CABLE THEORY FOR FINITE LENGTH DENDRITIC CYLINDERS WITH INITIAL AND BOUNDARY CONDITIONS

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ABSTRACT The cable equation is solved in the Laplace transform domain for arbitrary initial and boundary conditions. The cable potential is expressed directly in terms of the impedance of the terminations and the cable electrotonic length. A computer program is given to invert the transform. Numerical solutions may be obtained for any particular model by inserting expressions describing the terminations and parameter values into the program, without further computation by the modeler. For a finite length cable, sealed at one end, the solution is expressed in terms of the ratio of the termination impedance to the impedance of the finite length cable, a generalization of the steady-state conductance ratio. Analysis of a model of a soma with several primary dendrites shows that the dendrites may be lumped into one equivalent cylinder if they have the same electrotonic length, even though they may vary in diameter. Responses obtained under voltage clamp are conceptually predictable from measurements made under current clamp, and vice versa. The equalizing time constants of an infinite series expression of the solution are the negative reciprocals of the roots of the characteristic equation. Examination of computed solutions shows that solutions which differ theoretically may be indistinguishable experimentally.

INTRODUCTION

When a neuron is excited by a synaptic input, the synaptic current induces a membrane polarization which is distributed nonuniformly over the surface of the cell. After the brief period of synaptic activity, which roughly coincides with the rising phase of the synaptic potential, the charge across the membrane redistributes and decays, producing the falling phase of the synaptic potential. Assuming that the membrane remains passive in its electrical properties, and assuming that the duration of the synaptic permeability changes is indeed brief, the redistribution and decay of the membrane potential is well described by the one-dimensional cable equation (Rall, 1969 *b*).

Similarly, the neuron may be polarized by means of experimentally imposed voltages and currents. Again, the resulting time course of potential decay and redistribution over the surface of the fiber is well described by the one-dimensional cable equation (Clark and Plonsey, 1966; Pickard, 1969).

The cable equation model of passive nerve fibers can thus be a valuable tool both for analyzing the means by which a neuron combines a pattern of synaptic inputs to produce a specific computation, and for determining the functionally significant electrical parameters of the cell by measurements of the response to various applied currents. In order for the model to be of practical use, though, it must be possible first to set up the equation so that the boundary and initial conditions correspond to the anatomical, physiological, and experimental realities, and second, to solve the equation under these conditions.

The solution to the cable equation can be written in closed form in terms of known functions only for a few special cases, such as the infinite uniform cable (Hodgkin and Rushton, 1946) or the infinite cable terminated in a cell body (Rall, 1960). For more realistic models, such as a finite length cable, infinite series solutions have been found (Volkov and Platonova, 1970). Using a separation of variables approach, Rall (1962, 1969 *a*) has developed an infinite series form of solution applicable to the case of a finite length cable with a variety of different types of terminations. Each term of the sum is an exponentially decaying time function, the time constants of decay, the equalizing time constants, being the eigenvalues for the particular boundary conditions. This approach suffers from two disadvantages. First, minor changes in the nature of the boundary conditions require rather extensive changes in the nature of the equations used to determine the eigenvalues, and even in the eigenfunctions themselves. Second, numerical evaluation of the expected wave forms is difficult because the infinite series converges poorly for small values of time.

Using a Laplace transform approach, a theoretical framework can be developed in which both boundary and initial value conditions are expressed in concise and easily computed form. Using this framework, I shall develop the general form of solution to the cable equation for arbitrary boundary and initial conditions. The equalizing time constants in Rall's solution can be determined directly from the solution in the transform domain. In addition, I shall present a numerical method of inversion for the Laplace transform, so that any particular solution of interest can be readily computed and plotted.

The cable equation yields the same solutions, of course, no matter what method is used to determine and express the results. The special value of this approach is the ease with which numerical results are obtained. The experimenter can quickly test a series of models, changing numerical parameters such as the ratio of dendritic to soma impedance or the length of the dendritic cable, to compare the theoretical wave form resulting from applied currents with the experimental data.

THE CABLE EQUATION WITH INITIAL CONDITIONS

For a cable with longitudinal resistance r_L ohms/cm, transverse resistance r_m ohm-cm, and transverse capacitance c_m farads/cm, the transverse potential $v(x, t)$

and longitudinal current $i(x, t)$ satisfy the equations

$$\frac{1}{r_L}\frac{\partial^2 v(x,t)}{\partial x^2} - \frac{1}{r_m} v(x,t) - c_m \frac{\partial v(x,t)}{\partial t} = 0,$$

$$i(x,t) = -\frac{1}{r_L}\frac{\partial v(x,t)}{\partial x}. \qquad (1)$$

Both internal and external components of resistance are included in the longitudinal resistance, and the potential is measured as the deviation from resting. Substituting the normalized variables $X = x/\lambda$ and $T = t/\tau$

$$\frac{\partial^2 v(X,T)}{\partial X^2} - v(X,T) - \frac{\partial v(X,T)}{\partial T} = 0,$$

$$i(X,T) = -\frac{1}{r_L \lambda}\frac{\partial v(X,T)}{\partial X}. \qquad (2)$$

The Laplace transform of equation 2 is taken with respect to T, using s as the transform variable. Note that s is a dimensionless, normalized frequency. Laplace-transformed functions will be written in capitals

$$\frac{\partial^2 V(X,s)}{\partial X^2} - (1+s)V(X,s) = -V_0(X),$$

$$I(X,s) = -\frac{1}{r_L \lambda}\frac{\partial V(X,s)}{\partial X}, \qquad (3)$$

where $V_0(X)$ is the initial voltage distribution on the cable.

The formal solution to equation 3 is determined from the known solutions to the reduced equation by a variation of parameters technique. It is convenient to define $q = (1 + s)^{1/2}$. The solution is then written

$$V(X,s) = A(s)e^{-qX} + B(s)e^{qX} - (1/q)\int_0^X V_0(\xi)\sinh q(X-\xi)\, d\xi,$$

$$I(X,s) = \frac{q}{r_L \lambda}\left[A(s)e^{-qX} - B(s)e^{qX} + (1/q)\int_0^X V_0(\xi)\cosh q(X-\xi)\, d\xi\right], \qquad (4)$$

where the coefficients A and B are determined by the boundary conditions.

SPECIAL BOUNDARY CONDITIONS

The Infinite Cable

If the cable extends indefinitely far in the $+X$ direction, the appropriate boundary condition is the requirement that v and i, or equivalently V and I, remain bounded as $X \to \infty$. Expanding the sinh and cosh terms in equation 4 and ignoring all terms in exp $(-qX)$, which goes to 0 in the limit,

$$V(\infty, s) = \lim_{X\to\infty}\left\{\left[B(s) - \frac{1}{2q}\int_0^X V_0(\xi)e^{-q\xi}\,d\xi\right]e^{qX}\right\}.$$

In order for V to remain bounded in the limit

$$B(s) = \frac{1}{2q}\int_0^\infty V_0(\xi)e^{-q\xi}\,d\xi, \tag{5}$$

assuming that $V_0(X) \rightarrow 0$ as $X \rightarrow \infty$. The integral in equation 5 is just the Laplace transform of $V_0(X)$, transforming with respect to X and using q as the transform variable. The remaining coefficient $A(s)$ is determined by the other boundary condition.

