DISTRIBUTIONS OF POTENTIAL IN CYLINDRICAL COORDINATES AND TIME CONSTANTS FOR A MEMBRANE CYLINDER

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ABSTRACT A mathematical problem relating to membrane cylinders is stated and solved; its implications are illustrated and discussed. The problem concerns the volume distribution, in cylindrical coordinates, of the electric potential inside and outside a membrane cylinder of finite length (with sealed ends), during passive decay of an initially nonuniform membrane potential. The time constants for equalization with respect to the angle, θ, are shown to be typically about ten thousand times smaller than the time constant, $\tau_m = R_m C_m$, for uniform passive membrane potential decay. The time constants for equalization with respect to length are shown to agree with those from one-dimensional cable theory; typically, they are smaller than τ_m by a factor between 2 and 10. The relation of the membrane current density, $I_m(\theta, x, t)$, to the values (at the outer membrane surface) of the extracellular potential $\varphi_e(r, \theta, x, t)$ and of $\partial^2\varphi_e/\partial x^2$, is examined and it is shown that these quantities are not proportional to each other, in general; however, under certain specified conditions, all three of these quantities are proportional with each other and with $\varphi_i(r, \theta, x, t)$ and $\partial^2\varphi_i/\partial x^2$ (at the inner membrane surface). The relation of these results to those of one-dimensional cable theory is discussed.

INTRODUCTION

This paper is concerned with the volume distribution of electric potential, both inside and outside a membrane cylinder, during passive membrane potential decay. It is concerned specifically with cylinders of finite length, where both ends are sealed with membrane.

A major objective is to demonstrate and contrast two different sets of decay time constants: the time constants for equalization of membrane potential around the circumference of a passive membrane cylinder are shown to be several orders of magnitude shorter than those for equalization of membrane potential along the length of the cylinder, for length to diameter ratios relevant to neuronal dendritic trees.

By providing a complete mathematical solution for the transient distribution of interior and exterior potential, during passive membrane potential decay, the present results help clarify the approximations involved in standard nerve cable theory.

Historical Background

The earliest mathematical solutions of potential in cylindrical coordinates associated with a nerve membrane cylinder were provided by the classical studies of Weber (1873 *a*, *b*). Weber was a friend and colleague of Hermann during the early days of core conductor theory. It is noteworthy that Weber made basic contributions to the field of Bessel functions (see Watson (1944) p. 308–319 and 391–411), as well as basic contributions to mathematical physics (see classic textbook by Gray and Mathews (1895) in which Chapter 12, entitled "Steady Flow of Electricity or of Heat in Uniform Isotropic Media", is based explicitly on Weber's results). The third section of (Weber, 1873 *b*) presents his most general case; it includes volume distributions of potential both inside and outside the membrane cylinder, as a function of all three cylindrical coordinates. Weber dealt with complications associated with an electrode source and sink; however he did not present the results needed for the present paper: he did not consider decay transients; also, his insulating outer cylindrical boundary caused mathematical complications which are avoided in the present paper.

A more recent study, by Weinberg (1941), was built upon Weber's results. Weinberg's focus of attention was upon those solutions that are most relevant to propagation of an impulse in the iron wire model. He did not treat the class of solutions derived in the present paper.

The study by Lorente de Nó (1947) provided thoughtful discussion and computed (approximate) solutions of the distribution of current and potential in the volume surrounding a nerve cylinder. This study did not provide a rigorous solution of the relevant boundary value problem; it did provide a useful approximate solution by using one-dimensional cable theory to compute membrane current density, i_m, and then using i_m to compute the extracellular potential distribution.[1] This concept, that the extracellular potential distribution is that solution of Laplace's equation which matches the sources and sinks of current due to i_m plus any electrodes, has also been used to compute distributions of extracellular potential in the volume surrounding model dendritic neurons, both for the case of a single dendrite, and the several cases of multiple radiate dendrites (Rall, 1962); the full details of those results have not yet been published.

Recently, several authors (Plonsey, 1964; Clark and Plonsey, 1966, 1968; Geselowitz, 1966; Hellerstein, 1968; and Pickard, 1968) have contributed to the theoretical analysis and interpretation of potential distributions associated with membrane cylinders of infinite length. They have treated dependence upon two cylindrical coordinates, both inside and outside the membrane, and have clarified

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[1] A possible source of confusion can be avoided by using $\partial^2 V_i/\partial x^2$ (instead of $\partial^2 V_e/\partial x^2$) as the quantity that is proportional to i_m in the formulation of Lorente de No (1947, p. 396–407). This is because the intracellular potential distribution remains essentially unchanged by a change in extracellular volume, while the extracellular potential distribution is changed significantly; see sections *D* and *E*, as well as *C*, in part III below.

the relation of these results to one-dimensional cable theory. However, these authors did not treat cylinders of finite length, or dependence upon θ, or passive decay transients.

The papers of Falk and Fatt (1964) and Eisenberg (1967) do include the coordinate, θ, inside the axon, but treat the external volume as isopotential. They express their results in terms of transfer impedance, and do not treat the problem presented here. During my final revision of this manuscript, I received a preprint, from Eisenberg and Johnson, of a chapter to appear in Vol. 20 of *Progress in Biophysics*. This preprint also treats the external volume as isopotential; it does not treat the problem of the present paper. It does include useful discussion and detail relevant to eccentrically placed intracellular electrodes. Valuable discussion and review are also provided by Taylor (1963) and by Cole (1968).

I. STATEMENT AND SOLUTION OF CYLINDRICAL PROBLEM

Statement of the Problem

Let the axis of the cylinder coincide with the x-axis, and let the radius, r, and the angle, θ, complete the cylindrical coordinate system. Let $\varphi_i(r, \theta, x, t)$ represent the electric potential at every point inside the membrane cylinder, of radius, $r = a$, and let $\varphi_e(r, \theta, x, t)$ represent the electric potential at every point outside the membrane cylinder. Assume that the internal medium is purely resistive, homogeneous and isotropic, with a specific resistance, R_i (ohm cm); also assume that the external volume is purely resistive, homogeneous and isotropic, with a specific resistance, R_e (ohm cm). The assumption of pure resistance in both volumes implies that the potential distribution in each volume adjusts instantaneously[2] to the current sources and sinks provided by the membrane and by any electrodes; thus time dependence of this potential distribution can result only from changes in applied current and/or charging or discharging of the membrane capacity.

For all points not at the membrane and not at a source or sink of applied electric current, Laplace's equation holds both inside and outside (cf. Stratton 1941, No. 33, p. 222, as well as p. 162 and 195)

$$\nabla^2\varphi_i = 0, \qquad \text{for } r \leqq a \tag{1.1}$$

and

$$\nabla^2\varphi_e = 0, \qquad \text{for } r \geqq a \tag{1.2}$$

where θ runs from 0 to 2π, and x may be finite or infinite, depending upon the par-

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[2] The treatment by Pickard (1968) defers this simplifying assumption to a later stage of the analysis. Rosenfalck (see note added at the end of this paper) begins with Maxwell's equations and then examines simplifying assumptions.

ticular problem; the Laplacian, $\nabla^2\varphi$, in cylindrical coordinates, is expressed explicitly below in equation (1.6). In particular, φ_i is finite at $r = 0$, unless an electrode applies current at $r = 0$; also, φ_e is regular at infinity, unless an electrode applies current at infinity.

At the membrane, $r = a$, we require continuity of current normal to the membrane surface; this gives the boundary condition

$$(1/R_i)[-\partial\varphi_i/\partial r]_{r=a} = I_m = (1/R_e)[-\partial\varphi_e/\partial r]_{r=a} \tag{1.3}$$

which holds for any distribution of sources and sinks inside and outside. The membrane current density, I_m, is a function of θ and x, and can also be a function of time.

For a passive nerve membrane, the expression for membrane current density in terms of membrane resistance, R_m (ohm cm^2), and membrane capacitance, C_m (farad cm^{-2}), is well established

$$I_m = C_m(\partial V_m/\partial t) + (V_m - E_r)/R_m \tag{1.4}$$

where

$$V_m = \varphi_i(a, \theta, x, t) - \varphi_e(a, \theta, x, t)$$

and E_r, the resting membrane *EMF* (inside minus outside) is assumed to be independent of θ, x, and t.

For most of this paper, we restrict the range of x from 0 to ℓ, and we assume the boundary conditions

$$\left.\begin{aligned}\partial\varphi_i/\partial x &= 0\\ \partial\varphi_e/\partial x &= 0\end{aligned}\right\} \quad \text{at} \quad x = 0, \quad \text{and at} \quad x = \ell. \tag{1.5}$$

In other words, the membrane cylinder has sealed ends, and the external medium also has insulated boundaries[3] at $x = 0$ and $x = \ell$.

Separation of Variables

We will try the assumption that the potential (both interior and exterior) can be expressed as a product of four functions, each of three depends only upon one of the space variables, and the fourth depends only upon time; thus

$$\varphi(r, \theta, x, t) = F(r)G(\theta)H(x)Q(t).$$

Laplace's equation in these cylindrical coordinates is

$$\partial^2\varphi/\partial r^2 + (1/r)(\partial\varphi/\partial r) + (1/r^2)(\partial^2\varphi/\partial\theta^2) + \partial^2\varphi/\partial x^2 = 0. \tag{1.6}$$

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[3] The extension of the external volume to the range $0 \leqq x \leqq 2\ell$ is discussed and illustrated in part III, below.

If one uses the separated form of $\varphi(r, \theta, x, t)$ in equation 1.6, and one then multiplies through by $r^2/(FGH)$, one obtains

$$r^2F''/F + rF'/F + r^2H''/H + G''/G = 0 \tag{1.7}$$

where the primes indicate ordinary differentiation with respect to the relevant space variable, in each case.

Because this equation must hold for all values of r, θ and x, it follows that G''/G must be independent of θ, and also that H''/H must be independent of x; in other words, equation 1.7 can be separated into the three ordinary differential equations

$$d^2G/d\theta^2 = -n^2G \tag{1.8}$$

$$d^2H/dx^2 = -k^2H \tag{1.9}$$

and

$$r^2F'' + rF' - (k^2r^2 + n^2)F = 0 \tag{1.10}$$

where n^2 and k^2 are known as separation constants. Although separation constants of the opposite sign can be chosen, the advantages of the above choice will soon be apparent.

