z_{L_i} = \infty$, the solution $V(x,s)$ is obtained from the corresponding solution with $Z_{L_i} = 0$ by interchanging $\sinh\gamma_i L_i$ and $\cosh\gamma_i L_i$.

Dendritic Tree with Soma

For application to neurophysiology it is important to consider boundary conditions which approximate the effects of a soma. The simplest procedure is to represent the soma as a lumped impedance, $Z_0 = 1/(C_0 s + G_0)$ at the proximal boundary of the primary dendritic branch (Jack et al., 1971). In the appendix it is shown that the *structure* of the potential transform $V(x,s)$ is independent of boundary conditions. Therefore by suitably generalizing our graphical notation, the killed end solutions already derived, $Z_0 = 0$, can trivially lead to the more complicated soma boundary condition. An appropriate generalization of Eq. 14 is,

$$[\,\textcircled{Z_0}\overset{L}{\text{—}}] = Z_c \sinh\gamma L + Z_0 \cosh\gamma L, \tag{22}$$

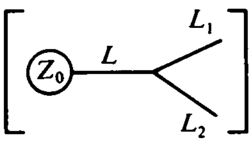
so that the solution corresponding to Eq. 4 is simply,

$$V(x,s) = \frac{[\,\textcircled{Z_0}\overset{x}{\text{—}}]\,[\overset{L\,-\,D}{\text{——}}]\cdot I^{*}(s)}{[\,\textcircled{Z_0}\overset{L}{\text{—}}]}. \tag{23}$$

This further suggests that the solution corresponding to Eq. 5 may be written as,

$$V(x,s) = \frac{Z_c Z_{c_1} Z_{c_2} [\;Z_0\;\;\overset{x}{\text{—}}]\,[\overset{L_1\,-\,D}{\text{——}}]\,[\overset{L_2}{\text{—}}]\, I^{*}(s)}{\left[\;\textcircled{Z_0}\overset{L}{\text{————}}<^{L_1}_{L_2}\;\right]}. \tag{24}$$

The validity of Eq. 24 is shown in the Appendix Eq. 44 where we must define



$$= \left\{ \begin{array}{l} Z_c Z_{c_1}[\,(Z_0)\overset{L}{\text{---}}][\overset{L_1}{\text{---}}][\overset{L_2}{\text{---}}]^* \\ + Z_c Z_{c_2}[\,(Z_0)\overset{L}{\text{---}}][\overset{L_1}{\text{---}}]^*[\overset{L_2}{\text{---}}] \\ + Z_{c_1} Z_{c_2}[\,(Z_0)\overset{L}{\text{---}}]^*[\overset{L_1}{\text{---}}][\overset{L_2}{\text{---}}] \end{array} \right\} \tag{25}$$

and

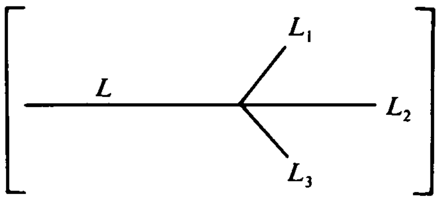
$$[\,(Z_0)\overset{L}{\text{---}}]^* = Z_c \cosh\gamma L + Z_0 \sinh\gamma L \tag{26}$$

is defined as the conjugate of Eq. 22. Note that the definition 25 preserves the natural symmetry of the dendritic system under consideration. That is, L_1 and L_2 may be interchanged in Eq. 25 leaving the result invariant.

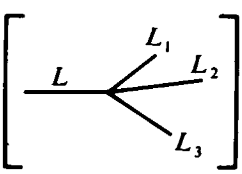
Multiple Branching

Thus far we have considered dendritic systems for which each primary branch of a dendritic tree can give rise to only two secondary branches. However it is possible to generalize our results to systems without such a constraint. Such configurations are considered in a recent paper by Rall and Rinzel (1973). We explicitly consider only the case of a primary dendritic branch with three secondary branches. The extension to further branches (see Fig. 3) being a rather obvious procedure given the results for $n = 2$ and 3. The expression for $V(x,s)$, the membrane potential transform at any point x along the primary branch, is derived in the Appendix. In our graphical notation this is shown to be,

$$V(x,s) = \frac{Z_c Z_{c_1} Z_{c_2} Z_{c_3}[\overset{x}{\text{---}}][\overset{L_1 - D_1}{\text{------}}][\overset{L_2}{\text{---}}][\overset{L_3}{\text{---}}]}{\text{(denominator: diagram below)}}, \tag{27}$$



where we define,



$$= \Pi Z_{c_i} \cdot \left\{ \begin{array}{l} Z_c Z_{c_1} Z_{c_2} \ \sinh\gamma L \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \cosh\gamma_3 L_3 \\ Z_c Z_{c_1} Z_{c_3} \ \sinh\gamma L \sinh\gamma_1 L_1 \cosh\gamma_2 L_2 \sinh\gamma_3 L_3 \\ + Z_c Z_{c_2} Z_{c_3} \ \sinh\gamma L \cosh\gamma_1 L_1 \sinh\gamma_2 L_2 \sinh\gamma_3 L_3 \\ + Z_{c_1} Z_{c_2} Z_{c_3} \cosh\gamma L \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \sinh\gamma_3 L_3 \end{array} \right\}. \tag{28}$$

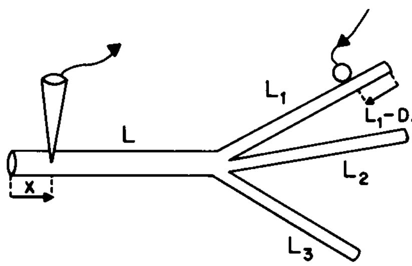


FIGURE 3 A multiply branched dendritic tree showing a recording electrode on the primary branch, and a current input on a secondary branch.

Again we note the cyclical symmetry of the graph definition, the expression remains invariant upon interchange of any pair of branches. The extension of Eq. 28 to the general case of n secondary branches arising from any primary branch is evident. In place of the four terms on the right-hand side of Eq. 28 we have $(n + 1)$ terms each of which is a product of n Z_{c_1} $\sinh\gamma_i L_i$ factors and a single $\cosh\gamma_j L_j$ factor.

DISCUSSION

We have developed a simple graphical calculus by which the investigation of branching dendritic systems may be facilitated. The power of the calculus is such that it allows the determination of membrane potential transients at any point in the dendritic tree for any configuration of synaptic inputs. In particular it incorporates the exhaustive treatment of cable transients by Jack et al. (1971) as a special case. For steady-state considerations it should be noted that the calculus immediately provides the appropriate algebraic solution. This follows since steady-state solutions are obtained from any Laplace transform $F(s)$, from the limit of $sF(S)$, as $s \to 0$, which implies in turn that $\gamma = 1/\lambda$. Thus there is no transform to invert, and the recent results of Rall and Rinzel (1973) on steady states in multiply branched trees can be immediately derived in closed form.

APPENDIX

Voltage transforms are derived for various finite, branched, and unbranched cables.