The Finite Cable

If the cable is of finite length, it must have two terminations, say at $X = 0$ and $X = L$. The terminations can be expressed as equivalent circuits (Fig. 1) with impedance $Z_1(s)$ and voltage source $V_1(s)$ at the left and $Z_2(s)$ and $V_2(s)$ at the right. The boundary conditions are

$$V(0, s) = V_1(s) - I(0, s)Z_1(s),$$
$$V(L, s) = V_2(s) + I(L, s)Z_2(s). \tag{6}$$

The sign difference results from the fact that $I(0, s)$ is positive into the cable while $I(L, s)$ is positive out of the cable. A pure current source termination at $X = 0$, with infinite impedance, is represented by the condition $I(0, s) = I_1(s)$, and similarly at $X = L$.

Since the initial conditions will always be expressed in terms of integrals of the form expressed in equation 4, it is convenient to define

$$\phi_s = \int_0^L V_0(\xi)\sinh q(L - \xi)\,d\xi,$$

$$\phi_c = \int_0^L V_0(\xi)\cosh q(L - \xi)\,d\xi.$$

Rewriting equation 6 in terms of the solutions in equation 4, the coefficients A and B can be obtained from the pair of equations

$$(1 + \mathbf{Z}_1)A(s) + (1 - \mathbf{Z}_1)B(s) = V_1,$$
$$e^{-qL}(1 - \mathbf{Z}_2)A(s) + e^{qL}(1 + \mathbf{Z}_2)B(s) = V_2 + (\phi_s + \mathbf{Z}_2\phi_c)/q, \tag{7}$$

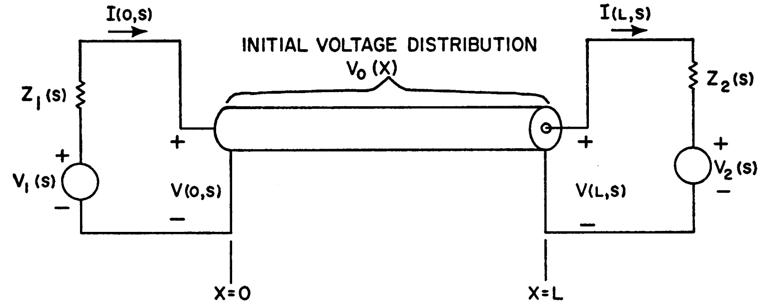

FIGURE 1 Finite length, initially excited cable, with generalized terminations.

where $\mathbf{Z}_i = qZ_i/(r_L\lambda)$ is a normalized impedance. Assuming the matrix of coefficients in this set of equations to be nonsingular, the coefficients are

$$A(s) = \frac{1}{2}\frac{(1+\mathbf{Z}_2)e^{qL}V_1 - (1-\mathbf{Z}_1)[V_2 + (\phi_s + \mathbf{Z}_2\phi_c)/q]}{(1+\mathbf{Z}_1\mathbf{Z}_2)\sinh qL + (\mathbf{Z}_1+\mathbf{Z}_2)\cosh qL},$$

$$B(s) = \frac{1}{2}\frac{-(1-\mathbf{Z}_2)e^{-qL}V_1 + (1+\mathbf{Z}_1)[V_2 + (\phi_s + \mathbf{Z}_2\phi_c)/q]}{(1+\mathbf{Z}_1\mathbf{Z}_2)\sinh qL + (\mathbf{Z}_1+\mathbf{Z}_2)\cosh qL}. \quad (8)$$

The significance of the singular points will be discussed later.

The complete solution for the boundary and initial value problem is found by inserting the appropriate impedances and voltage sources into equation 8, and using these expressions for A and B in equation 4. In many cases of interest, the resulting expressions may be greatly simplified. For example, the recording site may be located at one of the terminations, as would normally be the case if the termination were a cell body. If this termination is taken at $X = 0$, equation 4 reduces to $V(0, s) = A(s) + B(s)$. Furthermore, if the only excitation results from a current-passing electrode also inserted into the soma (cf. Fig. 2), the potential becomes

$$V(0, s) = \frac{(\tanh qL + \mathbf{Z}_2)Z_1I_1}{(1+\mathbf{Z}_1\mathbf{Z}_2)\tanh qL + (\mathbf{Z}_1+\mathbf{Z}_2)}. \quad (9)$$

Infinite Cable Terminations

If the cable is terminated with an infinitely long, initially unexcited cable, the corresponding V_i is 0 and the impedance is the input impedance of an infinite cable, $Z_i = Z_\infty = r_L\lambda/q$. The normalized impedance becomes $\mathbf{Z}_i = 1$; the normalization is with respect to the infinite cable impedance. If the termination occurs on the left, then $A(s) = 0$. Alternatively, if it occurs on the right then

$$B(s) = \frac{1}{2q}\int_0^L V_0(\xi)e^{-q\xi}\,d\xi.$$

In the limit, as $L \rightarrow \infty$, this expression reduces to equation 5.

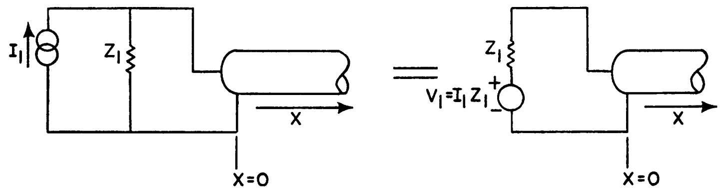

FIGURE 2 Cable excited by current source at left end, with equivalent circuit.

Combining the two types of termination, the potential on a doubly infinite cable (extending indefinitely far in both directions) with initial potential distribution $V_0(X)$ can be simplified into the form

$$V(X, s) = \frac{1}{2q} \int_{-\infty}^{\infty} V_0(\xi) e^{-q|X-\xi|} \, d\xi. \tag{10}$$

Finite Sealed Cable

If the cable is terminated in a sealed end, at that end the longitudinal current must be zero. Thus a cable sealed at $X = 0$ must satisfy $I(0, s) = (q/r_L\lambda)(A - B) = 0$ or $A(s) = B(s)$. The same result is obtained from equation 7 by allowing $Z_1 \rightarrow \infty$.