Solutions of the Separate Ordinary Differential Equations

The general solutions of equations 1.8 and 1.9 can be expressed

$$G(\theta) = C \cos (n\theta) + C_* \sin (n\theta)$$

and

$$H(x) = D \cos (kx) + D_* \sin (kx).$$

Because the value of θ goes only from 0 to 2π, we require that $G(0) = G(2\pi)$. This condition is satisfied whenever n is an integer or zero. Because we are not really interested in phase shift with respect to θ, we can choose the origin, $\theta = 0$, such that $C_* = 0$. Thus we are interested in the set of solutions of equations 1.8 having the form

$$G_n(\theta) = C \cos (n\theta) \tag{1.11}$$

where n is an integer or zero; the coefficient, C, is independent of θ.

We assume that the value of x goes only from 0 to ℓ, and that the boundary condition is $dH/dx = 0$ at $x = 0$ and $x = \ell$; see equation 1.5. This restricts our solutions of equation 1.9 to the set having the form

$$H_M(x) = D \cos (kx) \tag{1.12}$$

where

$$k = M\pi/\ell \tag{1.13}$$

and M is an integer or zero; the coefficient, D, is independent of x.

For the special case, $M = 0 = k$, which means that $H(x)$ and $\varphi(r, \theta, x, t)$ are independent of x, equation 1.10 becomes simplified and has a simple general solution,

$$F_{n,0}(r) = Ar^{n} + Br^{-n} \tag{1.14}$$

where the coefficient, A, must be set equal to zero for the exterior region, $r \geqq a$, which extends to $r = \infty$, and the coefficient, B, must be set equal to zero for the interior region, $r \leqq a$, which includes $r = 0$. The coefficients, A and B are independent of r.

For the more general case, where M and k are different from zero, equation 1.10 has the general solution

$$F_{n,M}(r) = AI_{n}(kr) + BK_{n}(kr) \tag{1.15}$$

where k is defined by equation 1.13 and I_n and K_n represent modified Bessel functions; see Olver (1964, section 9.6), Carslaw and Jaeger (1959, Appendix III), or part II, below. The coefficients, A and B, are independent of r. It may be noted that $I_n(kr)$ remains finite at $r = 0$, but, resembles exponential growth for large values of r; conversely $K_n(kr)$ resembles an exponential decay for large values of r, but blows up at $r = 0$. Therefore, as with equation 1.14, the coefficient, A, must be set equal to zero for the exterior region, $r \geqq a$, and the coefficient, B, must be set equal to zero for the interior region, $r \leqq a$.

Time Dependence

For each pair of values of n and M, above, there is a solution

$$\varphi_{n,M}(r, \theta, x, t) = F_{n,M}(r)G_{n}(\theta)H_{M}(x)Q_{n,M}(t)$$

which satisfies Laplace's equation as well as the several constraints introduced with equations 1.11–1.15. The time dependent function, $Q_{n,M}(t)$, can be different for each pair of values of n and M, and for different initial conditions. Its form must be determined from the membrane boundary conditions, equations 1.3 and 1.4. This will be done below, first for the case, $n = 1$, with $M = 0 = k$.

Example of Simplest Transient Involving Dependence upon θ

Consider $n = 1$ with $M = 0$. This provides for a dependence upon r, θ, and t, but not upon x; this avoids complication from Bessel functions. Let

$$\varphi_i(r, \theta, t) = E_r + A_{1,0}r \cos\theta \, Q_{1,0}(t) \tag{1.16}$$

and

$$\varphi_e(r, \theta, t) = B_{1,0}r^{-1} \cos\theta \, Q_{1,0}(t) \tag{1.17}$$

where the coefficients, $A_{1,0}$ and $B_{1,0}$ are independent of r, θ and t. It follows, from equation 1.3 that

$$\begin{aligned} I_m(\theta, t) &= -(A_{1,0}/R_i) \cos\theta \, Q_{1,0}(t) \\ &= a^{-2}(B_{1,0}/R_e) \cos\theta \, Q_{1,0}(t) \end{aligned} \tag{1.18}$$

and from this, that

$$B_{1,0} = -\,(R_e/R_i)a^2 A_{1,0} \, . \tag{1.19}$$

It follows from equations 1.4 and 1.19 that

$$I_m(\theta, t) = A_{1,0}(a + aR_e/R_i)[C_m(dQ_{1,0}/dt) + Q_{1,0}/R_m] \cos\theta. \tag{1.20}$$

When equations 1.18 and 1.20 are both multiplied by $R_i R_m$ and combined, rearrangement yields the differential equation

$$\tau_m(dQ_{1,0}/dt) = -\left(\frac{R_m + a(R_i + R_e)}{a(R_i + R_e)}\right) Q_{1,0} \tag{1.21}$$

where $\tau_m = R_m C_m$ is the passive membrane time constant. The solution of this differential equation is an exponential decay which can be expressed

$$Q_{1,0}(t) = Q_{1,0}(0) \exp\{-t/\tau_{1,0}\} \tag{1.22}$$

where the time constant, $\tau_{1,0}$, is defined

$$\tau_{1,0} = \left(\frac{a(R_i + R_e)}{R_m + a(R_i + R_e)}\right) \tau_m \, . \tag{1.23}$$

Typically, R_m is much larger than $a(R_i + R_e)$, with the result that $\tau_{1,0}$ is much smaller than τ_m. For example, if $R_m = 10^3$ ohm cm², $a = 10\mu = 10^{-3}$ cm, and $R_i + R_e = 10^2$ ohm cm, it follows that $\tau_{1,0}$ is smaller than τ_m by a factor of 10^4. For passive membrane potential decay, if the initial distribution of membrane potential consists of two components, one that is uniform (independent of θ and x), and another that is proportional to cos θ, these results imply that the θ-dependent component would decay (equalize) 10,000 times more rapidly than the uniform component.

Equalizing Time Constants For n ≠ 0, M = 0

By the same method illustrated in the previous section, one obtains the more general result

$$\tau_{n,0} = \left(\frac{a(R_i + R_e)}{nR_m + a(R_i + R_e)}\right)\tau_m. \tag{1.24}$$

For the typical case of R_m much larger than $a(R_i + R_e)$, we have approximately

$$\tau_{n,0} \simeq \left(\frac{a(R_i + R_e)}{nR_m}\right)\tau_m \tag{1.25}$$

which expresses an approximate inverse proportionality between $\tau_{n,0}$ and n. For the particular values cited in the preceding paragraph, this means that a component of membrane potential dependent upon cos $(n\theta)$ but not upon x, would decay (equalize) $n \times 10^4$ times more rapidly than would a component that was uniformly distributed. Note that the results above do not depend upon Bessel function properties.

Example of Transient Involving Dependence upon x as well as θ

Consider any particular pair of values, n and M, with the coefficients, $A_{n,M}$ and $B_{n,M}$ independent of r, θ, x and t. Using equation 1.15, we express

$$\varphi_i(r, \theta, x, t) = E_r + A_{n,M} I_n(kr) \cos(n\theta) \cos(kx)\ Q_{n,M}(t) \tag{1.26}$$

$$\varphi_e(r, \theta, x, t) = B_{n,M} K_n(kr) \cos(n\theta) \cos(kx)\ Q_{n,M}(t). \tag{1.27}$$

It follows from equation 1.3 that

$$\begin{aligned} I_m(\theta, x, t) &= -(A_{n,M}/R_i)[I_n'(kr)]_{r=a} \cos(n\theta) \cos(kx)\ Q_{n,M}(t) \\ &= -(B_{n,M}/R_e)[K_n'(kr)]_{r=a} \cos(n\theta) \cos(kx)\ Q_{n,M}(t) \end{aligned} \tag{1.28}$$

and that

$$B_{n,M} = (R_e/R_i)[I_n'(kr)/K_n'(kr)]_{r=a} A_{n,M} \tag{1.29}$$

where the "primed" notation designates differentiation with respect to r. From equations 1.4, 1.28, and 1.29 algebraic manipulations similar to those used to obtain previous equations 1.20 and 1.21 yield the differential equation

$$\tau_m(dQ_{n,M}/dt) = -\left(\frac{R_m + \alpha_n R_i - \beta_n R_e}{\alpha_n R_i - \beta_n R_e}\right) Q_{n,M} \tag{1.30}$$

where

$$\alpha_n = [I_n(kr)/I_n'(kr)]_{r=a} \tag{1.31}$$

and

$$\beta_n = [K_n(kr)/K_n'(kr)]_{r=a} \tag{1.32}$$

and, it can be shown (see equations 2.15 and 2.20 of part II, below) that for small values of ka, and $n > 0$

$$\alpha_n \simeq a/n \tag{1.33}$$

and

$$\beta_n \simeq -a/n. \tag{1.34}$$

When ka is not small, one should use the exact expressions for α_n and β_n provided by equations 2.17 and 2.22 of part II, below; see also Table I and the better approximations provided by equations 2.15, 2.25, and 2.26 of part II, below. The results for $n = 0$ differ, as shown in equations 1.38 and 1.39, below.

The solution of this differential equation 1.30 can be expressed

$$Q_{n,M}(t) = Q_{n,M}(0) \exp \{-t/\tau_{n,M}\} \tag{1.35}$$

where the time constant, $\tau_{n,M}$, is defined

$$\tau_{n,M} = \left(\frac{\alpha_n R_i - \beta_n R_e}{R_m + \alpha_n R_i - \beta_n R_e}\right) \tau_m. \tag{1.36}$$

It is interesting that for small values of ka, and $n > 0$, the approximations 1.33 and 1.34 give $\tau_{n,M}$ equal to the $\tau_{n,0}$ of previous equation 1.24. In other words, for ka small, the result obtained using Bessel functions (for $M > 0$) is the same as that obtained without Bessel functions (for $M = 0$). Also, for the usual case of R_m much larger than $a(R_i + R_e)$, this time constant is approximately

$$\tau_{n,M} \simeq \left(\frac{a(R_i + R_e)}{nR_m}\right) \tau_m \tag{1.37}$$

for $n \neq 0$.

This result implies that a component of membrane potential dependent upon θ and x, as in the product, $\cos(n\theta) \cos(kx)$, decays just as rapidly as when it is dependent upon θ, but not upon x (cf. equation 1.25). This result may be surprising at first glance; however, it can be understood intuitively on the basis that the equalization around the circumference of the cylinder is much more rapid than equalization with respect to length.[4] It may be noted that small $ka \equiv M\pi a/\ell$ implies a length of cylinder that is large compared with the radius. If ka were not small, either because of a short length or a large M, it can be seen, intuitively, that equalization with respect to length would be about as rapid as equalization around the circumference, and that $\tau_{n,M}$ should then be smaller than $\tau_{n,0}$; this expectation is confirmed by the fact that α_n and $-\beta_n$ both become smaller than a/n, as can be verified from equations 2.15, 2.25, and 2.26 as well as Table I in part II, below.