Finite Leaky Transmission Line

Consider first a cable of length L terminated with impedances $Z_0(s)$ and $Z_L(s)$, with a current source at $x = L$. Let $v(x,t)$ denote transmembrane potential, measured relative to the resting potential v_r. It is well known that the evolution of $v(x,t)$ is described by the cable equation (Rall, 1959):

$$\lambda^2(\partial^2 v/\partial x^2) - v - \tau(\partial v/\partial \tau) = 0, \tag{29}$$

where $\lambda^2 = (RG)^{-1}$, and $\tau = (RC)^{-1}$, and where R, C, and G are, respectively, the core resistance, membrane capacitance, and membrane conductance of the cable. In addition the core current is given by the equation

$$i(x,t) = -(1/R)(\partial v/\partial x). \tag{30}$$

To solve these equations, let $V(x,s)$ and $I(x,s)$ be the Laplace transforms of v and i, respectively. Then for zero initial conditions, Eqs. 29 and 30 become

$$(\mathrm{d}^2 V/\mathrm{d}x^2) - \gamma^2 V = 0, \tag{31}$$

$$(\mathrm{d}V/\mathrm{d}x) + RI = 0 \tag{32}$$

where

$$\gamma = (s\tau + 1)^{1/2}/\lambda. \tag{33}$$

As discussed in numerous textbooks, e.g., Weber (1965), there are two functionally equivalent forms of solution to Eq. 31 or 32. We follow Rall (1959) in the choice of hyperbolic functions as the more suitable for neurophysiological problems, i.e.,

$$V(x,s) = A\cosh\gamma x + B\sinh\gamma x \tag{34}$$

and

$$I(x,s) = -(1/Z_c)[A\sinh\gamma x + B\cosh\gamma x]. \tag{35}$$

where $Z_c = R/\gamma$ is known as the characteristic impedance of the cable. The unknowns $A(s)$ and $B(s)$ are determined from the boundary conditions. We assume a current source, $I^*(s)$, at $x = L$. The boundary conditions are:

$$V(0,s) = -Z_0 I(0,s), \tag{36}$$

$$V(L,s) = Z_L[I(L,s) + I^*(s)]. \tag{37}$$

Substituting 34 and 35 into Eqs. 36 and 37 we obtain

$$A(s) = k_0 B(s) \tag{38}$$

and

$$B(s) = \frac{Z_L I^*(s)}{(k_0 + k_L)\cosh\gamma L + (1 + k_0 k_L)\sinh\gamma L}, \tag{39}$$

where $k_0 = Z_0/Z_c$ and $k_L = Z_L/Z_c$ so that the membrane potential transform $V(x,s)$ may be written as,

$$V(x,s) = \frac{(\sinh\gamma x + k_0\cosh\gamma x)Z_L I^*(s)}{(k_0 + k_L)\cosh\gamma L + (1 + k_o k_L)\sinh\gamma L}. \tag{40}$$

Eq. 40 is a standard, textbook result in the theory of finite transmission lines (Weber, 1965) which we use as a jumping off point for developing a geometric scheme to obtain membrane potentials in branched, dendritic systems.

The current source $I^*(s)$, in the above, is assumed situated at $x = L$. Since a current source is our idealization of a synaptic input, it is important for neurophysiological applications to consider the case when the current source appears at an interior point D of cable (Fig. 1 *a*). This is not a difficult problem, but one that is not usually treated in the transmission line literature. Therefore we display the details of the calculation. The procedure involves two steps. First, since the current source is at $x = D$ consider the solution 40 for a cable of length D. Let the terminal impedances of this cable be Z_0 and Z_D rather than Z_0 and Z_L. Therefore the second step is to calculate Z_D. Z_D represents the original impedance Z_L as well as the impedance due to the remaining length of cable, $L - D$. The structure of Z_D suggests application of an input-output analysis, common in transmission line theory, whereby the line is represented as a four-pole. Thus the first step results in,

$$V(x,s) = \frac{(\sinh\gamma x + k_0 \cosh\gamma x)\cdot Z_D I^*(s)}{(k_0 + k_D)\cosh\gamma D + (1 + k_0 k_D)\sinh\gamma D}, \tag{41}$$

where $k_D = Z_D/Z_c$. The details of the four-pole aspects of a transmission line again may be found in Weber (1965). For a cable of length $L - D$, the result is:

$$\begin{pmatrix} V_D \\ I_D \end{pmatrix} = \begin{pmatrix} \cosh\gamma(L - D) & Z_c \sinh\gamma(L - D) \\ \frac{1}{Z_c}\sinh\gamma(L - D) & \cosh\gamma(L - D) \end{pmatrix} \begin{pmatrix} V_L \\ I_L \end{pmatrix} \tag{42}$$

where $V_D = V(D,s), I_D = I(D,s)$, and $V_L = V(L,s), I_L = I(L,s)$.

But by definition,

$$Z_D = V_D/I_D, Z_L = V_L/I_L, \tag{43}$$

so that trivially,

$$Z_D = Z_c \frac{Z_L \cosh\gamma(L - D) + Z_c \sinh\gamma(L - D)}{Z_L \sinh\gamma(L - D) + Z_c \cosh\gamma(L - D)}. \tag{44}$$

Substituting Eq. 44 into Eq. 41, and using the hyperbolic identities for $\sinh\gamma(D + L - D)$, $\cosh\gamma(D + L - D)$ finally leads to the relatively simple expression,

$$V(x,s) = \frac{(\sinh\gamma x + k_0 \cosh\gamma x)[Z_c \sinh\gamma(L - D) + Z_L \cosh\gamma(L - D)]I^*(s)}{(k_0 + k_L)\cosh\gamma L + (1 + k_0 k_L)\sinh\gamma L}. \tag{45}$$

The interesting aspect of Eq. 45 is that it is similar in structure to that of Eq. 40, the solution for the current source at $x = L$. The two equations differ only in that the factor $[Z_c \sinh\gamma(L - D) + Z_L \cosh\gamma(L - D)]$ in the numerator of Eq. 45 replaces the factor Z_L in the numerator of 40. This similarity is exploited heavily in much of what follows.

To complete the discussion it should be noted that Eq. 45 assumes $x < D$. If $x > D$, it is a straightforward exercise to show that the corresponding result is,

$$V(x,s) =$$

$$\frac{[\sinh\gamma D + k_0\cosh\gamma D][Z_c\sinh\gamma(L - x) + Z_L\cosh\gamma(L - x)]I^*(s)}{(k_0 + k_L)\cosh\gamma L + (1 + k_0k_L)\sinh\gamma L}. \quad (46)$$

Some important special cases of Eq. 45 are: (*a*) $Z_0 = Z_L = 0$, "killed ends," then,

$$V(x,s) = \frac{Z_c\sinh\gamma x\cdot\sinh\gamma(L - D)I^*(s)}{\sinh\gamma L}, \quad (47)$$

(*b*) $Z_0 = Z_L = \infty$, "sealed ends," then,

$$V(x,s) = \frac{Z_c\cosh\gamma x\cdot\cosh\gamma(L - D)I^*(s)}{\sinh\gamma L}, \quad (48)$$

and (*c*) $Z_0 = 0, Z_L = \infty$, then

$$V(x,s) = \frac{Z_c\sinh\gamma x\cdot\cosh\gamma(L - D)I^*(s)}{\cosh\gamma L}. \quad (49)$$

Branching Systems

Of more interest to the neurophysiology of dendritic systems are solutions for branching cables. The simplest such case is the Y-branched structure shown in Fig. 1 *b*. Let the primary branch be of length L and the peripheral branches be of lengths L_1 and L_2. For simplicity assume all terminal impedances are zero; i.e., $Z_0 = Z_{L_1} = Z_{L_2} = 0$. Let a current source transform, $I^*(s)$ be applied at any point D along the primary branch. The membrane potential transform $V(x,s)$, $x < D$, then follows immediately from Eq. 45 where Z_L is now the parallel impedance of the branches of lengths L_1 and L_2. Let Z_1 and Z_2 be the input impedances of the branches of length L_1 and L_2, respectively. Then we must have that,

$$1/Z_L = 1/Z_1 + 1/Z_2, \quad (50)$$

or

$$Z_L = Z_1Z_2/(Z_1 + Z_2). \quad (51)$$

But Z_1 and Z_2 may be determined from an input-output relation similar to Eqs. 42 and 44; i.e.

$$Z_1 = Z_{c_1}\cdot\frac{Z_{c_1}\sinh\gamma_1L_1 + Z_{L_1}\cosh\gamma_1L_1}{Z_{c_1}\cosh\gamma_1L_1 + Z_{L_1}\sinh\gamma_1L_1}, \quad (52)$$

and a similar expression for Z_2. The subscripts, 1, on the right-hand side of Eq. 52 simply serve to distinguish the transmission parameters of the branch of length L_1 from those of the primary branch of length L. Now since we are considering the simplest case, $Z_{L_1} = Z_{L_2} = 0$, substituting for Z_1 and Z_2 in Eq. 51 results in,

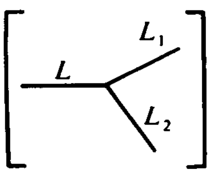
$$Z_L = \frac{Z_{c_1} Z_{c_2} \sinh\gamma_1 L_1 \sinh\gamma_2 L_2}{Z_{c_1} \sinh\gamma_1 L_1 \cosh\gamma_2 L_2 + Z_{c_2} \sinh\gamma_2 L_2 \cosh\gamma_1 L_1}. \tag{53}$$