If the cable, instead, is terminated in a sealed end at $X = L$, so that $Z_2 = \infty$, the coefficients become

$$A(s) = \frac{1}{2} \frac{e^{qL} V_1 - (1 - Z_1)\phi_c/q}{Z_1 \sinh qL + \cosh qL},$$

$$B(s) = \frac{1}{2} \frac{e^{-qL} V_1 + (1 + Z_1)\phi_c/q}{Z_1 \sinh qL + \cosh qL}. \tag{11}$$

A vertebrate spinal motoneuron may be modeled as a dendrite, or equivalent dendritic cylinder, sealed at the right and terminated at the left with a complex configuration of soma, axon, and other dendrites. If the recording site is in the soma, we are concerned only with $V(0, s)$ and $I(0, s)$. It is convenient to make a new normalization of impedance.

$$\rho = Z_1 \tanh qL = (qZ_1 \tanh qL)/(r_L\lambda) = Z_1/Z_L = Y_L/Y_1. \tag{12}$$

This ratio is the complex-valued ratio of dendritic to termination admittance, as a function of s. When evaluated at $s = 0$ it gives the steady-state conductance ratio defined by Rall (1959).

Using this ratio, the cable potential and current at the soma are

$$V(0, s) = \frac{1}{\rho + 1} V_1 + \frac{\rho}{\rho + 1} \frac{\phi_c}{q \sinh qL},$$

$$I(0, s) = \frac{1}{r_L \lambda (1 + \rho)} \left[qV_1 \tanh qL - \frac{\phi_c}{\cosh qL} \right]. \tag{13}$$

Since the excitation at $X = 0$ is usually in the form of a current source, equation 13 may be rewritten in terms of the equivalent voltage source (Fig. 2), $V_1 = I_1 Z_1$,

$$V(0, s) = r_L \lambda \frac{\rho}{\rho + 1} \frac{I_1}{q \tanh qL} + \frac{\rho}{\rho + 1} \frac{\phi_c}{q \sinh qL},$$

$$I(0, s) = \frac{\rho}{\rho + 1} I_1 - \frac{1}{r_L \lambda(\rho + 1)} \frac{\phi_c}{\cosh qL}. \quad (14)$$

The dependence of the potential and current on the particular nature of the termination is expressed completely by the ratio $\rho/(1 + \rho)$.

Both Ends Sealed. If the left end of the cable is also sealed, then $Z_1 = \infty$, so that $\rho = \infty$, corresponding to Rall's case of "complete dendritic dominance." The potential at the end of the cable resulting from a current excitation is $V = r_L \lambda I_1/(q \tanh qL)$. The potential distribution along the cable resulting from an initial distribution is obtained from equation 4 by setting $A = B = (1/2)\phi_c/(q \sinh qL)$:

$$V(X, s) = (1/q \sinh qL) \left[\cosh q(L - X) \int_0^X V_0(\xi) \cosh q\xi \, d\xi + \cosh qX \int_X^L V_0(\xi) \cosh q(L - \xi) \, d\xi \right]. \quad (15)$$

If the cable is initially uniformly charged, then $V_0(X) = V_0$ and the potential reduces to $V(X, s) = V_0/(1 + s)$, corresponding to a simple exponential decay with time constant τ along the entire length of cable.

Finite Cable Terminated in Soma

If the termination impedance represents a roughly spherical cell body with the same membrane properties as the cable itself, it can be modeled by a lumped RC equivalent circuit with time constant τ (Rall, 1960). Then $Z_1 = 1/(G_{soma} q^2)$ and

$$\rho = \frac{\tanh qL}{r_L \lambda G_{soma} q}. \quad (16)$$

The potential at the soma (equation 14) becomes

$$V(0, s) = \frac{I_1}{q \tanh qL + (1 + s) r_L \lambda G_{soma}} + \frac{\phi_c}{q \sinh qL + (1 + s) r_L \lambda G_{soma} \cosh qL}.$$

Cell Body with Dendrites. Any desired configuration of dendrites of varying lengths and diameters can be appended to the soma (Fig. 3) by making the

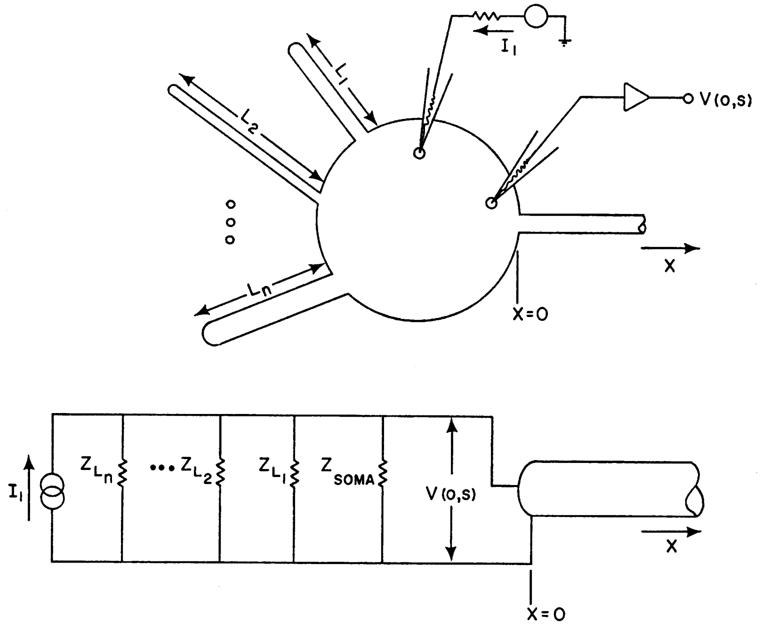

FIGURE 3 Cable terminated with soma and other dendrites, with equivalent circuit.

terminating impedance Z_1 the parallel combination of the soma impedance and each branch impedance, using $Z_L = (r_L\lambda)/(q \tanh qL)$ for the input impedance of a finite length sealed cable. Here L is the electrotonic length of the dendrite, measured relative to its own space constant. Since λ is proportional to $(\text{diameter})^{1/2}$ and r_L to $(\text{area})^{-1}$ or $(\text{diameter})^{-2}$, the product $r_L\lambda$ is proportional to $(\text{diameter})^{-3/2}$. By defining an impedance ratio for each dendrite separately, $\rho_k = Z_{soma}/Z_{L_k}$ and $\rho_0 = Z_{soma}/Z_L$, the impedance ratio ρ can then be expressed as $1/\rho = Z_{soma}/Z_1 = (1 + \sum_k \rho_k)/\rho_0$ or

$$\frac{\rho}{\rho + 1} \frac{(\tanh qL)/r_L\lambda)}{(\tanh qL)/(r_L\lambda) + \sum_k (\tanh qL_k)/(r_L\lambda)_k} \frac{\rho_{eq}}{\rho_{eq} + 1}, \tag{17}$$

where $\rho_{eq} = \rho_0 + \sum_k \rho_k$ is the impedance ratio for all the dendrites taken together.