Simplest Example of Transient Dependent upon x But Not θ

Here, $n = 0$, and the Bessel function ratios of equations 1.31 and 1.32 can be shown (see equations 2.3 and 2.8 of part II, below) to be well approximated, for ka small, by

$$\alpha_0 \simeq 2/(k^2a) = (2/a)(M\pi/\ell)^{-2} \tag{1.38}$$

$$\beta_0 \simeq a \log_e(ka) = a \log_e(M\pi a/\ell). \tag{1.39}$$

When ka is not small, one should use the exact expressions for α_0 and β_0 provided by equations 2.5 and 2.10 of part II, below; see also Table I and the better approximations provided by equations 2.3 and 2.8 of part II, below.

Consider first the special case where $R_e = 0$. Then equation 1.36 implies that

$$\tau_m/\tau_{0,M} = 1 + R_m/(\alpha_0 R_i). \tag{1.40}$$

For ka small, the value of α_0 from equation 1.38 yields

$$\begin{aligned}\tau_m/\tau_{0,M} &= 1 + (M\pi/\ell)^2(aR_m)/(2R_i)\\ &= 1 + (M\pi/L_0)^2 \end{aligned} \tag{1.41}$$

where

$$L_0 = \ell/\lambda_0 \tag{1.42}$$

and

$$\lambda_0 = \sqrt{aR_m/(2R_i)} \tag{1.43}$$

which constitutes a result of considerable relevance to one-dimensional nerve cable theory.

Significance for λ of Standard Nerve Cable Theory

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[4] This is discussed and illustrated in part III (Fig. 1) below; see also later footnote 5.

The definition of the characteristic length, λ, is

$$\lambda = \sqrt{r_m/(r_i + r_e)}$$

where

$$r_m = R_m/(2\pi a)$$
$$r_i = R_i/(\pi a^2)$$

and r_e is usually defined only when the external medium is a thin shell of conducting fluid which can be characterized by a resistance per unit length of cylinder. For large external volumes, it is customary to avoid mathematical complications by setting $R_e = 0$; e.g. (Rall, 1959, p. 495); then one can write

$$\lambda_0 = \sqrt{r_m/r_i}$$
$$= \sqrt{aR_m/(2R_i)}$$

which is the same as equation 1.43 above.

This demonstrates agreement between standard cable theory (for $R_e = 0$), and the results of the solution obtained here, using Laplace's equation for the interior (with $n = 0$ and ka small) and where the external volume is neglected by setting $R_e = 0$. Restating this, the equalizing time constants (equation 1.40) obtained for $\varphi_i(r, x, t)$, with $R_e = 0$, have simplified (with ka small) to the same form (equation 1.41) as that obtained from one-dimensional cable theory (Rall, 1969, equations 2 and 16): in both cases, the value of L (L_0 of equation 1.42) is based upon the same value for the characteristic length (equation 1.43). Because of this agreement for the special case, $R_e = 0$, it is of particular interest to explore the consequences of the present results when $R_e \neq 0$; cf. Clark and Plonsey (1966, 1968), Hellerstein (1968), and Pickard (1968) for cylinders of infinite length; see also Taylor (1963) and Cole (1968).

Effect of R_e upon Time Constants and upon λ

Here we note that

$$(\alpha_0 R_i - \beta_0 R_e)/R_m = (\alpha_0 R_i/R_m)(1 - (\beta_0/\alpha_0)(R_e/R_i))$$
$$= \gamma^2 L_0^2/(M\pi)^2$$

and, hence, from equation 1.36, that

$$\tau_m/\tau_{0,M} = 1 + (M\pi/\gamma L_0)^2 \qquad (1.44)$$

where L_0 is defined by equations 1.42 and 1.43, and γ is a correction factor defined exactly by

$$\gamma^2 = (\alpha_0/2)(k^2a)[1 - (\beta_0/\alpha_0)(R_e/R_i)] \tag{1.45}$$

where α_0 and β_0 are defined exactly by equations 2.5 and 2.10 in part II, below. When ka is small, one can use equations 1.38 and 1.39 to obtain the approximate expression

$$\gamma^2 \simeq 1 + (R_e/2R_i)(ka)^2 \log_e(1/ka) \tag{1.46}$$

In other words, when $R_e \neq 0$, $\tau_{0,M}$ is defined by equation 1.44, which differs from the previous result for $R_e = 0$ (equation 1.41) only by the correction factor, γ, which is typically close to unity. For example, if $R_e = 2R_i$, and if the quantity, $ka = M\pi a/\ell$, is 0.1, then equation 1.46 gives $\gamma^2 \simeq 1.023$, or $\gamma \simeq 1.01$; for this case, the appropriate value of λ would be about 1 per cent shorter than λ_0; the appropriate value of L would be about 1 per cent longer than L_0. Smaller values of ka result in even smaller correction factors.[5] Larger values of ka require that equation 1.45 be evaluated exactly. It should be noted that, for any particular value of $\pi a/\ell$, different values of M imply different values of γ; however, as long as $M\pi a/\ell$ remains less than 0.1, the differences are trivial.

General Class of Solutions to Present Problem

We have displayed several examples of solutions to the boundary value problem defined by equations 1.1 through 1.5. For each pair of values of n and M, we have obtained a separate solution. If we restrict the values of n and M to positive integers and zero, then all members of the resulting class of solutions are linearly independent of each other (negative values of n and M also provide solutions, but these solutions are not independent of the others). Because Laplace's equation is both linear and homogeneous, superpositions of these solutions are also solutions. Thus, we can define a much larger class of solutions consisting of all possible linear combinations of the separate solutions for different n and M, of the linearly independent class above. These will now be stated.

Consider the general initial condition of membrane potential,

$$\begin{aligned} V_m(\theta, x, 0) &\equiv \varphi_i(a, \theta, x, 0) - \varphi_e(a, \theta, x, 0) \\ &= E_r + \sum_{n=0}^{\infty} \left(\cos(n\theta) \sum_{M=0}^{\infty} C_{n,M} \cos(M\pi x/\ell) \right) \end{aligned} \tag{1.47}$$

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[5] Because frequent reference is made to small values of $ka = M\pi a/\ell$, it is useful to note the relation between $\pi a/\ell$ and L_0, for any given cylinder. For $R_m/R_i = 20$ cm, it follows from equations 1.42 and 1.43 that $\pi a/\ell = \sqrt{a}/L_0$, when the radius, a, is expressed in cm. For this R_m/R_i value, $\pi a/\ell = 0.1$ corresponds, for example, to $a = 1\ \mu$ with $L_0 = 0.1$, or to $a = 9\ \mu$ with $L_0 = 0.3$; also $\pi a/\ell = 0.01$ corresponds, for example, to $a = 1\ \mu$ with $L_0 = 1$, or to $a = 9\ \mu$ with $L_0 = 3$.

which may have been produced by some previous combination of applied current and/or membrane activity. We assume that all applied current and/or membrane activity is turned off at $t = 0$. Then, the decay of membrane potential, for completely passive membrane, can be expressed

$$V_m(\theta, x, t) = E_r + \sum_{n=0}^{\infty} \left(\cos(n\theta) \sum_{M=0}^{\infty} C_{n,M} \cos(M\pi x/\ell) \exp(-t/\tau_{n,M}) \right) \quad (1.48)$$

where the resting potential, E_r, and the coefficients, $C_{n,M}$, are independent of θ, x, and t; the time constants, $\tau_{n,0}$, are defined by equation 1.24 and can usually be approximated by equation 1.25, while, for $M > 0$, the time constants, $\tau_{n,M}$ are defined by equation 1.36 and can usually be approximated by equation 1.37 for $n > 0$, and by equation 1.44 for $n = 0$. It may be noted that $n = 0$ with $M = 0$ specifies a component of V_m that is independent of both θ and x, and that its time constant, $\tau_{0,0}$ equals τ_m, as it should. Also, for physiological values (see example following equation 1.23, the values of $\tau_{n,M}$ for $n > 0$ are smaller than τ_m by a factor of 10^4, while the value of $\tau_{0,1}$ is smaller than τ_m by a factor of from 2 to 5 for L values from $\pi/2$ to π (see equations 1.41 and 1.44).

The associated decay of potential in the interior region, $r \leqq a$, $0 \leqq \theta \leqq 2\pi$, $0 \leqq x \leqq \ell$, can be expressed

$$\varphi_i(r, \theta, x, t) = E_r + \sum_{n=0}^{\infty} \left(A_{n,0} r^n \cos(n\theta) \exp(-t/\tau_{n,0}) + \cos(n\theta) \sum_{M=1}^{\infty} A_{n,M} I_n(kr) \cos(kx) \exp(-t/\tau_{n,M}) \right) \quad (1.49)$$

where $k = M\pi/\ell$, and the time constants are the same as those specified for equation 1.48; the coefficients, $A_{n,M}$, are independent of r, θ, x, and t, and are related to $C_{n,M}$ as specified below in equations 1.51–1.53.

The associated decay of potential in the exterior region, $r \geqq a$, $0 \leqq \theta \leqq 2\pi$, $0 \leqq x \leqq \ell$, can be expressed

$$\varphi_e(r, \theta, x, t) = \sum_{n=0}^{\infty} \left(B_{n,0} r^{-n} \cos(n\theta) \exp(-t/\tau_{n,0}) + \cos(n\theta) \sum_{M=1}^{\infty} B_{n,M} K_n(kr) \cos(kx) \exp(-t/\tau_{n,M}) \right) \quad (1.50)$$

where $k = M\pi/\ell$, and the time constants are the same as those specified for equation 1.48; the coefficients, $B_{n,M}$ are independent of r, θ, x, and t, and are related to $C_{n,M}$ as specified below in equations 1.54–1.56.