Substituting the above value for Z_L and setting $Z_0 = 0$ in Eq. 45 finally leads to,

$$V(x,s) = \frac{Z_c \sinh\gamma x \left\{\begin{array}{ll} Z_c Z_{c_1} & \sinh\gamma(L - D) \sinh\gamma_1 L_1 \cosh\gamma_2 L_2 \\ + Z_c Z_{c_2} & \sinh\gamma(L - D) \cosh\gamma_1 L_1 \sinh\gamma_2 L_2 \\ + Z_{c_1} Z_{c_2} & \cosh\gamma(L - D) \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \end{array}\right\} I^*(s)}{\left\{\begin{array}{ll} Z_c Z_{c_1} & \sinh\gamma L \sinh\gamma_1 L_1 \cosh\gamma_2 L_2 \\ + Z_c Z_{c_2} & \sinh\gamma L \cosh\gamma_1 L_1 \sinh\gamma_2 L_2 \\ + Z_{c_1} Z_{c_2} & \cosh\gamma L \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \end{array}\right\}}. \tag{54}$$

It is apparent from Eq. 54 that analytic expressions for branched structures are complicated. Recall that this is the simplest case.

However if one looks closely at Eq. 54 there is some symmetry one can take advantage of to reduce most of the complexity. In the denominator of 54 there is a symmetry whereby L, L_1, L_2, and their respective subscripts may be interchanged without changing the result. The same is true of the term in parenthesis in the numerator except that in this case the parameters are $(L - D)$, L_1, and L_2. This invariance suggests a geometric notation which we can exploit. There are two topological structures which display the invariance of interest, a triangle and a "Y". We choose the latter for the obvious reason that it looks more like the physical geometry of the cables. Thus we propose a notation such that,

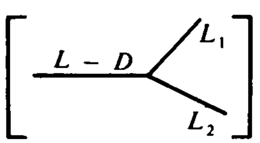
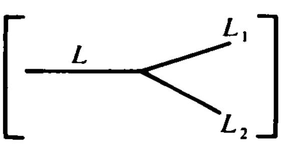


$$= Z_c Z_{c_1} Z_{c_2} \cdot \left\{\begin{array}{l} Z_c Z_{c_1} \sinh\gamma L \cdot \sinh\gamma_1 L_1 \cdot \cosh\gamma_2 L_2 \\ + Z_c Z_{c_2} \sinh\gamma L \cdot \cosh\gamma_1 L_1 \cdot \sinh\gamma_2 L_2 \\ + Z_{c_1} Z_{c_2} \cosh\gamma L \cdot \sinh\gamma_1 L_1 \cdot \sinh\gamma_2 L_2 \end{array}\right\}. \tag{55}$$

Further, let

$$[\stackrel{x}{\text{—}}] = Z_c \sinh\gamma x, \tag{56}$$

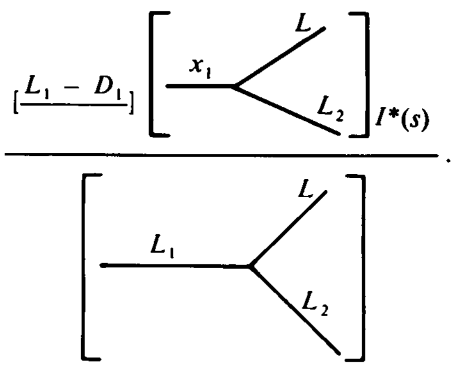
then Eq. 54 may be rewritten as,

$V(x,s) = [\stackrel{x}{\text{—}}] \cdot$  $I^*(s)$ divided by  . (57)

The factor, $Z_c Z_{c_1} Z_{c_2}$, in Eq. 55 appears in both the numerator and denominator of Eq. 57, thereby canceling out. Thus the inclusion of this factor in Eq. 55 is apparently artificial. However the reason for doing so is motivated by systems with more general boundary conditions than the simple ones considered here. These systems are discussed later.

Representing Eq. 54 by Eq. 57 is a trivial exercise. The important idea that we wish to discuss in this paper is that one can perform the same sort of trivial manipulation for *any* dendritic system. In this context the exercise becomes a powerful tool. In order to get some intuition for this statement we consider some further examples.

Similar to the above problem is one in which the current source transform, $I^*(s)$, appears at a point D_1 along the peripheral branch of length L_1 rather than on the primary branch. Let $V(x,s)$ and $V_1(x_1,s)$ be the potential transforms along the primary and the peripheral branches of length L and length L_1, respectively. We have that $0 \leq x \leq L$ and $0 \leq x_1 \leq L_1$. Assume x_1 is measured from the branch point. An expression for $V_1(x_1,s)$ follows immediately from the previous example by simply interchanging what is designated as "primary" and "peripheral"; i.e., L and L_1. Therefore,

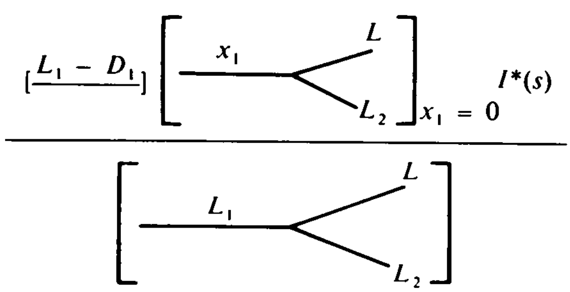
$V_1(x_1,s) =$ 

. (58)

To obtain $V(x,s)$ requires further consideration since we now are asking for the potential transform on a branch *different* from that with the current source transform. Quite generally we know that $V(x,s)$ is of the form of Eq. 34, i.e., $V(x,s) = A \cosh\gamma x + B \sinh\gamma x$, so that it is necessary to determine again the coefficients A and B. These follow from two constraints, the assumed boundary condition, $Z_0 = 0$ and a continuity condition,

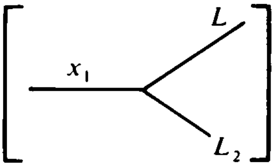
$$V(L,s) = V_1(0,s). \tag{59}$$

The boundary condition $Z_0 = 0$ implies $A = 0$, and the continuity condition results in,

$B \sinh\gamma L =$ 

. (60)

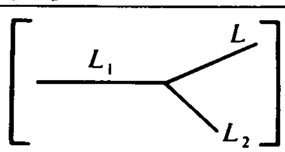
However by definition 55,



$$_{x_1=0} = Z_c^2 Z_{c_1} Z_{c_2}^2 \sinh\gamma L \sinh\gamma_2 L_2. \tag{61}$$

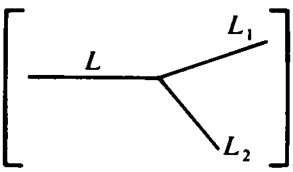
Therefore,

$$B = \frac{Z_c^2 Z_{c_1} Z_{c_2}^2 \sinh\gamma_2 L_2 \left[\overset{L_1 - D_1}{\text{———}}\right] I^*(s)}{\text{(diagram below)}}. \tag{62}$$



Substituting Eq. 62 in the relation $V(x,s) = B \sinh\gamma x$ as well as the definition 56 results in,

$$V(x,s) = \frac{Z_c Z_{c_1} Z_{c_2} \left[\overset{x}{\text{—}}\right] \left[\overset{L_2}{\text{—}}\right] \left[\overset{L_1 - D_1}{\text{———}}\right] I^*(s)}{\text{(diagram below)}}. \tag{63}$$



Note that in going from 62 to 63 we have interchanged L and L_1 in the denominator. As discussed earlier the result is invariant under this operation. The reason for choosing this orientation is simply to emphasize the similarity in solutions for this example and the previous one, Eq. 57.

The striking feature of the solutions 57 and 63 is that the denominators display a symmetry corresponding to the topology of the original, physical dendritic system. The location of the current source transform, $I^*(s)$ affects only the numerators of Eqs. 57 and 63. Remarkably however, the location of the current source transform affects the numerator in a systematic manner. This observation is one of the major features of our paper. Anticipating a proof of the general case derived in a later section we now state the rule, or operation, from which numerators may be constructed. There are two parts to this rule, one corresponding to determining the geometric structures in the numerator of the membrane potential transform, the other corresponding to determining an algebraic factor, a product of characteristic impedances, Z_{c_i}.