The potential at the soma due to current excitation (equation 14) becomes

$$V(0, s) = \frac{\rho_{eq}}{\rho_{eq} + 1} \frac{I_1}{(q \tanh qL)/(r_L\lambda) + \sum_k (q \tanh ql_k)/(r_L\lambda)_k}. \tag{18}$$

If all the dendrites have the same electrotonic length, $L_k = L$ for all k, then $\rho/(\rho + 1) = K\rho_{eq}/(\rho_{eq} + 1)$ where K is a real constant depending only on the relative diameters of the various dendrites. Then any potential or current expression, whose dependence on the terminating impedance is contained solely in the form $\rho/(\rho + 1)$, can be written using ρ_{eq} in place of ρ, with only a constant factor error. Inspection of equations 13 and 14 shows that the potential at the soma due to either dendritic initial conditions or to applied currents satisfies this condition. The ratio ρ_{eq} represents an equivalent dendritic cylinder with all the dendrites lumped into one thicker cylinder.

Any measurement of ρ made from the soma will, in fact, be an estimate of ρ_{eq}. This estimate must not then be used in calculations for which lumping is prohibited, as in computing the spread of current of potential from one dendrite into another, or the potential distribution along a dendrite.

When lumping is permitted, ρ_{eq} may be estimated from morphological data in terms of the ratio of total dendritic area to soma area (Rall, 1959), $\rho_{eq} = (\text{area}_{\text{dend}}/\text{area}_{\text{soma}})\ (\tanh qL)/(qL)$. Otherwise, each separate ρ_k can be computed from this formula using the area for that dendrite.

Voltage Clamp. A perfect voltage clamp occurs when a voltage source with zero internal impedance is imposed across the cable. If the clamp is introduced at $X = 0$, then $Z_1 = 0$ and $V(0, s) = V_1(s) = V_{\text{clamp}}$. Thus $\rho = 0$, corresponding to Rall's (1969 *a*) case of vanishing dendritic admittance.

To compare voltage and current clamping, consider the neuron model with a finite length dendrite sealed at $X = L$ and terminated at $X = 0$ in a soma, axon, and dendrite combination with impedance Z_1 and ratio ρ. The voltage response to a current applied at the soma (current clamp) is given by equation 14.

If a voltage clamp is imposed on the soma, two components of clamp current will flow, one into the cable and one through Z_1. The ratio of these components is simply ρ, while the current through Z_1 is V_{clamp}/Z_1. The clamp current is thus $(\rho + 1)\ V_{\text{clamp}}/Z_1$ or:

$$I_{\text{clamp}} = \frac{1}{r_L \lambda} \frac{\rho + 1}{\rho} q\ (\tanh qL) V_{\text{clamp}}. \qquad (19)$$

The voltage clamp response of the initially unexcited cable is described by the equivalent clamp load admittance $I_{\text{clamp}}/V_{\text{clamp}}$ in equation 19. The current clamp response of the initially unexcited cable is similarly described by the equivalent load impedance $V(0, s)/I_1$ in equation 14. Since the current clamp impedance is exactly the reciprocal of the voltage clamp admittance, the two responses are equivalent. That is, it is conceptually possible to measure a transient response in one clamp mode, compute the corresponding admittance and impedance, and predict the response to an arbitrary command signal in the other clamp mode.

The same conclusion is reached for the more general model of a finite, arbitrarily terminated cable with voltage clamp imposed at a point, or for the comparison of the current response in voltage clamp mode to the voltage response in current clamp mode due to initial conditions. The only information about a cable that can be obtained from measurements made at a single point relates to the effective driving point impedance of the cable at that point, no matter what the mode of excitation

EQUALIZING TIME CONSTANTS

Rall's method (1969 *a*) for the solution of the cable equation involves a separation of variables and an eigenfunction expansion, resulting in an infinite series expression, each term with exponential decay. The time constants of decay, the equalizing time constants, are the eigenvalues of the system.

Both the infinite series expression and the equalizing time constants are computable directly from the transform solutions by means of a partial fraction development of the transform (van der Pol and Bremmer, 1964, Sec. VII.10). The terms in the partial fraction expansion depend on the singularities of V and I, considered as functions of the complex variable s. Since the integrals and exponential terms in equation 4 are analytic functions of q, the singularities of V and I are just those of A and B, considered as functions of q. These, in turn, are just the singularities in the set of simultaneous equations, equation 7. The location of the singular points can be obtained from the roots of the characteristic equation $(1 + \mathbf{Z}_1\mathbf{Z}_2) \sinh qL + (\mathbf{Z}_1 + \mathbf{Z}_2) \cosh qL = 0$, which can be written

$$\tanh qL = -\frac{\mathbf{Z}_1 + \mathbf{Z}_2}{1 + \mathbf{Z}_1\mathbf{Z}_2}. \tag{20}$$

If the cable is sealed at $X = L$, then $\mathbf{Z}_2 = \infty$, and the characteristic equation becomes $\tanh qL = 1/\mathbf{Z}_1$.

If the cable is sealed at both ends, the singular points are the roots of $\tanh qL = 0$, at $q_n = n\pi j/L$, where $j^2 = -1$, for all positive and negative integers n. Using the mapping $s = q^2 - 1$, the roots in the s plane become $s_n = -n^2\pi^2/L^2$. By retaining both positive and negative values of n in the development, an effective path of integration is produced that avoids the branch cuts from the mapping $q \rightarrow s$. Thus, each term in the development results from a simple pole on the negative real axis in the s plane, corresponding to simple exponential decay. The time constants of decay, the equalizing time constants, are the negative reciprocals of the roots of the characteristic equation $\tau_n = -1/s_n = (1 + n^2\pi^2/L^2)^{-1}$. Note that these are already normalized to the membrane time constant. The coefficients in the expansion are the residues evaluated at s_n and, after taking into consideration both positive and negative values of n, reduce exactly to Rall's coefficients.

For the voltage-clamped finite cable, $Z_1 = 0$ and the singular points are the roots of $\tanh ql = \infty$. The poles are shifted to $q_n = (2n + 1)\pi j/(2L)$, or $\tau_n = [1 + \pi^2(2n + 1)^2/(4L^2)]^{-1}$. The imposition of the voltage clamp thus shifts the location of the singular points. Since $s = -1$ is not a singular point, there is no component of decay with the natural membrane time constant, as emphasized by Rall (1969 *a*).

For other terminations of the finite cable sealed at the far end, the characteristic equation can be expressed quite simply, remembering that ρ is a function of s:

$$\rho = -1. \tag{21}$$

For the cable terminated in a soma, ρ is given equation 16. The characteristic equation becomes $\tanh qL = -K\,qL$, where $K = r_L\lambda\, G_{soma}/L$, corresponding to equation 21 of Rall (1969 *a*).

INVERTING THE TRANSFORM

The preceding sections show how the Laplace transform representation of the cable potential and current can be obtained for a variety of boundary conditions and initial conditions. These calculations are to no avail, however, unless they can be used to predict the time course of the potential and current wave forms. Certain properties of the solution can, in fact, be determined by known properties of the Laplace transform, such as initial values, final values, integrals, and derivatives of the solution.