The relation between the coefficients $A_{n,M}$ and $B_{n,M}$ follows from the boundary condition (equation 1.3), and has already been stated explicitly by equation 1.19 for the case $n = 1$ with $M = 0$, and by equation 1.29, for $M > 0$. The corresponding result for $M = 0$ with $n > 1$ can be expressed

$$B_{n,0} = -(R_e/R_i)a^{2n}A_{n,0}\,.$$

The dependence of the coefficients upon the $C_{n,M}$ of equation 1.47 can be obtained by substituting equations 1.49 and 1.50 into equation 1.47, and noting that $B_{0,0}$ must be zero, because we have assumed zero applied current. Thus, we find that

$$A_{0,0} = C_{0,0} \tag{1.51}$$

$$A_{n,0} = \left(\frac{R_i a^{-n}}{R_i + R_e}\right) C_{n,0} \tag{1.52}$$

$$A_{n,M} = \left(\frac{\alpha_n R_i/I_n(ka)}{\alpha_n R_i - \beta_n R_e}\right) C_{n,M} \tag{1.53}$$

and that

$$B_{0,0} = 0 \tag{1.54}$$

$$B_{n,0} = \left(\frac{-R_e a^n}{R_i + R_e}\right) C_{n,0} \tag{1.55}$$

$$B_{n,M} = \left(\frac{\beta_n R_e/K_n(ka)}{\alpha_n R_i - \beta_n R_e}\right) C_{n,M} \tag{1.56}$$

where $ka = M\pi a/\ell$ (see equation 1.13), and α_n and β_n are the Bessel function ratios defined by equations 1.31 and 1.32. For ka small, equations 1.33, 1.34, 1.38, 1.39, 2.13, and 2.18 yield the approximations

$$A_{0,M} \simeq \left(\frac{2R_i}{2R_i + (ka)^2 R_e \log_e (1/ka)}\right) C_{0,M} \tag{1.57}$$

and, for $n > 0$

$$A_{n,M} = \left(\frac{R_i (ka/2)^{-n} n!}{R_i + R_e}\right) C_{n,M} \tag{1.58}$$

also

$$B_{0,M} \simeq \left(\frac{-(ka)^2 R_e}{2R_i + (ka)^2 R_e \log_e (1/ka)}\right) C_{0,M} \tag{1.59}$$

and, for $n > 0$

$$B_{n,M} \simeq \left(\frac{-2(ka/2)^n R_e/(n-1)!}{R_i + R_e}\right) C_{n,M} \tag{1.60}$$

These results are discussed in part III, below.

II. APPROXIMATIONS TO CERTAIN BESSEL FUNCTION RATIOS

The modified Bessel functions, $I_n(z)$ and $K_n(z)$, are available in tabulated form and can also be approximated by means of series expansions. A convenient reference for both tables and series expansions is provided by the chapter (Olver, 1964) in the Handbook of Mathematical Functions, edited by Abramowitz and Stegun. The properties of these functions and their series expansions are summarized in many places (e.g. Carslaw and Jaeger, 1959, Appendix III); these functions are also known as "Bessel functions of purely imaginary argument" (Watson, 1944, p. 77–80). Here, we require expressions for several ratios of modified Bessel functions and their derivatives with respect to r. Because we are interested in approximations appropriate for small values of the argument, ascending series are required.

Results for $n = 0$

The first three terms of the ascending series for $I_0(z)$, (see equation 9.6.12 of Olver, 1964), provide the approximation

$$I_0(kr) \simeq 1 + (kr)^2/4 + (kr)^4/64 \tag{2.1}$$

for small values of kr; the derivative with respect to r can be expressed

$$I_0'(kr) \simeq k^2r/2 + k^4r^3/16 \tag{2.2}$$

Therefore, we can express the ratio

$$\frac{I_0(kr)}{I_0'(kr)} \simeq \left(\frac{2}{k^2r}\right)\left(\frac{1 + (kr)^2/4}{1 + (kr)^2/8}\right). \tag{2.3}$$

Where $r = a$, and ka is small, this reduces to previous equation 1.38 for α_0.

To obtain the exact expression for this ratio, we make use of the Bessel function property,

$$I_0'(kr) = kI_1(kr) \tag{2.4}$$

where the "prime" designates differentiation with respect to r. The ratio, α_0, can be expressed

$$\begin{aligned}\alpha_0 &\equiv [I_0(kr)/I_0'(kr)]_{r=a}\\ &= (1/k)I_0(ka)/I_1(ka)\end{aligned} \tag{2.5}$$

and can be evaluated by using Table 9.8 of Olver (1964).

In order to test the two levels of approximation suggested by equation 2.3, con-

TABLE I

APPROXIMATE AND EXACT VALUES OF RATIOS

	α_0/a*	β_0/a‡	α_1/a§	β_1/a‖
ka = 0.1				
1° Approx.	200.0	−2.3026	1.0	−1.0
2° Approx.	200.25	−2.4631	0.9975	−0.9753
Exact	200.25	−2.4631	0.9975	−0.9760
ka = 0.5				
1° Approx.	8.0	−0.6931	1.0	−1.0
2° Approx.	8.242	−1.1026	0.9429	−0.7887
Exact	8.247	−1.1162	0.9417	−0.9729
ka = 1.0				
1° Approx.	2.0	0.0	1.0	−1.0
2° Approx.	2.222	−0.5708	0.8182	−0.7720
Exact	2.240	−0.6995	0.8063	−0.5884

* For α_0, exact values from equation 2.5; 1° and 2° approx. from equation 2.3.

‡ For β_0, exact values from equation 2.10; 1° and 2° approx. from equation 2.8.

§ For α_1, exact values from equation 2.17; 1° and 2° approx. from equation 2.15.

‖ For β_1, exact values from equation 2.22; 1° and 2° approx. from equation 2.25.

sider numerical examples for the three cases, $ka = 0.1$, 0.5, and 1. For $ka = 0.1$, the exact value to five significant figures, is $\alpha_0 = 200.25a$, from equation 2.5. The second order approximation obtained with equation 2.3 agrees with all five of these significant figures. The first order approximation (equation 1.38) gives $200a$, which differs only by about 0.1%. The first column of Table I summarizes these results together with those obtained for $ka = 0.5$ and 1.0; it can be seen that the first order approximation differs by about 3 and 12% respectively, while the second order approximation differs by less than 1% in both cases.

For $K_0(kr)$, the limiting form, as $kr \rightarrow 0$, (equation 9.6.8 of Olver, 1964) is simply

$$K_0(kr) \simeq -\log_e(kr).$$

Differentiation with respect to r yields simply, $-(1/r)$, with the result that the limiting value of the ratio, $K_0(kr)/K_0'(kr)$ is simply $r \log_e(kr)$, as $kr \rightarrow 0$. For $r = a$, and ka very small, this agrees with previous equation, 1.39, for β_0.

By using the first few terms of the ascending series (see equations 9.6.13 and 9.8.5 of Olver, 1964), we can express the approximation

$$K_0(kr) \simeq -\log_e(kr/2)\ [1 + (kr/2)^2] - 0.5772 + 0.4228\ (kr/2)^2 \tag{2.6}$$

Differentiation with respect to r yields

$$K_0'(kr \simeq -(1/r)[1 + (kr/2)^2(0.1544 + 2\log_e(kr/2))]. \tag{2.7}$$

Thus, the approximate ratio can be expressed

$$\frac{K_0(kr)}{K_0'(kr)} \simeq \frac{r \log_e (kr)[1 + (kr/2)^2] - r[0.116 + 1.116(kr/2)^2]}{1 + (kr/2)^2[2 \log_e (kr) - 1.232]} \qquad (2.8)$$

It can be seen also here that when $r = a$ and ka is small, this approximation reduces in the limit to previous equation 1.39, for β_0.

To obtain the exact expression for this ratio, we make use of the Bessel function property,

$$K_0'(kr) = -kK_1(kr) \qquad (2.9)$$

where the "prime" designates differentiation with respect to r. The ratio,

$$\begin{aligned} \beta_0 &\equiv [K_0(kr)/K_0'(kr)]_{r=a} \\ &= -(1/k)K_0(ka)/K_1(ka) \qquad (2.10) \end{aligned}$$

can be evaluated by using Table 9.8 of Olver (1964). A comparison of the two levels of approximation suggested by equation 2.8, with the exact value from equation 2.10, is provided by the illustrative examples shown in the second column of Table I. It can be seen that the second order approximation agrees to five significant figures for $ka = 0.1$, and differs only by about 1% for $ka = 0.5$; it differs by nearly 20% for $ka = 1$. Although the first order approximation does differ by about 6%, for $ka = 0.1$, this is not critical because β_0 is nearly 100 times smaller than α_0. The first order approximation differs by nearly 40% for $ka = 0.5$ and by 100% for $ka = 1$.

From these results, it can be concluded that equation 1.38 and 1.39 provide good approximations to equations 2.5 and 2.10 when ka is less than 0.1; however, for $ka = 1$, it is necessary to use at least the better approximations provided by equations 2.3 and 2.8.

Equations 2.4 and 2.9 can also be used to provide an exact expression for the ratio

$$I_0'(kr)/K_0'(kr) = -I_1(kr)/K_1(kr) \qquad (2.11)$$

which can be evaluated from tables. However, if kr is small, one can use equations 2.2 and 2.7 to obtain an approximation whose limiting form is

$$I_0'(kr)/K_0'(kr) \simeq -(1/2)(kr)^2 \qquad (2.12)$$

This is relevant to previous equation 1.29 when $n = 0$ and kr is small.

Results for $n > 0$

When n is a positive integer the first two terms of the ascending series for $I_n(z)$, (see equation 9.6.10 of Olver, 1964), provide the approximation

$$I_n(kr) \simeq (kr/2)^n/n! + (kr/2)^{n+2}/(n+1)! \tag{2.13}$$

or small values of kr; the derivative with respect to r can be expressed

$$I_n'(kr) \simeq (kr/2)^{n-1}(nk/2n!) + (kr/2)^{n+1}(n+2)(k/2)/(n+1)! \tag{2.14}$$

Therefore, we can express the ratio

$$\frac{I_n(kr)}{I_n'(kr)} \simeq \left(\frac{r}{n}\right)\left(\frac{1 + (kr/2)^2/(n+1)}{1 + (kr/2)^2(n+2)/n(n+1)}\right). \tag{2.15}$$

When $r = a$, and ka is small, this reduces to previous equation 1.33, for α_n.