Deletion Rule: For any dendritic tree delete the direct path *from* the point at which the membrane potential is desired *to* the location of the current source. This deletion in general dismembers the dendritic tree. Then (*a*) the geometric structure of the numerator simply corresponds to the product of the resulting disjoint sets of dendritic branches; and (*b*) for each bifurcation point deleted there appears an algebraic product of three characteristic impedances in the numerator. If the bifurcation point is the junction of branches of length L_i, L_j, L_k the product is $Z_{c_i} Z_{c_j} Z_{c_k}$.

Thus far we have been assuming rather simple boundary conditions, $Z_0 = Z_{L_1} = Z_{L_2} = 0$. To indicate that the proposed reduction technique is independent of boundary constraints we consider again the first branching problem with arbitrary Z_0, Z_{L_1}, and Z_{L_2}. Then $V(x,s)$ is determined by a procedure analagous to that in Eqs. 50–54. The computational burden in these equations stems from the expressions for Z_1 and Z_2. Therefore we introduce a more general geometric notation to circumvent this problem. Let,

$$\left[\overset{L_1}{\text{—}} Z_{L_1}\right] = Z_{c_1}\sinh\gamma_1 L_1 + Z_{L_1}\cosh\gamma_1 L_1 \tag{64}$$

and

$$\left[\overset{L_1}{\text{—}} Z_{L_1}\right]^* = Z_{c_1}\cosh\gamma_1 L_1 + Z_{L_1}\sinh\gamma_1 L_1, \tag{65}$$

so that Eq. 52 may be rewritten as

$$Z_1 = Z_{c_1}\frac{\left[\overset{L_1}{\text{—}} Z_{L_1}\right]}{\left[\overset{L_1}{\text{—}} Z_{L_1}\right]^*} \tag{66}$$

with a similar representation for Z_2. We refer to Eq. 65 as the "conjugate" graph of 64. The conjugacy operation is simply an interchange of sinh's and cosh's. Then corresponding to Eq. 53 for Z_L we have that,

$$Z_L = \frac{\left[Z_{c_1}Z_{c_2}\overset{L_1}{\text{—}} Z_{L_1}\right]\left[\overset{L_2}{\text{—}} Z_{L_2}\right]}{Z_{c_1}\left[\overset{L_1}{\text{—}} Z_{L_1}\right]\left[\overset{L_2}{\text{—}} Z_{L_2}\right]^* + Z_{c_2}\left[\overset{L_2}{\text{—}} Z_{L_2}\right]\left[\overset{L_1}{\text{—}} Z_{L_1}\right]^*}. \tag{67}$$

Eq. 67 must then be used to substitute for Z_L in Eq. 45. This latter equation we can rewrite in a more suggestive form. Multiply the numerator and denominator on the right-hand side of Eq. 45 by Z_c^2. Then a rearrangement of the terms in the denominator results in,

$$V(x,s) = \frac{Z_c[Z_c\sinh\gamma x + Z_0\cosh\gamma x]\,[Z_c\sinh\gamma(L - D) + Z_L\cosh\gamma(L - D)]I^*(s)}{Z_c[Z_c\sinh\gamma L + Z_0\cosh\gamma L] + Z_L[Z_c\cosh\gamma L + Z_0\sinh\gamma]}. \tag{68}$$

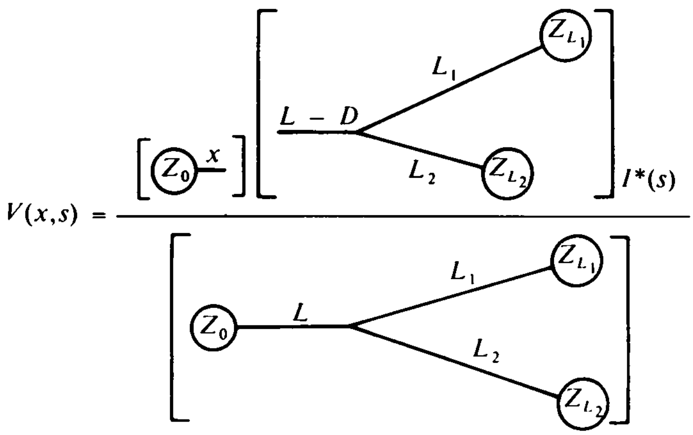
The structure of Eq. 68 suggests that we let,

$$\left[Z_0 \overset{L}{\text{—}}\right] = Z_c\sinh\gamma L + Z_0\cosh\gamma L \tag{69}$$

with the conjugate,

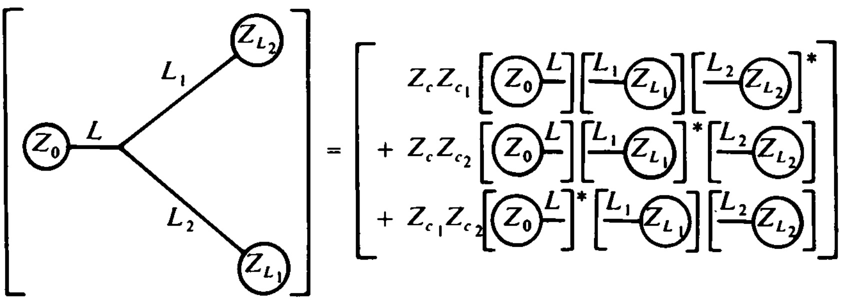
$$\left[\textcircled{\scriptsize Z_0}\overset{L}{\text{—}}\right]^* = Z_c \cosh\gamma L + Z_0 \sinh\gamma L. \tag{70}$$

Note that this notation is consistent with that of Eq. 63; we have simply inverted the left-right orientation to correspond to the underlying physical cable structure. Then substituting Eqs. 67, 69, and 70 into 68 leads to a result in which the full topological symmetry of the cable structure is exploited, i.e.,



(71)

where we have defined,



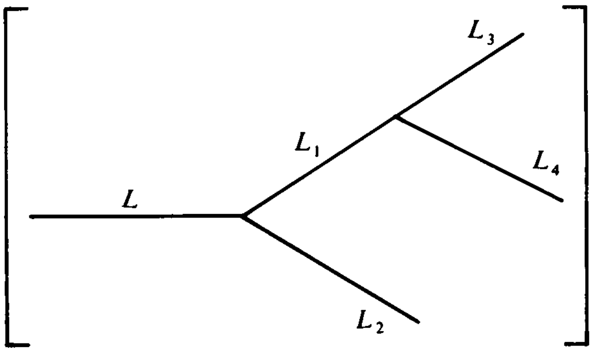
(72)

Note that Eq. 72 displays the same symmetry as Eq. 55, to which 72 reduces when $Z_0 = Z_{L_1} = Z_{L_2} = 0$. That is L, L_1, and L_2 may be interchanged in Eq. 72 leaving the result invariant. Thus it appears that the geometric formalism we are introducing is independent of boundary conditions.

Higher Order Branching

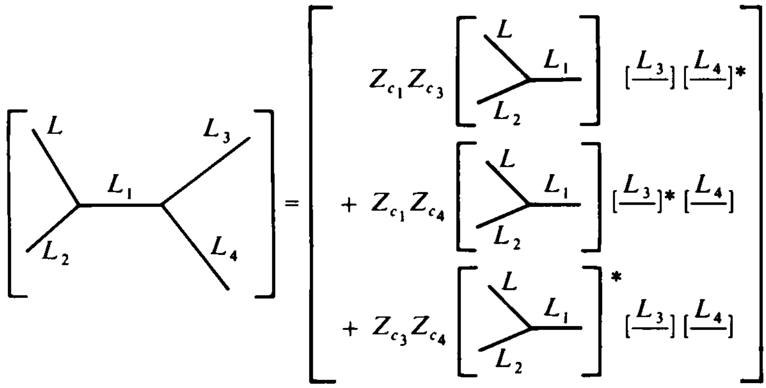
In the preceding we have simply considered a system with one branch junction or bifurcation point. Here we consider an example with two such points. The generalization to more complex structures will be apparent.