The transforms obtained for the cable equation have the property that they are analytic in the right half-plane, as seen from the determination of the equalizing time constants. The imaginary axis can be used as the path of integration in the inversion of the Laplace transform, reducing the formula to a Fourier inversion integral with the correspondence $s = jw$, where w is normalized radian frequency, $w = 2\pi f\tau$. The Fourier transform is performed numerically using the "Fast Fourier Transform" program derived by Cooley and Tukey (1965) and available in the IBM scientific subroutine package for FORTRAN and PL/I (see also Mejia and Chang, 1970). The details of the inversion program, along with a discussion of the resulting errors of approximation and problems of spectral folding or aliasing are discussed in Appendix II.

The direct numerical inversion of the Laplace transform has several advantages over series methods of solution. The computations involved in computing the transform are relatively straightforward. The effect of varying cable length or of changing details of the terminating impedances is easily incorporated. No integration is needed to compute the transform for the initially quiescent cable, nor must transcendental equations be solved. For the initially excited case, the integrals ϕ_c and ϕ_s involve products of the initial distribution with exponentials, integrals that can be evaluated analytically if the initial conditions can be expressed as polynomials, exponentials, or trigonometric functions. Similar integrals must be evaluated, in any case, to obtain the coefficients in the series expansion solutions.

The principal advantage of the direct numerical inversion is the fact that approximation errors in the numerical computations can be treated exactly. There are no difficulties with convergence, for either large or small values of time, and the inversion is easily programmed for routine computer use.

USE OF THE EQUATIONS

On advantage of this treatment of the cable equation is that numerical solutions for particular models may be found with little or no computation on the part of the experimenter. In this section, the rules for applying the equations to the most useful models will be explained.

Equation 4 expresses the general form of the solution to the cable equation. If the main interest is in finding the potential resulting from applied currents, the initial conditions $[V_0(X), \phi_c$ and $\phi_s]$ are zero. Pick a specific value of X (measured in space constants) for the recording site. The variables s and q are assigned complex values in the computer program for numerical inversion (Appendix II). The only task for the programmer is to write expressions for A and B in terms of s and q. Equation 8 gives these expressions in the general case of the finite length cable modeled in Fig. 1. The normalized impedances $\mathbf{Z}_1$ and $\mathbf{Z}_2$ can be taken from Table I for particular terminations.

One useful model involves a cable excited only by means of a current-passing microelectrode. The recording site is located at or near the stimulating site, as would occur with a bridge circuit or a double-barreled electrode. In this case, equation 9 expresses the potential in terms of the terminating impedance and I_1 the Laplace transform of the current. A current impulse is $I_1 = 1$, while a step of magnitude 1 is

TABLE I

IMPEDANCES AND NORMALIZED IMPEDANCE RATIOS FOR TERMINATIONS OF A CABLE OF ELECTROTONIC LENGTH L AND RADIUS a

Case	Termination Type	Z	$\mathbf{Z}$	ρ
1	Short circuit, killed end, or voltage clamp	0	0	0
2	Sealed cable, current clamp	∞	∞	∞
3	Imperfect clamp, electrical coupling through resistance	R	$qR/(r_L\lambda)$	$\frac{qR \tanh qL}{r_L\lambda}$
4	Soma with conductance G_{soma}	$\frac{1}{G_{soma}(1+s)}$	$\frac{1}{G_{soma}\, r_L\, \lambda\, q}$	$\frac{\tanh qL}{G_{soma}\, r_L\, \lambda\, q}$
5	Infinite length cable	Z_∞	1	$\tanh qL$
6	Sealed cable, length L'	Z_L'	$1/\tanh qL'$	$\frac{\tanh qL}{\tanh qL'}$
7	Sealed cable, electrotonic length L', radius a'	Z_L'	$\frac{(a/a')^{3/2}}{\tanh qL'}$	$\frac{(a/a')^{3/2} \tanh qL}{\tanh qL'}$
8	Branching terminations, with separate impedances Z_a, Z_b, ...	$\frac{1}{1/Z_a + 1/Z_b + \ldots}$	$\frac{1}{1/\mathbf{Z}_a + 1/\mathbf{Z}_b + \ldots}$	$\frac{1}{1/\rho_a + 1/\rho_b + \ldots}$

$I_1 = [1\text{-exp}(-10s)]/s$. The step is turned on for 10 time constants, then turned off to obtain proper convergence of the inversion. To avoid division by zero, specify $I_1 = 10$ for $s = 0$.

If the cable model is terminated at $X = L$ in a sealed or closed end, equation 11 gives the expressions for A and B. For the potential at the site of the current-passing electrode, equation 14 is used with $\phi_c = 0$. The termination is expressed in terms of the normalized impedance ratio ρ, also listed in Table I for the various termination types.

SUMMARY AND CONCLUSIONS

The Laplace transform provides a concise language for expressing the general solution to the cable equation for arbitrary boundary and initial conditions. The cable voltage or current for any particular model is obtained as a special case of the general result. Given the computer program in Appendix II for numerically inverting the transform, any particular model can easily be simulated, following the guide in the previous section for the most common physiological models.

In this formulation, the cable terminations can take on a very complex character. In addition to the sealed end, the soma, or the soma plus dendrite cases developed in the text, the terminations can include electrical coupling between cells, changes in fiber diameter, or fiber branching, as indicated in Table I. To model electrotonic coupling, V_2 is equated with the transform of the potential in the driving neuron, while Z_2 represents the impedance between the cells (case 3, Table I). A change in diameter is expressed through its influence on the parameters r_L and λ (case 7, Table I). If the termination is a branch point, the terminating impedance is the parallel combination of the individual branch impedances (case 8, Table I). A general treatment of branching dendritic networks will be treated in a separate paper.

The particular termination is expressed by its terminating impedance. For the general finite cable, impedance is normalized with respect to the impedance of an infinite cable to simplify the expressions. If the cable is sealed at one end, it is more convenient to normalize the termination impedance at the other end with respect to the impedance of the finite sealed cable, equation 12. The resulting ratio ρ expresses the complex-valued impedance ratio as a function of complex frequency s. Evaluated at $s = 0$ (or $q = 1$) it reduces exactly to Rall's steady-state conductance ratio.

One special case of dendritic branching is of interest as a model of a vertebrate spinal motor neutron, or other multipolar cell. In this case, several primary dendrites, each modeled by a single equivalent cylinder, arise from a cell body. In the context of the cable model considered here, one dendritic cylinder is singled out for consideration and is terminated in the combination of the soma plus all the other dendrites. In practice, with a recording and stimulating electrode in the soma, the dendrites are indistinguishable, and are lumped into one thicker equivalent cylinder. A consideration of the exact terminating impedance ratio (equation 17) confirms that, in general, the lumped equivalent cylinder model is valid only if the various dendrites have the same electrotonic length, even though they may differ in diameter (Rall, 1962). Even so, the lumped equivalent impedance ratio cannot be used when the termination impedance is not expressed in the form $\rho/(\rho + 1)$.