To obtain the exact expression for this ratio, we make use of the Bessel function property,

$$I_n'(kr) = kI_{n-1}(kr) - (n/r)I_n(kr) \tag{2.16}$$

where the "prime" designates differentiation with respect to r. The ratio,

$$\begin{aligned} \alpha_n &\equiv [I_n(kr)/I_n'(kr)]_{r=a} \\ &= \frac{a/n}{(ka/n)I_{n-1}(ka)/I_n(ka) - 1} \end{aligned} \tag{2.17}$$

can be evaluated by using Table 9.8 of Olver (1964). A comparison of the two levels of approximation suggested by equation 2.15, with the exact value from equation 2.17 is provided by the illustrative examples shown in the third column of Table I.

For $K_n(kr)$, the limiting form, as $kr \to 0$, (equation 9.6.9 of Olver, 1964) is simply

$$K_n(kr) \simeq (1/2)(n-1)!\,(kr/2)^{-n}. \tag{2.18}$$

Its derivative with respect to r yields

$$K_n'(kr) \simeq -(nk/4)(n-1)!\,(kr/2)^{-n-1}. \tag{2.19}$$

Thus, we can express the limiting ratio

$$K_n(kr)/K_n'(kr) \simeq -(r/n) \tag{2.20}$$

as $kr \to 0$. For $r = a$, this agrees with previous equation 1.34, for β_n.

To obtain the exact expression for this ratio, we make use of the Bessel function property,

$$K_n'(kr) = -kK_{n-1}(kr) - (n/r)K_n(kr) \tag{2.21}$$

where the "prime" designates differentiation with respect to r. The ratio,

$$\begin{aligned}\beta_n &\equiv [K_n(kr)/K_n'(kr)]_{r=a} \\ &= \frac{-a/n}{(ka/n)K_{n-1}(ka)/K_n(ka) + 1}\end{aligned} \tag{2.22}$$

can be evaluated by using Table 9.8 of Olver (1964).

When using the ascending series for $K_n(z)$, the specification of the second largest term depends upon n; (see equations 9.6.11 and 9.8.7 of Olver, 1964). When $n = 1$, the resulting approximation for small kr can be expressed.

$$K_1(kr) \simeq (kr)^{-1} + (kr/2)\log_e(kr/2). \tag{2.23}$$

Its derivative with respect to r yields

$$K_1'(kr) \simeq -k(kr)^{-2} + (k/2)[1 + \log_e(kr/2)]. \tag{2.24}$$

Therefore, we can express the ratio

$$\frac{K_1(kr)}{K_1'(kr)} \simeq (-r)\left(\frac{1 + 2(kr/2)^2 \log_e (kr/2)}{1 - 2(kr/2)^2[1 + \log_e (kr/2)]}\right) \tag{2.25}$$

for kr small. Similarly, for $n = 2$, we can obtain

$$\frac{K_2(kr)}{K_2'(kr)} \simeq \left(\frac{-r}{2}\right)\left(\frac{1 - (kr/2)^4 \log_e (kr/2)}{1 + (kr/2)^4[1/2 + \log_e (kr/2)]}\right) \tag{2.26}$$

for kr small. Both equations 2.25 and 2.26 agree with the limiting form (equation 2.20) as $kr \to 0$. Illustrative numerical values are given in Table I.

Equations 2.16 and 2.21 can also be used to provide an exact expression for the ratio

$$\frac{I_n'(kr)}{K_n'(kr)} = -\frac{krI_{n-1}(kr) - nI_n(kr)}{krK_{n-1}(kr) + nK_n(kr)} \tag{2.27}$$

which occurs in previous equation 1.29; note that for $n = 0$, equation 2.11 applies. These can be evaluated from Table 9.8 of Olver (1964). However, if kr is small, one can use equations 2.14 and 2.19 to obtain the limiting form

$$I_n'(kr)/K_n'(kr) \simeq -2[(kr/2)^n/n!] \tag{2.28}$$

for kr small; note that when $n = 0$, equation 2.12 applies.

III. DISCUSSION, EXTENSION AND CONCLUSION

A. Three Kinds of Time Constants Contrasted

The mathematical results in part I, above, provide a rigorous basis for distinguishing between three kinds of time constants in the passive decay of initially nonuniform membrane potential, for the case of a membrane cylinder with sealed ends. These time constants are distinguished formally by the values of n and M; conceptually, it is useful to distinguish between components[6] of membrane potential which are (*1*) independent of both θ and x, (*2*) dependent upon x, but not upon θ, and (*3*) dependent upon θ and possibly also upon x.

1. The passive membrane time constant, $\tau_m = R_m C_m$, is also designated $\tau_{0,0}$ because it corresponds to $n = 0 = M$; $n = 0$ means that this component does not depend upon θ; $M = 0$ means that this component does not depend upon x. In equations 1.47 and 1.48, $C_{0,0}$ represents the difference between the initial uniform component of membrane potential and its resting value, E_r. The passive decay of this component can thus be expressed

$$C_{0,0} \exp(-t/\tau_m). \tag{3.1}$$

2. The set of time constants, $\tau_{0,M}$, for M equal to any positive integer, corresponds to decay with respect to x of components of membrane potential that are independent of θ. These correspond to the "equalizing" time constants obtained from one-dimensional cable theory (Rall, 1969). The passive decay of each such component in equation 1.48 can be expressed

$$C_{0,M} \cos(M\pi x/\ell) \exp(-t/\tau_{0,M}). \tag{3.2}$$

The distribution of current flow during such "equalizing" decay is indicated schematically in Fig. 1 (*b*), for the case, $M = 1$. These time constants are smaller than τ_m, but not too small to measure electrophysiologically when the effective electrotonic length, $L = \ell/\lambda$, of the cylinder lies in the range from about 1 to about 3. Over this range, the value of the ratio, $\tau_m/\tau_{0,1}$, ranges from about 11 to about 2; see equations 1.41 and 1.44. Thus, the value of this ratio can be used to obtain an indirect estimate of L, which can be expressed

$$L = \pi(\tau_m/\tau_{0,1} - 1)^{-1/2} \tag{3.3}$$

3. The additional set of time constants, $\tau_{n,M}$, for n equal to any positive integer, with M equal to either zero or any positive integer, corresponds to decay with respect to θ of components of membrane potential that are dependent upon θ and that may also be dependent upon x. The passive decay of each such component in equa-

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[6] These components are the individual terms in the infinite series defined by equations 1.47–1.50; each component corresponds to a particular value of n with a particular value of M.

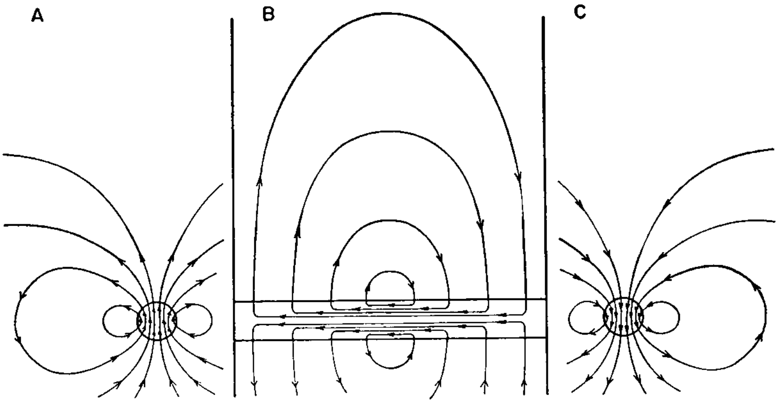

FIGURE 1 Schematic diagrams sketching the direction of electric current flow in the external and internal volumes. (*a*) Cross-section of membrane cylinder, with approximate sketch of current flow for a component that depends upon θ with $n = 1$. (*b*) Section along axis of membrane cylinder, with approximate sketch of current flow for a component that depends upon x with $M = 1$. (*c*) Cross-section of membrane cylinder, with approximate sketch of current flow near $x = \ell$ for a component that depends upon θ and x, with $n = 1$ and $M = 1$; *a*, *b*, and *c* together represent different aspects of the case $n = 1$ with $M = 1$.

tion 1.48 can be expressed

$$C_{n,M} \cos (n\theta) \cos (M\pi x/\ell) \exp (-t/\tau_{n,M}). \tag{3.4}$$

The distribution of current flow during such decay is indicated schematically in Fig. 1 *a* for $n = 1$. For the particular case ($n = 1$, $M = 0$), the current flow would be the same for all cross-sections of the cylinder (i.e. for all values of x). Such decay is typically about 1,000 times faster than for the previous case ($n = 0$, $M = 1$) corresponding to Fig. 1 *b*. This can be understood intuitively on the basis that the membrane capacity discharges itself by means of current which flows through much smaller resistance in flow pattern (Fig. 1 *a*) than in flow pattern (Fig. 1 *b*), especially for cylinder lengths that are much greater than the diameter. In other words, the longitudinal core resistance is much greater than the resistance across the core.

In the case ($n = 1$, $M = 1$), for a component which depends upon both θ and x, the current flow would resemble Fig. 1 *a* for cross-sections over the half-length from $x = 0$ to $x = \ell/2$; however, it would be reversed (as in Fig. 1 *c*) over the other half-length. It should be added that there would also be some simultaneous current flow of the kind in Fig. 1 *b*; however, because the time constant, $\tau_{1,1}$, is typically a thousand times smaller than $\tau_{0,1}$, this means that the component ($n = 1$, $M = 1$) decays so rapidly by means of current flow patterns (Fig. 1 *a*) over one half of the length, with (Fig. 1 *c*) over the other half of the length, that this component of nonuniformity has collapsed essentially to zero long before any appreciable amount of current flows through the higher resistance pattern of Fig. 1 *b*. Only if the length of the cylinder is small (comparable to its diameter), does the current flow pattern of Fig. 1 *b*, compete effectively with the pattern of (Fig. 1 *a* paired with Fig. 1 *c*); in that case, $\tau_{1,1}$ is less than $\tau_{1,0}$; see paragraph following equation 1.37 in part I.

It should be noted that a nonuniform membrane potential could contain both a component ($n = 0, M = 1$) and a component ($n = 1, M = 1$). In such a case, there would be rapid decay of component ($n = 1, M = 1$) through the current flow pattern of Fig. 1 *a* with Fig. 1 *c*, according to equation 3.4, and there would be slower decay of the other component ($n = 0, M = 1$) through the higher resistance current flow pattern of Fig. 1 *b*, according to equation 3.2.