Assume a dendritic system with primary branch of length L bifurcating into branches of length L_1 and L_2. Let L_1 further bifurcate into branches of length L_3 and L_4. For simplicity assume all terminal impedances are zero, i.e., $Z_0 = Z_{L_2} = Z_{L_3} = Z_{L_4} = 0$. The membrane potential transform at any point in the dendritic tree for any placement of the current source is a quotient. The numerator in this quotient we can obtain rapidly in our geometric notation using the deletion operation discussed earlier. The denominator in our notation is simply a structure topologically isomorphic to the physical dendritic system which in this case is,



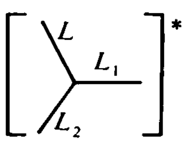
(73)

The difficulty in diagram 73 is to relate it to some already known geometric structures, e.g., Eq. 55 and 56. The reduction procedure is quite trivial. We simply consider the branches of length L and L_2 as a terminal load on the branch of length L_1. That is for the moment we consider the original five-branched dendritic structure reduced to three branches of lengths L_1, L_3, and L_4, with L_1 having some terminal impedance. Then definition 72 is applicable, i.e.,



(74)

where

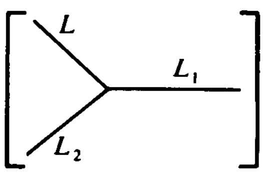


$$= Z_c Z_{c_1} Z_{c_2} \left[\begin{array}{l} Z_{c_1} Z_{c_2} \cosh\gamma_1 L_1 \cdot \cosh\gamma_2 L_2 \cdot \sinh\gamma L \\ +\ Z_{c_1} Z_c \cosh\gamma_1 L_1 \cdot \sinh\gamma_2 L_2 \cdot \cosh\gamma L \\ +\ Z_c Z_{c_2} \sinh\gamma_1 L_1 \cdot \cosh\gamma_2 L_2 \cdot \cosh\gamma L \end{array} \right] . \quad (75)$$

Eq. 75 is simply the conjugate of 55, and is constructed by an interchange of sinh's and cosh's. It is apparent then that there is a simple reduction procedure for expressing any such denominator in terms of known structures and ultimately in terms of sinh's and cosh's. However there is a more elegant procedure which again appeals to the given symmetry of the dentritic geometry. Multiply the first two terms on the right of Eq. 74 by Z_{c_1} $\sinh\gamma_1 L_1$ and the third term by Z_{c_1} $\cosh\gamma_1 L_1$. Then if one considers the terms in Eqs. 55 and 75 one observes that if the following commutative operation, ⊗, is defined:

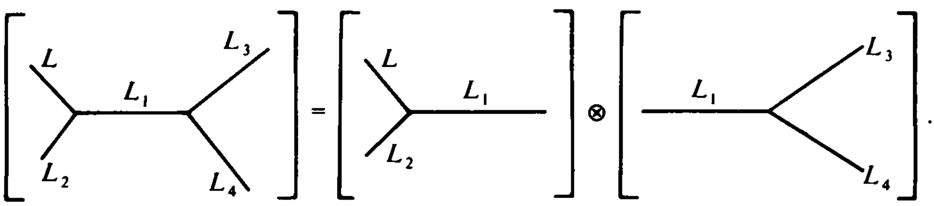
$$\begin{aligned} Z_{c_1}\sinh\gamma_1 L_1 \otimes Z_{c_1}\sinh\gamma_1 L_1 &\rightarrow Z_{c_1}\sinh\gamma_1 L_1 \\ Z_{c_1}\cosh\gamma_1 L_1 \otimes Z_{c_1}\cosh\gamma_1 L_1 &\rightarrow Z_{c_1}\sinh\gamma_1 L_1 \\ Z_{c_1}\cosh\gamma_1 L_1 \otimes Z_{c_1}\sinh\gamma_1 L_1 &\rightarrow Z_{c_1}\cosh\gamma_1 L_1 \end{aligned} \tag{76}$$

then it may be verified that the right-hand side of Eq. 74 may be rewritten as,



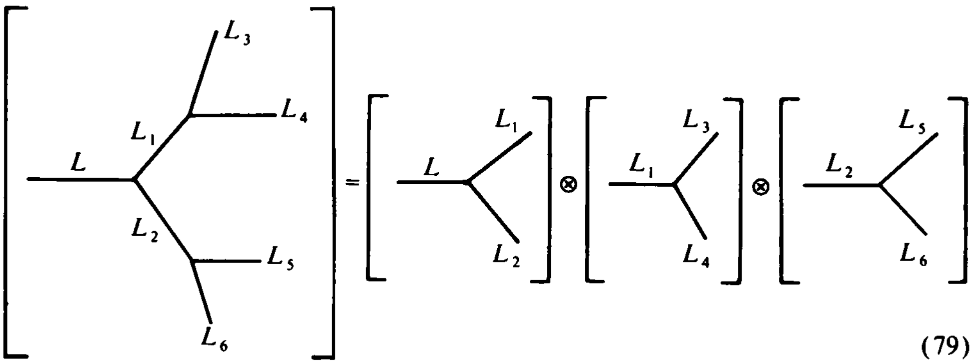
$$\otimes \begin{bmatrix} Z_{c_1}Z_{c_3}[\underline{\;L_1\;}]\,[\underline{\;L_3\;}]\,[\underline{\;L_4\;}]^* \\ +\, Z_{c_1}Z_{c_4}[\underline{\;L_1\;}]\,[\underline{\;L_3\;}]^*\,[\underline{\;L_4\;}] \\ +\, Z_{c_3}Z_{c_4}[\underline{\;L_1\;}]^*\,[\underline{\;L_3\;}]\,[\underline{\;L_4\;}] \end{bmatrix}. \tag{77}$$

But the term in parenthesis in expression 77 is simply definition 55 with parameters L_1, L_3, L_4 instead of L, L_1, L_2. Therefore using definition 55 and the operation, ⊗, we finally obtain that



(78)

The important advantage of Eq. 78 over 74 is that all the symmetries of the resulting sinh-cosh expansion are immediately displayed. In particular the invariance of replacing L and L_2 by L_3 and L_4, respectively, is an immediate consequence of the commutativity of the operator ⊗. However besides this aesthetic aspect there are as well computational advantages to the more sophisticated reduction. Consider that each of our graphs represents a sum of products of sinh's and cosh's. Each such product contains a factor $\sinh\gamma_i L_i$ or $\cosh\gamma_i L_i$ for every branch i in the graph. The enormity of the task may be appreciated by considering the simplest case in which all terminal impedances are set equal to zero. In this case it is not difficult to show that the number of terms in the summation is equal to the cube of the number of bifurcation points. Thus for example if there are two complete levels of branching, i.e. a dendritic tree with seven branches and three bifurcation points, we have 27 terms in the summation. Further each of these terms is the product of seven hyperbolic functions. On the other hand Eq. 78 leads to the decomposition

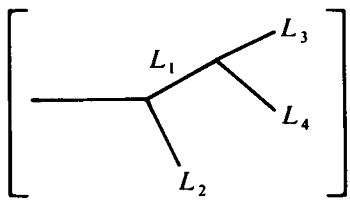


(79)

There are three factors, each of which is the sum of three terms, each of which is a product of three hyperbolic functions. Since the operator $\otimes$ may be easily programmed using logical variables on a computer, one can completely avoid having to deal with the full analytic expansion.

Returning to the dendritic tree with five branches, our discussion indicates that if $V(x,s)$ is the membrane potential transform at a point x along the primary branch of length L and if a current source transform is applied at a point D_3 along the branch of length L_3, then

$$V(x,s) = \pi_\alpha \left[\frac{x}{\;}\right]\left[\frac{L_2}{\;}\right]\left[\frac{L_4}{\;}\right]\left[\frac{L_3 - D_3}{\;}\right] \Big/ \quad (80)$$



where

$$\pi_\alpha = Z_c Z_{c_1}^2 Z_{c_2} Z_{c_3} Z_{c_4}. \quad (81)$$

Sealed Ends

For applications to neurophysiology it is more interesting to consider the boundary conditions $Z_{L_i} = \infty$ rather than $Z_{L_i} = 0$. The condition $Z_{L_j} = \infty$ corresponds to Rall's (1959) sealed end solutions. We have already discussed the fact that the structure of $V(x,s)$ is independent of boundary conditions. That is, by a suitable graphical notation, solutions for arbitrary boundary conditions have essentially the same form as those with boundary conditions $Z_{L_i} = 0$, killed ends. However for the special case where $Z_{L_i} = \infty$, sealed ends, the explicit solution, i.e. the function of hyperbolic sines and cosines, may be trivially obtained from the corresponding killed end solution. The procedure is simply to interchange all sinh's and cosh's to get sealed end solutions from killed end solutions.