A comparison of voltage clamp and current clamp excitation shows the data from one clamp mode to be predictable from measurements made in the other clamp mode; hence the two types of experiment are conceptually equivalent. The prediction requires determining the impedance or admittance of the clamp load, by Fourier or Laplace transformation of a transient response or by measuring amplitude and phase response as a function of frequency. The two modes are not identical, though, and a particular analytic technique, such as fitting exponentials to the data, will yield different information for the two types of response. If noise and bandwidth limitations preclude the more complete analysis, the two types of response will then yield complementary information about the neuron.

The equalizing time constants, in Rall's sense, are obtained from the transform by solving the characteristic equation (equation 20). The equalizing time constants, normalized with respect to τ, are the negative reciprocals of the roots of the characteristic equation. If the cable is sealed at one end, the characteristic equation can be expressed simply as $\rho = 1$. The characteristic equation is, of course, the same whether derived through the Laplace transform or directly from the boundary conditions (Rall, 1969 *a*). The advantage of this approach is that the roots of the characteristic equation are not needed to compute the solution.

It is interesting to note that, for the infinite cable, the temporal Laplace transform (transforming with respect to T) of the potential is closely related to the spatial Laplace transform (transforming with respect to X) of the initial condition (equations 5 and 10). Initial conditions are thus easily expressed for the infinite cable.

APPENDIX I

Examples

To illustrate the techniques described in this paper, voltage transients are computed for several types of cables and excitations. The specific numerical values for the parameters are chosen to model a cat spinal motoneuron. Thus, the electrotonic length of the cable L is 1.5 space constants, and the steady-state impedance ratio for the termination is 7.5 (Nelson and Lux, 1970). The constant $r_L\lambda$, which only affects the scale of the response, is ignored.

The voltage response at the site of an applied current step for five cable models is shown in Fig. 4, computed from the expressions in Table II. Each response has been normalized to the same steady-state value of 1.0. For the extended cable model, the cable is extended a distance L' to the left of the electrode site, the length L' being chosen to mimic the soma model. Thus, the steady-state value of the impedance ratio ρ is set at 7.5, so $\tanh L' = (\tanh L)/7.5$, or $L' = 0.12$.

The responses in Fig. 4 show each cable model to respond faster than a simple exponential rise with time constant τ. The initial slope for the infinite, the finite, and the extended finite cables are theoretically infinite, while the soma termination should show finite initial slope due to the soma capacitance. Yet the soma and the extended cable models have responses which are indistinguishable in the plot. They differ by less than 0.1% of the final value for $T > 0.2$ and by only 0.5% at $T = 0.02$. To distinguish these cases experimentally in a cat spinal motoneuron, where $\tau = 4$ msec and the current is chosen to hold potentials below

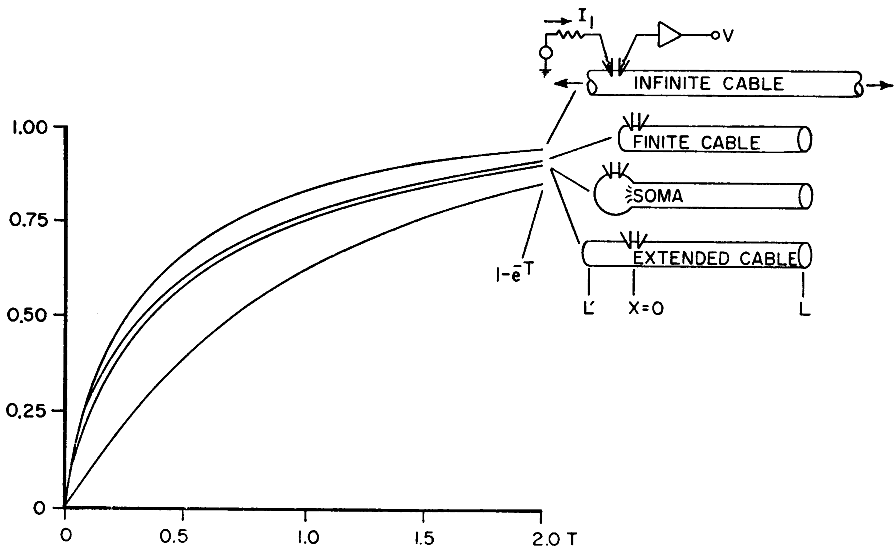

FIGURE 4 Potential response at site of applied current step for different cable models. All responses are normalized to approach 1.0 asymptotically. Cable parameters are chosen to model cat spinal motoneuron: $L = 1.5$, steady-state $\rho = 7.5$, and $L' = 0.12$. The expressions for potential for these responses are listed in Table II.

TABLE II

EXPRESSIONS FOR CABLE POTENTIAL IN FIGS. 4 AND 6

Model	Fig. 4*	Fig. 6‡
Exponential rise, $1 - e^{-T}$	$I_1/(1 + s) = I_1/q^2$	—
Doubly infinite cable	I_1/q	$(e^{-0.25q} - e^{-0.75q})/(1 + s)$
Finite cable, $L = 1.5$	$0.905\ I_1/(q \tanh 1.5q)$	$\phi_c/(q \sinh 1.5q)$
Finite cable, $L = 1.0$	—	$\phi_c/(q \sinh q)$
Cable with soma (steady-state $\rho = 7.5$)	$\dfrac{1.026\ I_1/(q \tanh 1.5q)}{1 + \dfrac{q \tanh 1.5}{7.5 \tanh 1.5q}}$	$\dfrac{\phi_c/(q \sinh 1.5q)}{1 + \dfrac{q \tanh 1.5}{7.5 \tanh 1.5q}}$
Extended cable, $L' = 0.12$	$\dfrac{1.026\ I_1/(q \tanh 1.5q)}{1 + \dfrac{\tanh 0.12q}{\tanh 1.5q}}$	—

* $I_1 = (1 - e^{-10s})/s$ for $s \neq 0$, $I_1 = 10$ for $s = 0$. Curves normalized so that transform has value 1.0 for $s = 0$, $q = 1$, ignoring I_1. (Step response approaches steady-state value 1.0.)
‡ $\phi_c = (\sinh 0.75q - \sinh 1.25q)/q$.

5 mv, would require measurements accurate to the microvolt level during the first millisecond of response.

Fig. 5 illustrates the voltage response at the site of an applied current step for a sealed cable of length $L = 1.5$, for different placements of the recording and current-passing electrodes. As the electrode is moved from the end of the cable the response slows. The potential is computed from equation 14, assuming a cable of length X_0 to be terminated in a cable of length $1.5 - X_0$, where X_0 is the distance of the electrode site from the end of the cable. Thus $\rho = \tanh qX_0/\tanh q(1.5 - X_0)$ and $V = (r_L\lambda I_1/q)$ $[\tanh qX_0 + \tanh q(1.5 - X_0)]$.