B. Relative Contributions of φ_i and φ_e to V_m

The solution provided by equations 1.47–1.50, with equations 1.51–1.60, implies different contributions of the intracellular potential, φ_i, and the extracellular potential, φ_e, to the components of membrane potential, V_m. Let $(V_m)_{n,M}$ represent the component of $V_m(\theta, x, t)$ in equation 1.48 corresponding to each pair of values (n, M). Similarly, let $(V_i)_{n,M}$ represent the corresponding component of $\varphi_i(r, \theta, x, t)$ of equation 1.49, when $r = a$, and let $(V_e)_{n,M}$ represent the corresponding component of $\varphi_e(r, \theta, x, t)$ of equation 1.50, when $r = a$. Then one can obtain the ratios $(V_i)_{n,M}/(V_m)_{n,M}$ and $(V_e)_{n,M}/(V_m)_{n,M}$ which express, respectively, the fraction of V_m contributed by φ_i and φ_e for each pair of values (n, M). These fractions have been evaluated and tabulated in Table II, for the particular example, $R_e = 2R_i$.

It can be seen in Table II that the contribution of φ_e to V_m is very small for those components which are independent of θ (i.e. $n = 0$). For the uniform case ($n = 0$, $M = 0$) the contribution of φ_e is zero because we have assumed zero applied current. For dependence upon x, but not θ (i.e. $n = 0$, $M = 1$ or 2), the contribution of φ_e is small because the external volume provides much less resistance to longitudinal current flow than does the restricted internal volume, when the length of the cylinder is large compared with its diameter; see lines of current flow in Fig. 1 *b*.

TABLE II

CONTRIBUTIONS OF φ_i AND φ_e TO V_m

n	M	$\pi a/\ell$	$(V_i)_{n,M}/(V_m)_{n,M}$	$(V_e)_{n,M}/(V_m)_{n,M}$
0	0	any	1.0	0.0
0	1	0.1	0.977	−0.023
		0.01	0.9995	−0.0005
0	2	0.1	0.88	−0.12
		0.01	0.9979	−0.0021
1	0	any	1/3	−2/3
>1	0	any	1/3	−2/3
>1	M	$0.1/M$	0.34	−0.66

* Here, $R_e = 2R_i$. See text for definitions.

For those components which depend upon θ (i.e. $n > 0$), the contributions of φ_i and φ_e to V_m are proportional to the specific resistances, R_i and R_e; if $R_e = R_i$, the two contributions would be equal. Looking at the lines of current flow (Fig. 1 *a* and 1 *c*), this can be explained intuitively by saying that the greater cross-section available for external current flow is balanced by the greater length of the paths of external current flow.

C. Extension of External Volume

In the boundary value problem that was both stated and solved in part I, above, the external volume was confined between a plane at $x = 0$ and another plane at $x = \ell$; the value of r was allowed to extend to infinity. As can be seen in the schematic diagram of Fig. 1 *b*, all lines of external current flow are confined to the region between these two planes. This restriction of the external volume resulted from the

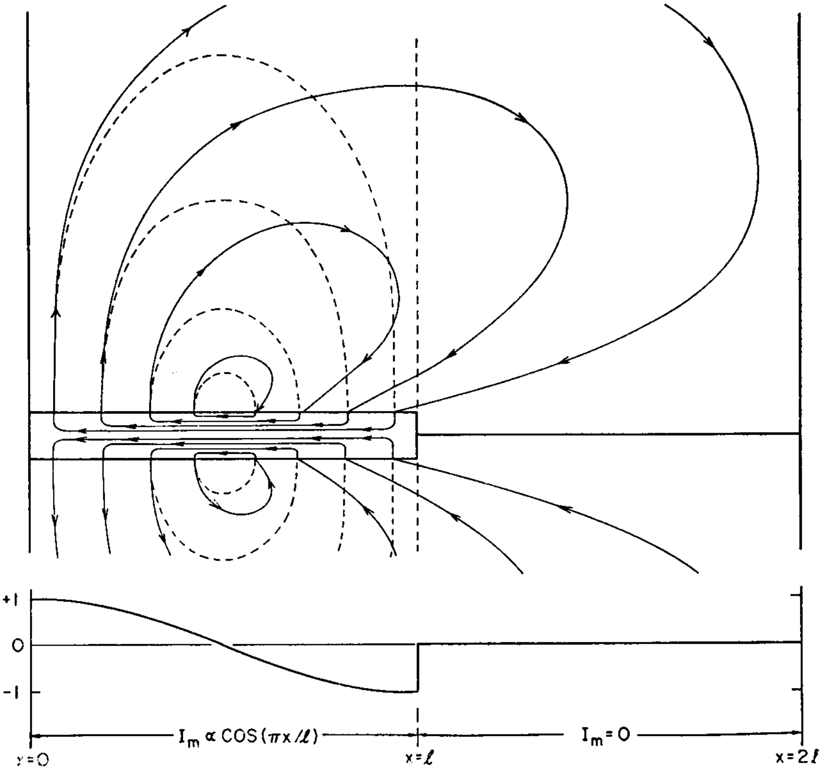

FIGURE 2 Schematic diagram sketching the spread of extracellular current beyond $x = \ell$ when the outer insulating boundary is moved from $x = \ell$ to $x = 2\ell$; the dashed lines indicate the situation before the boundary was moved. The diagram at the bottom shows the membrane current density, I_m, to which the normal derivative, $[\partial\varphi_e/\partial r]_{r=a}$, of extracellular potential at $r = a$, was matched by means of Fourier coefficients; note that I_m is proportional to $\cos(\pi x/\ell)$ from $x = 0$ to $x = \ell$, and that $I_m = 0$ from $x = \ell$ to $x = 2\ell$.

boundary condition, $\partial \varphi_e / \partial x = 0$ at $x = 0$ and $x = \ell$, which was chosen to match that for the interior region; see equations (1.5) in part I. This had the advantage that $H(x)$ (equation 1.12) could be the same inside and outside the membrane, for each value of M, and this, in turn, made it easy to satisfy the membrane boundary conditions (equations 1.3 and 1.4).

Here we wish to explore the possibility of extending the external volume beyond $x = \ell$, while preserving the internal boundary condition for the sealed end of the cylindrical membrane at $x = \ell$. One example of such an extension of the external volume is illustrated schematically in Fig. 2, where the insulating boundary has been removed from $x = \ell$ and placed at $x = 2\ell$ (for the external volume only). This insulating boundary could be placed even farther away, but the essence of the problem can be treated most simply with this example.

For this new boundary value problem, equations 1.1, 1.3, 1.4, and 1.5 apply to $\varphi_i(r, \theta, x, t)$ as before, for the interior region, $r \leqq a$, $0 \leqq \theta \leqq 2\pi$, $0 \leqq x \leqq \ell$. However, equation 1.2 now applies to $\varphi_e(r, \theta, x, t)$ for the extended exterior region, $r \geqq a$, $0 \leqq \theta \leqq 2\pi$, $0 \leqq x \leqq 2\ell$, plus perhaps also the small region $r < a$ for $\ell < x \leqq 2\ell$; (it is simpler, but not necessary to exclude this small additional region by regarding it as filled by a glass rod or similar insulator). The important point is that the membrane boundary condition (equation 1.3) can be used for φ_e, provided that we set

$$I_m = 0, \quad \text{for} \quad \ell < x \leqq 2\ell. \tag{3.5}$$

This means

$$\left.\begin{aligned} &\partial \varphi_e / \partial r = (R_e / R_i) \partial \varphi_i / \partial r \\ &\text{at} \quad r = a, \quad \text{for} \quad 0 \leqq x \leqq \ell \end{aligned}\right\} \tag{3.6}$$

and

$$\left.\begin{aligned} &\partial \varphi_e / \partial r = 0 \\ &\text{at} \quad r = a, \quad \text{for} \quad \ell < x \leqq 2\ell. \end{aligned}\right\} \tag{3.7}$$

Also, we have

$$\left.\begin{aligned} &\partial \varphi_e / \partial x = 0 \\ &\text{at } x = 0, \quad \text{and at} \quad x = 2\ell. \end{aligned}\right\} \tag{3.8}$$

This last boundary condition tells us that $H(x)$ outside differs from $H(x)$ inside; instead of previous equation 1.12, here we have, for the exterior region,

$$H_N(x) = D_N \cos (k_e x) \tag{3.9}$$

where

$$k_e = N\pi / 2\ell \tag{3.10}$$

and N is an integer or zero. It should be noted that the infinitely many roots, k_e, defined by equation 3.10 are twice as dense as the $k = M\pi/\ell$ of equation 1.13 for the interior. In other words, when N has even values, $M = N/2$ provides the same function for $H_N(x)$ outside as for $H_M(x)$ inside. However, for odd values of N, there is no matching $H_M(x)$ inside. This peculiarity cannot be avoided because the even values of N all imply that $dH_N/dx = 0$ at $x = \ell$; they could not provide any gradient of potential driving current from the region $x < \ell$ to the region $x > \ell$. The odd values of N are essential because they provide $dH_N/dx \neq 0$ at $x = \ell$.

The most useful example is the case ($n = 0$, $M = 1$) inside. Then, from equation 1.49, we can write

$$\varphi_i(r, x, t) = E_r + A_{0,1}I_0(kr) \cos (kr) \exp (-t/\tau_{0,1}) \tag{3.11}$$

where $k = \pi/\ell$. For the range, $0 \leqq x \leqq \ell$, we can use equations 1.3, 2.4, and 3.11 to obtain

$$I_m(x, t) = -(\pi/\ell)(A_{0,1}/R_i)I_1(\pi a/\ell) \cos (\pi x/\ell) \exp (-t/\tau_{0,1}) \tag{3.12}$$

For $t = 0$, we write the initial distribution of membrane current density more simply as

$$I_m(x, 0) = C_1 \cos (\pi x/\ell) \quad \text{for} \quad 0 \leqq x \leqq \ell \tag{3.13}$$

where

$$C_1 = -(\pi/\ell)(A_{0,1}/R_i)I_1(\pi a/\ell). \tag{3.14}$$

For the range, $\ell < x \leqq 2\ell$, equation 3.5 applies. This case is the one illustrated at the bottom of Fig. 2.