The explanation for this procedure may be traced to the impedances Z_1 and Z_2 (in the simple case of two peripheral branches) given by Eq. 52. In general, the load impedance Z_i due to the ith branch is,

$$Z_i = Z_{c_i} \cdot \frac{Z_{c_i} \sinh\gamma_i L_i + Z_{L_i} \cosh\gamma_i L_i}{Z_{c_i} \cosh\gamma_i L_i + Z_{L_i} \sinh\gamma_i L_i}. \quad (82)$$

Therefore if the terminal impedance $Z_{L_i} = 0$,

$$Z_i = Z_{c_i}\frac{\sinh\gamma_i L_i}{\cosh\gamma_i L_i}, \tag{83}$$

and if $Z_{L_i} = \infty$,

$$Z_i = Z_{c_i}\frac{\cosh\gamma_i L_i}{\sinh\gamma_i L_i}. \tag{84}$$

It is apparent that Eq. 84 follows from Eq. 83 by a simple interchange of sinh's and cosh's. Since the boundary condition Z_{L_i} enters the solution for $V(x,s)$ only through the branch impedance Z_i the simple conjugacy rule follows: if the solution $V(x,s)$ is known for the boundary condition $Z_{L_i} = 0$, then the solution for $V(x,s)$ with $Z_{L_i} = \infty$ follows by replacing "$\sinh\gamma_i L_i$ with $\cosh\gamma_i L_i$" and "$\cosh\gamma_i L_i$ with $\sinh\gamma_i L_i$." In model experiments on the computer we normally do not consider hybrid boundary conditions, i.e., some terminals sealed, some killed. Thus in the homogeneous case, where *all* branches have $Z_{L_i} = \infty$, the conjugacy rule is stated as *all* sinh's and cosh's are interchanged to derive the sealed end solution from the killed end one. To illustrate, consider Eq. 67 with $Z_{L_1} = Z_{L_2} = \infty$. In this case Z_L becomes,

$$Z_L = \frac{Z_{c_1}Z_{c_2}\cosh\gamma_1 L_1\cosh\gamma_2 L_2}{Z_{c_1}\cosh\gamma_1 L_1\sinh\gamma_2 L_2 + Z_{c_2}\cosh\gamma_2 L_2\sinh\gamma_1 L_1}. \tag{85}$$

The solution $V(x,s)$ for the three-branched dendritic system with the current source on the primary branch is then obtained by substituting Eq. 85 in Eq. 45. If we assume $Z_0 = 0$, the result may be shown to be

$$V(x,s) = \frac{Z_c\sinh\gamma x\begin{Bmatrix} Z_cZ_{c_1}\sinh\gamma(L-D)\cosh\gamma_1 L_1\sinh\gamma_2 L_2 \\ +\,Z_cZ_{c_2}\sinh\gamma(L-D)\sinh\gamma_1 L_1\cosh\gamma_2 L_2 \\ +\,Z_{c_1}Z_{c_2}\cosh\gamma(L-D)\cosh\gamma_1 L_1\cosh\gamma_2 L_2\end{Bmatrix} I^*(s)}{\begin{Bmatrix} Z_cZ_{c_1}\sinh\gamma L\cosh\gamma_1 L_1\sinh\gamma_2 L_2 \\ +\,Z_cZ_{c_2}\sinh\gamma L\sinh\gamma_1 L_1\cosh\gamma_2 L_2 \\ +\,Z_{c_1}Z_{c_2}\cosh\gamma L\cosh\gamma_1 L_1\cosh\gamma_2 L_2\end{Bmatrix}}, \tag{86}$$

and if we assume the homogeneous case where $Z_0 = \infty$, the result is,

$$V(x,s) = \frac{Z_c\cosh\gamma x\begin{Bmatrix} Z_cZ_{c_1}\sinh\gamma(L-D)\cosh\gamma_1 L_1\sinh\gamma_2 L_2 \\ +\,Z_cZ_{c_2}\sinh\gamma(L-D)\sinh\gamma_1 L_1\cosh\gamma_2 L_2 \\ +\,Z_{c_1}Z_{c_2}\cosh\gamma(L-D)\cosh\gamma_1 L_1\cosh\gamma_2 L_2\end{Bmatrix} I^*(s)}{\begin{Bmatrix} Z_cZ_{c_1}\cosh\gamma L\cosh\gamma_1 L_1\sinh\gamma_2 L_2 \\ +\,Z_cZ_{c_2}\cosh\gamma L\sinh\gamma_1 L_1\cosh\gamma_2 L_2 \\ +\,Z_{c_1}Z_{c_2}\sinh\gamma L\cosh\gamma_1 L_1\cosh\gamma_2 L_2\end{Bmatrix}}. \tag{87}$$

Observe that Eq. 86 is symmetric in L_1 and L_2 as it should be. However whereas the denominator in Eq. 87 is symmetric in L, L_1, and L_2, the numerator is symmetric in only L_1 and L_2.

In terms of the conjugacy rule, this asymmetry results since the branch of length $(L - D)$ does not in effect have a terminal impedance equal to infinity.

Multiple Branching

The development of membrane potential transforms for dendritic systems with multiple branching parallels the derivation given for systems with binary branching. Firstly, a solution is computed for the case when the intracellular recording electrode and the current input are along the same branch and then this expression is applied to the case when electrode and current input are on separate branches.

As before we assume for simplicity that all terminal impedances are identically equal to zero so that for the first part of the problem Eq. 45 is applicable with $k_0 = 0$. Then Z_L is determined by a relationship analogous to Eq. 41

$$\frac{1}{Z_L} = \frac{1}{Z_1} + \frac{1}{Z_2} + \frac{1}{Z_3}, \tag{88}$$

or

$$Z_L = \frac{Z_1 Z_2 Z_3}{Z_1 Z_2 + Z_2 Z_3 + Z_3 Z_1}, \tag{89}$$

where Z_1, Z_2, Z_3 are given by expressions similar to Eq. 52. For the special case of zero terminal impedances,

$$Z_j = Z_{c_j} \frac{\sinh \gamma_j L_j}{\cosh \gamma_j L_j}, \tag{90}$$

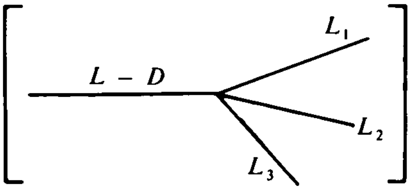
so that substituting into Eq. 82

$$Z_L = \frac{Z_{c_1} Z_{c_2} Z_{c_3} \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \sinh\gamma_3 L_3}{\begin{bmatrix} Z_{c_1} Z_{c_2} \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \cosh\gamma_3 L_3 \\ + Z_{c_2} Z_{c_3} \cosh\gamma_1 L_1 \sinh\gamma_2 L_2 \sinh\gamma_3 L_3 \\ + Z_{c_1} Z_{c_3} \sinh\gamma_1 L_1 \cosh\gamma_2 L_2 \sinh\gamma_3 L_3 \end{bmatrix}}. \tag{91}$$