To illustrate initial conditions, a distributed synapse is modeled in Fig. 6. Here the synaptic current is distributed over the cable, so that after the initial permeability change the cable

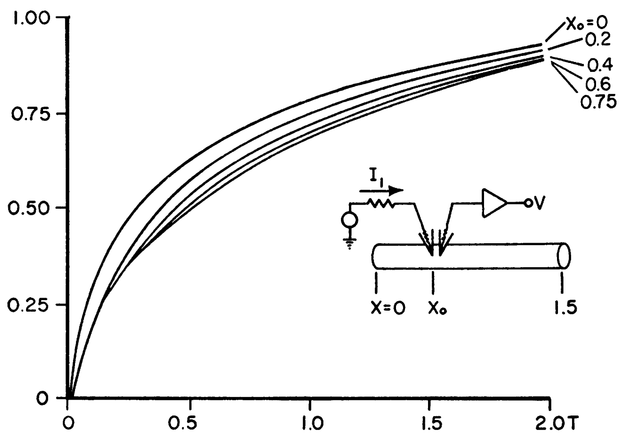

FIGURE 5 Potential response at site of applied current step in a finite length cable sealed at both ends, as a function of electrode placement. Cable length $L = 1.5$.

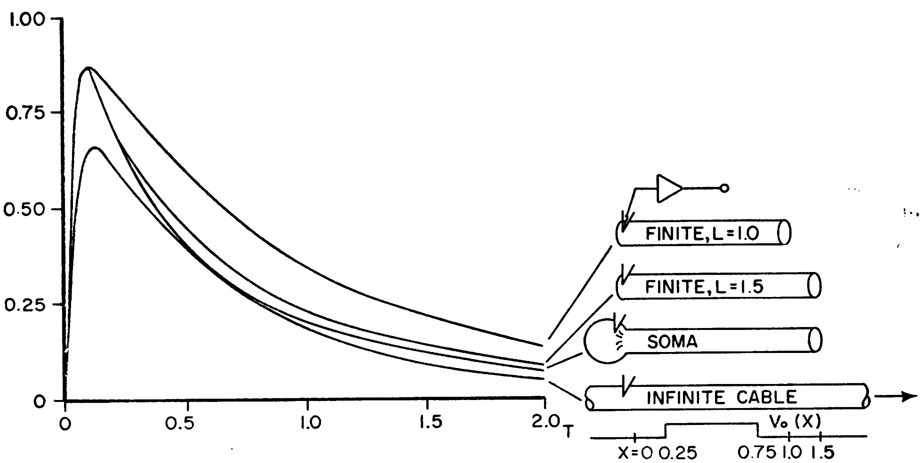

FIGURE 6 Potential response to distributed synaptic input for different cable models. The synaptic current leaves a uniform initial potential distribution on the cable from $X = 0.25$ to $X = 0.75$. The expressions for potential for these responses are listed in Table II.

is left with a potential distribution roughly proportional to the synaptic current at each point. In Fig. 6, a uniform initial distribution from $X = 0.25$ to $X = 0.75$ is assumed, giving $\phi_c = \int_{0.25}^{0.75} \cosh (L - \xi)\, d\xi = [(\sinh q(L - 0.75) - \sinh q(L - 0.25)]/q$. The time course of the response is much sharper for the infinite cable than for the finite cables. For the cable of length 1, the decay after the peak is indistinguishable from pure exponential decay with time constant τ. The effect of the soma on the potential is to weaken and broaden the peak. The voltage transforms for the cable models in Fig. 6 are listed in Table II.

APPENDIX II

Numerical Inversion of Transform

The inversion formula for the Laplace transform requires evaluating a contour integral over a path in the complex plane. By replacing the variable s with jw, the Laplace transform is converted to a Fourier transform,

$$f(T) = \left(\frac{1}{2\pi}\right) \int_{-\infty}^{\infty} F(w) \exp (jwT)\, dw, \qquad (A\,1)$$

which is an integral of a (complex-valued) function of a real variable. This step is justified since the transform has no singularities to the right of the imaginary axis in the s plane.

The Fast Fourier Transform (Cooley and Tukey, 1965) computes the finite, discrete transform:

$$f_k = \sum_{m=0}^{N-1} F_m \exp (2\pi jmk/N). \qquad (A\,2)$$

By writing $T_k = k\Delta T$ and $w_m = m\Delta w$, where $\Delta w = 2\pi/(N\Delta T)$, equation A 2 becomes

$$f(T_k) = (N\Delta T) \left(\frac{1}{2\pi}\right) \sum_{m=0}^{N-1} F(w_m) \exp(jw_k T_k)\Delta w, \qquad (A\,3)$$

which is the finite, stepwise approximation to equation A 1 except for a constant factor of $N\Delta T$.

The errors in making the approximation can be computed exactly. They are of three kinds, resulting (*a*) from truncation of the spectrum, so that only a finite bandwidth is considered, (*b*) from sampling of the spectrum, so that only discrete values of frequency are considered, and (*c*) from sampling of the computed transform, so that only discrete values of time are considered.

The effect of truncation is computed by considering the true spectrum $F(w)$ to be multiplied by a window $H(w)$ which is nonzero only within the finite frequency range considered. The effect of this truncation is to convolve the time function with the transform of H.

$$F_1(w) = F(w)H(w); \qquad f_1(t) = \int_{-\infty}^{\infty} f(\tau)h(t - \tau)\, d\tau. \qquad (A\,4)$$

The effect of sampling the spectrum is to multiply the transform by an impulse comb of spacing Δw, which is equivalent to making the time function periodic with period $2\pi/\Delta w =$

$N\Delta T$:

$$F_2(w) = \begin{cases} F(w_m), & w = m\Delta w \\ 0, & \text{elsewhere} \end{cases}, \qquad f_2(T) = \sum_{n=-\infty}^{\infty} f_1(T + nN\Delta T).$$

Note that if $f_1(T)$ is zero for $T > N\Delta T$, then each cycle of f_2 will exactly reproduce f_1.

The effect of computing the inverse only for equally spaced values of T, sampling in the time domain, is to make the spectrum periodic (folding or aliasing in the terminology of Blackman and Tukey, 1958):

$$F_3(w) = \sum_{n=-\infty}^{\infty} F_2(w + nN\Delta w).$$

Combining these three effects, if

$$F_m = F_3(w_m) = \sum_{n=-\infty}^{\infty} F(m\Delta w + nN\Delta w)H(m\Delta w + nN\Delta w), \qquad \text{(A 5)}$$

then the result of applying the discrete Fourier transform in equation A 2 is the desired function $f_k = f(k\Delta T)$, except for the constant factor of $N\Delta T$ and the effect of the convolution given by equation A 4. Thus the value f_k will be influenced by the values f_{k-r} and f_{k+r}, the amplitude of the influence being given by $h(r\Delta t)$, where $h(t)$ is the inverse transform of the window $H(w)$. Blackman and Tukey (1958) discuss the choice of spectral windows to minimize this effect, which is the only error in the computation. In practice, this influence will be negligible except when the cable response is discontinuous, a situation which requires impulsive current flows when the experimental record is also subject to transient errors.