For the matching exterior potential, we try the expression

$$\varphi_e(r, x, 0) = \sum_{N=1}^{\infty} B_{0,1,N}K_0(k_e r) \cos (k_e x) \tag{3.15}$$

where k_e is defined by equation (3.10). From equation (1.3) we can write that

$$I_m(x, 0) = \sum_{N=1}^{\infty} B_N \cos (N\pi x/2\ell) \tag{3.16}$$

where

$$\begin{aligned} B_N &= -(B_{0,1,N}/R_e)[K_0'(N\pi r/2\ell)]_{r=a} \\ &\simeq -(B_{0,1,N}/R_e)\left(\frac{K_0(N\pi a/2\ell)}{a \log_e (N\pi a/2\ell)}\right) \end{aligned} \tag{3.17}$$

The approximate form (based on equation 2.8) being valid when $N\pi a/2\ell$ is small enough.

Equation 3.16 matches equation 3.13 together with equation 3.5 when the coefficients, B_N, are the Fourier coefficients defined by

$$B_N = (2/2\ell)\left[C_1\int_0^{\ell}\cos(\pi x/\ell)\cos(N\pi x/2\ell)\,dx + \int_{\ell}^{2\ell}0\cdot dx\right]$$

or

$$B_N/C_1 = (2/\pi)\int_0^{\pi/2}\cos(2\theta)\cos(N\theta)\,d\theta \qquad (3.18)$$

For $N = 1$, 2 and 3, the values obtained from equation 3.18 are 0.212, 0.50, and 0.382, respectively. For $N = 4$, and for all subsequent even values of N, the Fourier coefficients are zero. For odd values of N, the subsequent coefficients alternate in sign and decrease in absolute value according to the expression

$$B_N/C_1 = (-1)^{(N+1)/2}(2N/\pi)/(N^2 - 4). \qquad (3.19)$$

The values of this ratio for $N = 5$, 7, and 9 are -0.152, $+0.099$, and -0.074, respectively. By going to large enough values of N, a truncated Fourier series based on equations 3.16–3.18 can be obtained to match equations 3.13 and 3.5 to any desired precision.

At first this result might seem to solve this boundary value problem rigorously. However, there is a difficulty which should be pointed out, even though it does not lead to significant error when $N\pi a/2\ell$ is small enough. The difficulty is that although one membrane boundary condition equation 1.3 is satisfied, the related condition (equation 1.4) for current in the membrane, is not rigorously satisfied. Both $\partial\varphi_i/\partial t$ and $(\varphi_i - E_r)$ share with equation 3.12 and with equations 3.16 plus 3.18 a dependence upon x that is $\cos(\pi x/\ell)$ over the range, $0 \leqq x \leqq \ell$; however, equation 3.15 for φ_e does not have this dependence upon x. The two Fourier series, equations 3.15 and 3.16 differ in their dependence upon x because the coefficient ratio

$$\frac{B_{0,1,N}K_0(k_e a)}{B_N} = \frac{-R_e K_0(k_e a)}{[K_0'(k_e r)]_{r=a}}$$

$$\simeq aR_e \log_e(2\ell/N\pi a) \qquad (3.20)$$

(see equations 3.15–3.17) is not independent of N. For example, if $2\ell/\pi a = 100$, then $\log_e(2\ell/N\pi a)$ has values of 4.6, 3.9, 3.5, 3.2, and 3.0, approximately, for N values of 1, 2, 3, 4, and 5 respectively. This feature plays a positive role, because without it, not only $\partial\varphi_e/\partial r$, but also φ_e would be zero at $r = a$, for $\ell < x \leqq 2\ell$. Furthermore, the deviation of $\varphi_e(a, x)$ from proportionality with $\varphi_i(a, x)$ is tempered by the fact that the magnitude of $\varphi_e(a, x)$ is less than 0.01% of $\varphi_i(a, x)$, when $\pi a/\ell = 0.01$; see Table II, above, for $n = 0$, $M = 1$. In fact, the magnitude of

$\varphi_e(a, x)$ should be slightly smaller in Fig. 2 than in Fig. 1 *b*, because the current can spread out more. This means that $V_m - E_r$ and $\partial V_m/\partial t$ can be expected to deviate from proportionality with $\partial \varphi_i/\partial r$, at $r = a$, and with $\partial \varphi_e/\partial r$, at $r = a$, by less than 0.01 % for the example($n = 0$, $M = 1$, with $\pi a/\ell = 0.01$) considered here.

Once one appreciates the negligible contribution that φ_e makes to V_m and $\partial V_m/\partial t$, one obtains an intuitive basis for the paramount importance of matching $\partial \varphi_e/\partial r$, at $r = a$, to $\partial \varphi_i/\partial r$, at $r = a$. It was already shown earlier, that setting $R_e = 0$ has little effect upon the time constant (equation 1.44) and upon λ; these are determined almost entirely by the membrane and the interior region, for typical values of the relevant parameters. Thus, we can obtain an excellent approximation to the transient solution of the present problem, by associating the interior potential of equation 3.11, for $0 \leqq x \leqq \ell$, with an exterior potential defined by

$$\varphi_e(r, x, t) = \exp\left(-t/\tau_{0,1}\right) \sum_{N=1}^{\infty} B_{0,1,N} K_0(k_e r) \cos(k_e x) \qquad (3.21)$$

for $0 \leqq x \leqq 2\ell$, where k_e is defined by equation 3.10 and the coefficients, $B_{0,1,N}$ are defined by equations 3.17–3.20.

Similarly, for each component (n, M) of an interior solution (equation 1.49) we can define a corresponding approximate exterior component

$$\varphi_{e_{n,M}}(r, x, t) = \exp\left(-t/\tau_{n,M}\right) \sum_{N=1}^{\infty} B_{n,M,N} K_n(k_e r) \cos(k_e x) \qquad (3.22)$$

for $0 \leqq x \leqq 2\ell$ where k_e is the same as above, and the coefficients, $B_{n,M,N}$, are obtained in the same manner as $B_{0,1,N}$ above.

D. Relation of I_m to V_e and to $\partial^2 V_e/\partial x^2$

There has been some confusion in the neurophysiological lore about the relation of membrane current density, I_m, to the derivative, $\partial^2 V_e/\partial x^2$, and to the potential, V_e, at the external membrane surface. It is well known that both $\partial^2 V_e/\partial x^2$ and $\partial^2 V_i/\partial x^2$ are proportional to I_m in one-dimensional cable theory, where the internal and external media are both assumed to have such small cross-sections that they provide only resistance per unit length of the cylinder; this applies to an axon placed in oil or in air. If such an axon is placed in a large volume of external conducting medium, the distribution of extracellular potential during an action potential is obviously different. Although I_m remains essentially proportional to $\partial^2 V_i/\partial x^2$, the value of $\partial^2 \varphi_e/\partial x^2$ at the external membrane surface is not proportional to I_m, in general; see Lorente de Nó (1947), Plonsey (1964), Clark and Plonsey (1966, 1968), Geselowitz (1966), Hellerstein (1968), and Pickard (1968). Here we take the opportunity to reexamine this question in the context of the present study, i.e. for cylinders of finite length, with sealed ends.

The relation of membrane current density to the extracellular potential distribution is defined by the membrane boundary condition (equation 1.3); thus we write

$$I_m(\theta, x, t) = (1/R_e)[-\partial\varphi_e/\partial r]_{r=a}\,. \tag{3.23}$$

When the external volume is confined between the planes $x = 0$ and $x = \ell$, as in Fig. 1 *b*, we have equation 1.50 for $\varphi_e(r, \theta, x, t)$, with $B_{0,0} = 0$ during passive membrane potential decay. For $n = 0$, with $M > 0$, we obtain, for each M

$$\begin{aligned}(R_e)[I_m(x, t)]_{0,M} &= (-1/\beta_0)\varphi_e(a, x, t)\\ &\simeq \varphi_e/[a \log_e (M\pi a/\ell)]\end{aligned} \tag{3.24}$$

where β_0 is defined by equations 2.10, and approximated by equations 2.8 and 1.39 for ka small. The important point to note is that whenever φ_e can be represented by a single component, with $n = 0$ and some particular $M > 0$, $I_m(x, t)$ is proportional to $\varphi_e(a, x, t)$. However, as soon as φ_e becomes a linear combination of several components having different values of M, this simple proportionality is lost.

Next, consider $n > 0$. Then for $M = 0$

$$(R_e)[I_m(\theta, t)]_{n,0} = (n/a)\varphi_e(a, \theta, t) \tag{3.25}$$

and for $M > 0$

$$\begin{aligned}(R_e)[I_m(\theta, x, t)]_{n,M} &= -(1/\beta_n)\varphi_e(a, \theta, x, t)\\ &\simeq (n/a)\varphi_e(a, \theta, x, t),\end{aligned} \tag{3.26}$$

where β_n is defined by equations 1.32 and 2.22 and approximated by equation 1.34 for ka small. From these results, we see that φ_e can be composed of several components with several different values of M, and, provided that they all have the same value of n (i.e. some positive integer), and provided that ka is small, $I_m(\theta, x, t)$ is effectively proportional to $\varphi_e(a, \theta, x, t)$. Note that the proportionality found here does not apply to the extended external volume of Fig. 2.

With regard to $\partial^2 V_e/\partial x^2$, it follows from equation 1.50 that, for each value of M,

$$[\partial^2\varphi_e/\partial x^2]_{r=a} = -(M\pi/\ell)^2\varphi_e(a, \theta, x, t). \tag{3.27}$$

For $M = 0$, this equals zero, which is clearly not proportional to equation 3.25, for $n > 0$. When both n and M are greater than zero, equations 3.26 and 3.27 show that $[\partial^2\varphi_e/\partial x^2]_{r=a}$ is proportional to $I_m(\theta, x, t)$ when there is only a single component (n, M); however, for a linear combination of several components, $[\partial^2\varphi_e/\partial x^2]_{x=a}$ is neither proportional to $\varphi_e(a, \theta, x, t)$ nor to $I_m(\theta, x, t)$. Also, it should be added that the proportionality for a single component, for n and M both greater than zero, applies only to the restricted external volume of Fig. 1, and not to the extended external volume of Fig. 2.

The conclusion is that, in general, when φ_e consists of several components having different values of n and M, the surface value of neither φ_e nor $\partial^2\varphi_e/\partial x^2$ is proportional to I_m. However, when φ_e can be represented by a single component, both φ_e and $\partial^2\varphi_e/\partial x^2$ are proportional to I_m, provided that the external volume and the internal volume are both confined by the zero slope boundary condition (equation 1.5) at $x = 0$ and $x = \ell$.