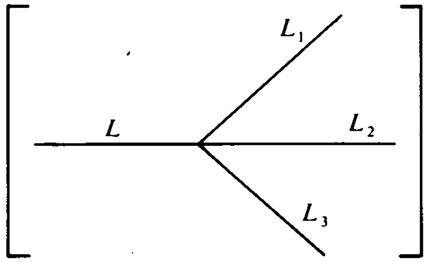
Substituting this expression for Z_L in Eq. 45 results in,

$$V(x,s) = Z_c \sinh\gamma x \frac{\begin{bmatrix} Z_c Z_{c_1} Z_{c_3} \sinh\gamma(L-D) \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \cosh\gamma_3 L_3 \\ + Z_c Z_{c_1} Z_{c_3} \sinh\gamma(L-D) \sinh\gamma_1 L_1 \cosh\gamma_2 L_2 \sinh\gamma_3 L_3 \\ + Z_c Z_{c_2} Z_{c_3} \sinh\gamma(L-D) \cosh\gamma_1 L_1 \sinh\gamma_2 L_2 \sinh\gamma_3 L_3 \\ + Z_{c_1} Z_{c_2} Z_{c_3} \cosh\gamma(L-D) \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \sinh\gamma_3 L_3 \end{bmatrix} I^*(s)}{\begin{bmatrix} Z_c Z_{c_1} Z_{c_2} \sinh\gamma L \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \cosh\gamma_3 L_3 \\ + Z_c Z_{c_1} Z_{c_3} \sinh\gamma L \sinh\gamma_1 L_1 \cosh\gamma_2 L_2 \sinh\gamma_3 L_3 \\ + Z_c Z_{c_2} Z_{c_3} \sinh\gamma L \cosh\gamma_1 L_1 \sinh\gamma_2 L_2 \sinh\gamma_3 L_3 \\ + Z_{c_1} Z_{c_2} Z_{c_3} \cosh\gamma L \sinh\gamma_1 L_1 \sinh\gamma_2 L_2 \sinh\gamma_3 L_3 \end{bmatrix}}, \tag{92}$$

or applying a graph definition analogous to Eq. 55 we have,

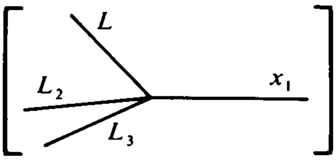
$V(x,s) =$ $\left[\frac{x}{\ }\right]$ 

$I^*(s)$

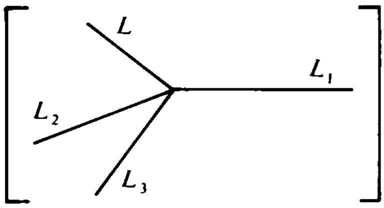


(93)

This expression is the membrane potential transform when recording electrode and current input are on the same branch. To consider the more general case when they are on different branches, for example the current input at some point D_1 along the branch of length L_1, we again have a boundary value problem characterized by the condition 59. Therefore $V(x,s)$ must be of the form $B \sinh\gamma x$. It then remains to determine the unknown B which is accessible once we have $V_1(x_1,s)$. But the latter is simply a form of Eq. 93; i.e.,

$V_1(x_1,s) =$ $\left[\frac{L_1 - D_1}{\ }\right]$ 

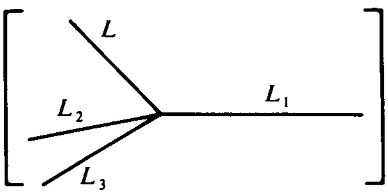
$I^*(s)$



(94)

Letting x_1 approach zero and substituting in Eq. 59 yields,

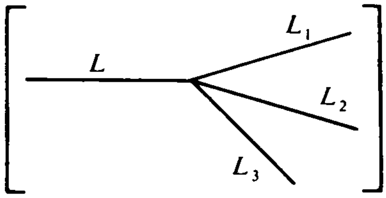
$B \sinh\gamma L =$ $Z_c Z_{c_1} Z_{c_2} Z_{c_3} \left[\frac{L_1 - D_1}{\ }\right]\left[\frac{L}{\ }\right]\left[\frac{L_2}{\ }\right]\left[\frac{L_3}{\ }\right] I^*(s)$



(95)

The resulting expression for B is then substituted into Eq. 56 to yield the desired result

$$V(x,s) = \frac{Z_c Z_{c_1} Z_{c_2} Z_{c_3} \left[\frac{x}{\ }\right] \left[\frac{L_1 - D_1}{\ }\right] \left[\frac{L_2}{\ }\right] \left[\frac{L_3}{\ }\right] I^*(s)}{\left[\quad\right]}. \qquad (96)$$



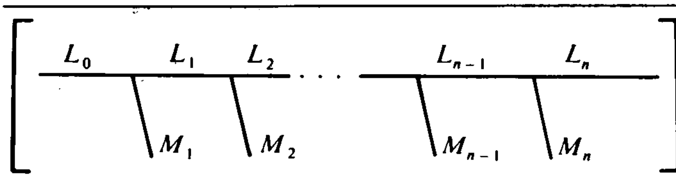
Theorem

On a dendritic tree of arbitrary geometry the membrane potential transform $V(x,s)$ at a point x on any branch due to a current source transform $I^*(s)$ at a point D the same or any other branch of the tree is a quotient. The numerator and denominator of this quotient are expressions involving sums and products of the hyperbolic trigonometric functions sinh and cosh. Then there exists a geometric notation whereby the denominator is represented by a graph structure topologically isomorphic to the physical dendritic tree and the numerator is given by the following deletion rule: For any dendritic tree delete the direct path *from* the point x at which the membrane potential is desired *to* the location D of the current source. This deletion dismembers the dendritic tree into disjoint connected sets. Then (a) the geometric notation of the numerator simply corresponds to a product of structures topologically isomorphic to the resulting disjoint sets of connected dendritic branches; and (b) for each bifurcation point deleted in the tree there corresponds an algebraic product of three characteristic impedances in the numerator. If the bifurcation point is the junction of branches labelled i, j, k, the product is $Z_{c_i} Z_{c_j} Z_{c_k}$.

Proof

We prove the theorem for the dendritic configuration of Fig. 4 where the membrane potential transform $V(x,s)$ is desired at a point n levels, or generations, of branching removed from the current source transform $I^*(s)$. There is no loss of generality in considering this special case. Additional branching simply corresponds to altering the terminal impedances of the dendritic tree of Fig. 4 a. We have demonstrated in Eq. 71 that the geometric symmetries which motivate the graph structures are independent of boundary conditions. Therefore the general case follows if, for the dendritic system illustrated in Fig. 4 a, the membrane potential transform $V(x,s)$ is given by,

$$V(x,s) = \frac{(Z_{c_0}/Z_{c_n}) \left[\frac{x}{\ }\right] \left[\frac{D}{\ }\right] \prod_{k=1}^{n-1} Z^2_{c_k} Z'_{c_k} \left[\frac{M_k}{\ }\right] I^*(s)}{\left[\quad\right]}. \qquad (97)$$



The proof is by simple induction. The theorem has already been demonstrated for one level of

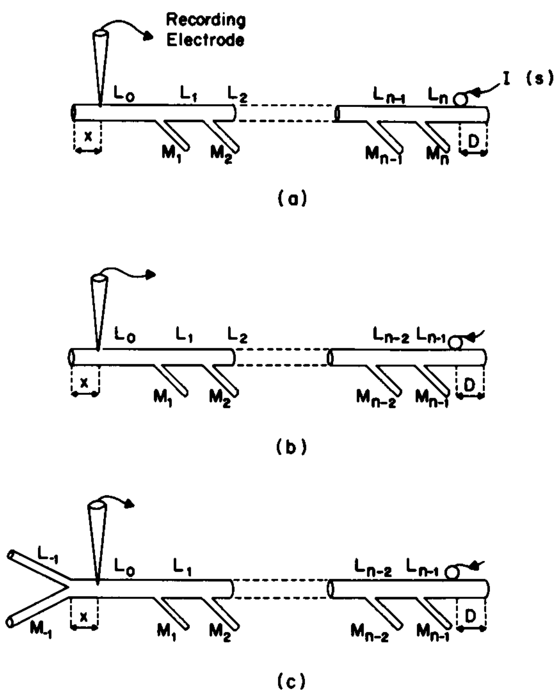
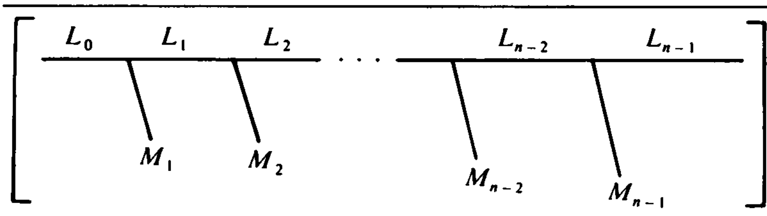


FIGURE 4 The general dendritic tree: recording electrode on the primary branch; current input on a terminal branch.