The time increment ΔT must be chosen small enough to adequately sample the fastest responses anticipated. The parameter N must be chosen to allow the signal to vanish after time $N\Delta T$. Transients decaying exponentially will fall to less than 0.01% in 10 time constants, so N must be at least 500 for $T = 0.02$. In order to simulate a maintained potential, such as the response to a step input, we can merely turn on the step for 10 time constants, allowing all transients to decay, then turn off the step, allowing another 10 time constants for decay before reexcitation. Thus N must be at least 1000. Since N must be a power of 2 for the Fast Fourier Transform, $N = 2^{10} = 1024$. The window $H(w)$ is chosen to extend only to $w = 2\pi/\Delta T$. The coefficients in the Fast Fourier Transform (equation A 5) become

$$F_m = F\left(\frac{2\pi m}{N\Delta T}\right) + F\left(\frac{2\pi(m - N)}{N\Delta T}\right),$$
$$= F\left(\frac{2\pi m}{N\Delta T}\right) + F^*\left(\frac{2\pi(N - m)}{N\Delta T}\right),$$

where F^* is the complex conjugate of F.

A PL/I program[1] for the numerical inversion using this window, with $T = 0.02$ and $N =$

[1] A FORTRAN program with sample input and output, and more descriptive information on its parameters, will be supplied on request.

1024, is given in Fig. 7. On the IBM 360/65 computer this program requires about 4 sec of execution time to compute and invert one spectrum.

The computation is accurate to five significant figures for $T > 0.06$ in the computation of $1 - \exp(-T)$, that is, the inversion of $s^{-1}(1 + s)^{-1}$. For $T = 0.02$, the first value computed,

```
CAB_EQ:  PROC OPTIONS (MAIN);
      /*  COMPUTE INVERSE LAPLACE TRANSFORM   */
      /*  FOR SOLUTION TO CABLE EQUATION      */
DECLARE (C(2048),L,X,RL_LAMBDA) BINARY,
        (A,B,RHO,S,V,CURRENT)   COMPLEX BINARY;
DELTA_T =0.02;      N = 1024; /* COMPUTE N TIME STEPS SPACED DELTA_T */
L = -----;  RL_LAMBDA = -----;  /* SET CABLE PARAMETERS */
PI = 4*ATAN(1);

LOOP1:   DO I = 0 TO N-1;
    S = 2I * PI * I/(N * DELTA_T);
    Q = SQRT(1. + S);

    RHO = -----;          /* INSERT EXPRESSIONS FOR RHO AND */
    CURRENT = -----;      /* TRANSFORM OF CURRENT PULSE     */

    V = RL_LAMBDA * (RHO/(RHO + 1.)) * CURRENT /(Q * TANH(Q*L));

       /* OR ELSE DO:   X = -----;                */
       /*               A = -----;                */
       /*               B = -----;                */
       /*      V = A * EXP(-Q*X) + B * EXP(Q*X);  */

   V = V/(N * DELTA_T);
   C(2*I+1) = REAL(V);  C(2*I+2) = IMAG(V);
END LOOP1;

LOOP2:   DO I = 1 TO N/2;     /*  FOLD SPECTRUM */
   K = 2*I+1;   L = 2*(N-I)+1;
   C(K) = C(K)+C(L);    C(K+1) = C(K+1)-C(L+1);
   C(L) = C(K);         C(L+1) = -C(K+1);
END LOOP2;

    /*  V IS THE FUNCTION TO BE INVERTED,  C IS THE FOLDED */
    /*  SPECTRUM WITH REAL AND IMAGINARY PARTS SEPARATED   */

CALL FFT(C,1011B,'3');     /* PERFORM FOURIER TRANSFORM */

    /*  THE FIRST ARGUMENT IS THE PREPARED SPECTRUM, THE SECOND */
    /*  IS 2*N IN BINARY, THE THIRD INDICATES INVERSE TRANSFORM */
    /*  THE RESULT FOR TIME = I*DELTA_T IS THE VALUE OF C(2*I+1)*/

PUT EDIT (('TIME','FUNCTION' DO J = 0 TO 4))   /* PRINT RESULTS */
   (PAGE,SKIP(1),(5)(X(10),A,X(4),A));
PUT SKIP;
DO J = 0 TO 4;   DO J1 = 0 TO 9;
   I = 10*J+J1;   T = I*DELTA_T;   T1 = 50*DELTA_T;   K = 2*I+1;
   PUT EDIT ((T+M*T1,C(K+100*M) DO M = 0 TO 4))
         (SKIP(1),(5)(F(14,2),F(12,6)));
END; PUT SKIP; END;

END CAB_EQ;
```

FIGURE 7 PL/I program for computation and inversion of Laplace transform. Values for L and $r_L\lambda$ must be defined. The potential at $X = 0$ for a finite cable, sealed at $X = L$, with applied current, is computed from equation 14, given expressions for ρ and I_1. Alternatively, the potential is computed from equation 4, given a value for X and expressions for A and B.

the error is only 0.2% of true value. The error is larger in the computation of exp $(-T)$, the inversion of $(1 + s)^{-1}$, which has a jump of magnitude 1 at $T = 0$. The error, in percentage of the true value, is less than 5% a $T = 0.02$, decreasing to less than 1% for $T > 0.10$.

SYMBOLS

Cable Parameters

c_m	Transverse capacitance, farads/cm.
r_m	Transverse resistance, ohm-cm.
r_L	Longitudinal resistance, ohms/cm.
τ	Time constant, sec.
λ	Space constant, cm.
L	Equivalent length of finite cable, in units of λ.
Variables	
x	Distance, cm.
t	Time, sec.
X	x/λ, normalized distance.
T	t/τ, normalized time.
s	Normalized complex frequency, transform of T.
q	$(1 + s)^{1/2}$.
$v(x, t)$, $v(X, T)$	Cable potential, deviation from resting potential.
$i(x, t)$, $i(X, T)$	Longitudinal current.
$V(X, s)$	Laplace transform of potential.
$I(X, s)$	Laplace transform of current.
$V_0(X)$	Initial voltage distribution at $T = 0$.
ϕ_s	$\int_0^L V_0(\xi) \sinh q(L - \xi)\, d\xi$.
ϕ_c	$\int_0^L V_0(\xi) \cosh q(L - \xi)\, d\xi$.
$A(s)$, $B(s)$	Coefficients in cable equation solution (equations 4, 8).
$Z_1(s)$, $Z_2(s)$	Terminating impedances at left and right (Fig. 1).
$V_1(s)$, $V_2(s)$	Terminating potentials at left and right (Fig. 1).
I_1	Current source at left termination (Fig. 2).
$Z_\infty = r_L\lambda/q$	Input impedance of infinite cable.
$Z_L = r_L\lambda/(q \tanh qL)$	Input impedance of finite cable, length L, sealed at far end.
$\mathbf{Z} = Z/Z_\infty$	Normalized impedance for general finite cable (equation 8).
$\rho = Z_1/Z_L$	Normalized impedance for finite cable sealed on right (equation 12).

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