E. Relation of $\partial^2 V_i/\partial x^2$ to I_m and to $\partial^2 V_e/\partial x^2$

Because it is widely held that I_m is proportional to $\partial^2 V_i/\partial x^2$, not only for one-dimensional cable theory, but also when there is a large external volume, this question merits examination as well. In analogy with equation 3.27, it follows from equation 1.49 that, for each value of M,

$$[\partial^2\varphi_i/\partial x^2]_{r=a} = -(M\pi/\ell)^2\varphi_i(a, \theta, x, t). \qquad (3.28)$$

Referring to equations 1.53 and 1.56, as well as equation 3.27, it follows that:

$$[\partial^2\varphi_i/\partial x^2]_{r=a} = (\alpha_n R_i/\beta_n R_e)[\partial^2\varphi_e/\partial x^2]_{r=a} \qquad (3.29)$$

for $M > 0$. For $n = 0$, α_0/β_0 depends upon M (see equations 1.38 and 1.39); however, for $n > 0$, $\alpha_n/\beta_n \simeq -1$, for ka small (see equations 1.33 and 1.34). Thus equation 3.29 implies proportionality between $[\partial^2\varphi_i/\partial x^2]_{r=a}$ and $[\partial^2\varphi_e/\partial x^2]_{r=a}$ for any single component,[7] and also for any linear combination which excludes $n = 0$ with $M > 0$. Linear combinations including $n = 0$ with $M > 0$ do not provide proportionality. No proportionality occurs when the external volume is extended as in Fig. 2.

In analogy with equations 3.23–3.26, we can write, for $n = 0$ with $M > 0$,

$$\begin{aligned}(R_i)[I_m(x, t)]_{0,M} &= (-1/\alpha_0)\varphi_i(a, x, t)\\ &\simeq (-a/2)(M\pi/\ell)^2\varphi_i(a, x, t), \qquad (3.30)\end{aligned}$$

where α_0 is defined by equation 2.5 and approximated by equations 2.3 and 1.38 for

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[7] This proportionality holds also for the corresponding first derivatives with respect to x, at $r = a$. This proportionality gives a legitimate meaning to r_e, the external resistance per unit length, for the special case where there is only a single component and where this component has $n = 0$, with $M > 0$. Then $r_e/r_i = -(\beta_0/\alpha_0)(R_e/R_i)$, and, using equations 1.38 and 1.39 (see also equations 1.45 and 1.46), we obtain the approximation, $r_e/r_i \simeq (R_e/2R_i)(ka)^2 \log_e (1/ka)$, for ka small. Thus, $R_e = 2R_i$ and $ka = 0.1$ would imply that $r_e = 0.023\, r_i$. It should be noted that here concern has been restricted to a single cylinder placed in a volume. For the case of a population of parallel cylinders acting synchronously, it becomes meaningful to define a longitudinal resistance per unit length, per cylinder, and to make use of results from one-dimensional cable theory.

ka small. Comparing equation 3.30 with equation 3.28, it can be seen that $I_m(x, t)$ is approximately proportional to $[\partial^2\varphi_i/\partial x^2]_{r=a}$ for any linear combination involving $n = 0$ with different values of M, provided that ka is small. In other words when there is no dependence upon θ, and the length of the cylinder is large compared with its diameter, this proportionality is essentially valid, and this is changed negligibly by extending the external volume, as in Fig. 2. This result agrees with Clark and Plonsey (1966, 1968), Hellerstein (1968), and Pickard (1968). However, this proportionality does not hold for linear combinations which include any dependence upon θ, because, for $n > 0$, we have (for $M = 0$)

$$(R_i)[I_m(\theta, t)]_{n,0} = -(n/a)\varphi_i(a, \theta, t) \tag{3.31}$$

and for $M > 0$

$$\begin{aligned}(R_i)[I_m(\theta, x, t)]_{n,M} &= -(1/\alpha_n)\varphi_i(a, \theta, x, t)\\ &\simeq -(n/a)\varphi_i(a, \theta, x, t)\end{aligned} \tag{3.32}$$

where α_n is defined by equations 1.31 and 2.17, and approximated by equations 2.15 and 1.33, for ka small. From these results we see that a linear combination of several components with different values of M, but a single value of n, provides approximate proportionality of $I_m(\theta, x, t)$ with $\varphi_i(a, \theta, x, t)$, but not with $[\partial^2\varphi_i/\partial x^2]_{r=a}$ because of equation 3.28. Furthermore, if the linear combination includes several values of n, $I_m(\theta, x, t)$ is neither proportional to $\varphi_i(a, \theta, x, t)$, nor to $[\partial^2\varphi_i/\partial x^2]_{r=a}$.

Thus, we see that the widely held belief that I_m is proportional to $\partial^2 V_i/\partial x^2$ is not even approximately correct, in general. It is strictly correct only for one-dimensional cable theory, and it is approximately correct for the three dimensional problem when there is no dependence upon θ, and when the cylinder length is large compared with its diameter. When there are components that depend upon θ together with other components which depend upon x but not θ, then the very rapid equalization with respect to θ is relevant here; after a few microseconds of decay, the θ-dependent components will have decayed essentially to zero, and the remaining x-dependent components then meet the proportionality requirement just discussed.

F. Validity of One-Dimensional Equalizing Time Constants for Estimate of L

This paper was stimulated by the desire to show that the equalizing time constants from one-dimensional cable theory (Rall, 1969) provide a valid means of estimating the electrotonic length of a membrane cylinder having sealed ends. Thus, it is appropriate to note in conclusion, that the result presented as equations 1.44–1.46 defines precisely the correction factor relating those time constants obtained here from a rigorous three-dimensional boundary value problem, to those obtained from the one-dimensional boundary value problem (equation 1.41 and Rall, 1969). For typical values of the parameters, R_i, R_e, R_m, a, and ℓ, the correction factor differs from unity by less than 1 %. Furthermore, the extension of the external volume from $x = \ell$ to $x = 2\ell$ (see Fig. 2) would tend to bring this correction factor even closer to unity. This is because extension of the external volume further reduces the already small contribution of R_e to results that are dominated by R_m/R_i and ℓ/a. However, if future applications require estimates outside this range of values, the present theoretical results provide a rigorous basis for correcting results obtained from one-dimensional cable theory.

SUMMARY

1. The mathematical boundary value problem for the transient volume distribution of extracellular potential, $\varphi_e(r, \theta, x, t)$ and of intracellular potential, $\varphi_i(r, \theta, x, t)$ during passive decay of membrane potential for a membrane cylinder with sealed ends, has been stated and solved for a large variety of nonuniform initial distributions.

2. The simplest case involving dependence upon the angle θ, as well as r and t, does not involve any complications with Bessel functions. This case establishes that equalization of a membrane potential nonuniformity, which depends upon θ but not upon x, is several orders of magnitude faster than uniform decay. The time constant, $\tau_{1,0}$, is defined by equation 1.23, and is typically about 10,000 times smaller than $\tau_m = R_m C_m$.

3. Nonuniformity that depends upon $\cos(n\theta)$ but not upon x equalizes even more rapidly according to the time constant, $\tau_{n,0}$, defined by equation 1.24.

4. For nonuniformity that depends upon both θ and x, Bessel functions complicate the analysis. However, for cylinders whose lengths are large compared with their diameters, the Bessel function ratios can be approximated by simple expressions, and the time constants, $\tau_{n,M}$, defined by equation 1.36 can be shown to be essentially equal to the $\tau_{n,0}$. This means that equalization with respect to θ dominates in such cases, as is explained further in the discussion associated with Fig. 1.

5. For nonuniformity that depends upon x, but not upon θ, results are obtained which can be compared with those of one-dimensional cable theory. For cylinders whose lengths are large compared with their diameters, these results provide equalizing time constants, $\tau_{0,M}$, defined by equation 1.44, which agree with those from one-dimensional cable theory within 1 %. If the external resistivity is set equal to zero, the agreement is even better, and the standard characteristic length, λ, for $R_e = 0$ is also obtained; for $R_e \neq 0$, the appropriate value of λ becomes shorter, usually by less than 1 %, while the appropriate value of $L = \ell/\lambda$ becomes longer, usually by less than 1 %. For L values between 1 and 3, the value of $\tau_{0,1}$ is smaller than τ_m by a factor between 11 and 2.

6. For components of membrane potential that are independent of θ, the extracellular contribution is very small, for cylinders whose lengths are large compared

with their diameters. In contrast, for components of membrane potential that depend upon θ, the extracellular and intracellular contributions are comparable; they are proportional to R_e and R_i, respectively. Numerical examples are provided by Table II and intuitive explanations are provided in the associated discussion.

7. In part I, the external volume is confined between $x = 0$ and $x = \ell$; however, in part III-C the external volume is extended out to $x = 2\ell$. An approximate solution, is obtained for this more complicated boundary value problem, and is illustrated ischematically in Fig. 2. It can be concluded that there is only negligible modification of the membrane potential, $V_m(\theta, x, t)$, and the intracellular potential, $\varphi_i(r, \theta, x, t)$, but that there is a significant change in the extracellular potential, $\varphi_e(r, \theta, x, t)$.

8. It is demonstrated that the value of $\varphi_e(r, \theta, x, t)$ and that of $\partial^2\varphi_e/\partial x^2$, at the outer membrane surface ($r = a$) should not be regarded as proportional to membrane current density, $I_m(\theta, x, t)$, in general. Only when the extracellular and intracellular volume are both confined by the zero slope boundary condition equation 1.5 at $x = 0$ and $x = \ell$, and when, furthermore, the potentials can be expressed in terms of a single component (n, M), do we find the special situation where $I_m(\theta, x, t)$ remains proportional to both $\varphi_e(r, \theta, x, t)$ and $\partial^2\varphi_e/\partial x^2$ at the outer surface, $r = a$.

9. It also demonstrated that $\partial^2\varphi_i/\partial x^2$ at the inner membrane surface, $r = a$, is not proportional to $I_m(\theta, x, t)$ in general; it is essentially proportional when there is dependence upon x but not upon θ, provided that the cylinder length is large compared with its diameter. Even when there is dependence upon θ, these two quantities become approximately proportional after the first few microseconds of decay, because the θ-dependent components decay so rapidly, leaving the x-dependent components to decay more slowly.

Added Note Just as this paper was ready for submission, I received a copy of an interesting 168 page monograph (doctoral dissertation) by Poul Rosenfalck, of the University of Copenhagen. That monograph, entitled "Intra- and extracellular potential fields of active nerve and muscle fibres", contains many useful mathematical results, numerical calculations, and experimental tests; the emphasis is on action potentials in cylinders of infinite length.

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