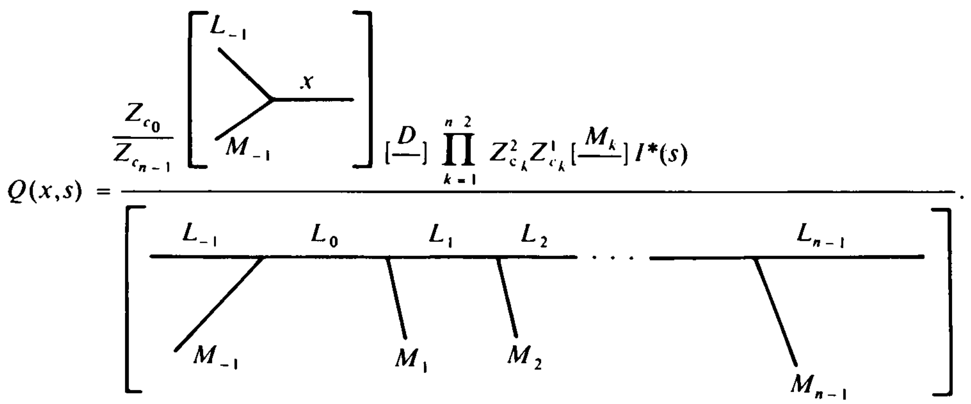
branching, Eq. 71. Therefore we assume it to be true for $n - 1$ levels of branching and use this result to derive the theorem for n levels of branching. Assume then that the membrane potential transform $P(x,s)$ for a system of $n - 1$ levels of branching (Fig. 4 *b*) is given by

$$P(x,s) = \frac{(Z_{c_0}/Z_{c_{n-1}})\left[\frac{x}{\;}\right]\left[\frac{D}{\;}\right]\prod_{k=1}^{n-2} Z_{c_k}^2 Z'_{c_k}\left[\frac{M_k}{\;}\right] I^*(s)}{\left[\;\cdot\;\right]}. \tag{98}$$



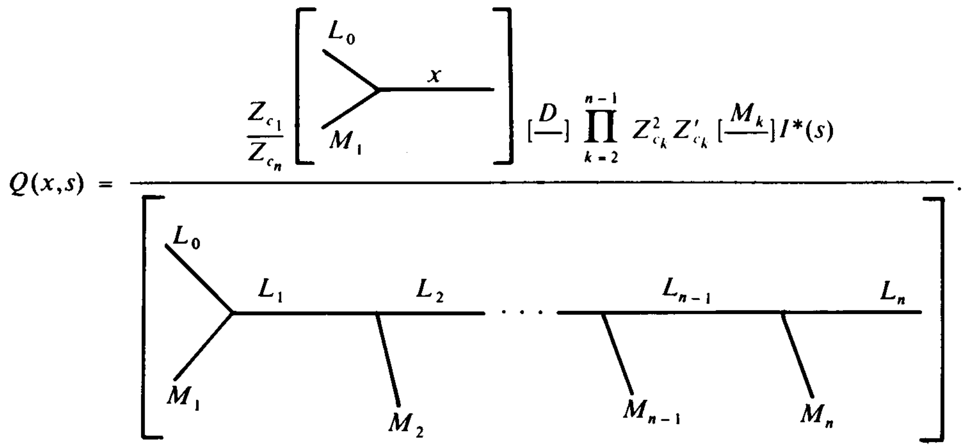
(98)

However $P(x,s)$ is simply a special case of the solution $Q(x,s)$ corresponding to the more general system shown in Fig. 4 *c*. In Fig. 4 *c* the terminal impedance of the branch of length L_0 represents the parallel impedances of the branches of lengths L_{-1} and M_{-1}. Then by the discussion leading to Eq. 71, on the independence of the geometric symmetry on the boundary conditions, $Q(x,s)$ may be represented as,



(99)

Since the dendritic tree of Fig. 4 *c* has *n* levels of branching, relabel the branch lengths and characteristic impedances to correspond to Fig. 4 *a*; i.e., $L_k \rightarrow L_{k+1}$, $M_k \rightarrow M_{k+1}$, $Z_{c_k} \rightarrow Z_{c_{k+1}}$, $Z'_{c_k} \rightarrow Z'_{c_{k+1}}$. Therefore $Q(x,s)$ may be rewritten as,



(100)

In this form $Q(x,s)$ may be interpreted as the membrane potential transform at any point x along the branch of length L_1 in the dendritic system of Figure 4 *a*. Since we wish to determine $V(x,s)$, the membrane potential transform at any point x along the branch of length L_0, we must have the continuity condition

$$V(L,s) = Q(0,s). \tag{101}$$

But $V(x,s)$ is the solution of a partial differential equation of the form of Eq. 29 and thus must be of the form

$$V(x,s) = A \cosh\gamma_0 x + B \sinh\gamma_0 x. \tag{102}$$

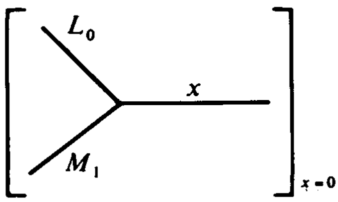
If Z_0 is the terminal impedance of the branch of length L_0 Eq. 102 may then be written as,

$$V(x,s) = (B/Z_{c_0})\,[Z_{c_0}\sinh\gamma_0 x + Z_0\cosh\gamma_0 x], \tag{103}$$

or in our graph notation,

$$V(x,s) = (B/Z_{c_0})\,[\overset{x}{\text{—}}]. \tag{104}$$

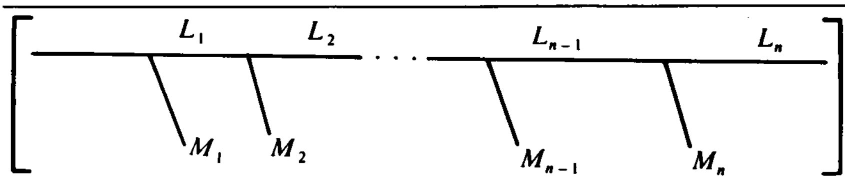
The unknown B is determined from the continuity condition 101. From Eq. 72



$$= Z_{c_0} Z_{c_1} Z'_{c_1} [\overset{L_0}{\text{—}}]\,[\overset{M_1}{\text{—}}]. \tag{105}$$

Therefore,

$$B = \frac{(Z^2_{c_0}/Z_{c_n})[\overset{D}{\text{—}}] \prod_{k=1}^{n-1} Z^2_{c_k} Z'_{c_k} [\overset{M_k}{\text{—}}] I^*(s)}{\text{(see diagram)}}.$$



(106)

Substituting Eq. 106 into 104 leads finally to the desired result, Eq. 97.

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REFERENCES

CAJAL, S. R. 1909. Histologie du Système Nerveux de l'Homme et des Vertébrés. S. A. Maloine, Paris, France.

JACK, J. J. B., S. MILLER, R. PORTER, and S. J. REDMAN. 1971. *J. Physiol.* **215**:353.

RALL, W. 1959. *Exp. Neurol.* **1**:491.

RALL, W. 1962 *a*. *Biophys. J.* **2**:145.

RALL, W. 1962 *b*. *Ann. N. Y. Acad. Sci.* **96**:1071.

RALL, W. 1964. *In* Neural Theory and Modelling. R. F. Reiss, editor. Stanford University Press, Stanford, Calif. 73–97.
RALL, W. 1967. *J. Neurophysiol.* **30**:1138.
RALL, W. 1969 *a*. *Biophys. J.* **9**:1483.
RALL, W. 1969 *b*. *Biophys. J.* **9**:1509.
RALL, W., and J. RINZEL. 1973. *Biophys. J.* **13**:648.
WEBER, E. 1965. *Linear Transient Analysis.* Vol. II. John Wiley & Sons, New York.