VOLUME CONDUCTOR FIELDS OF ACTION CURRENTS

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ABSTRACT The formulation of Lorente de Nó for the potential distribution in a volume conductor due to a contained bioelectric source is reviewed. The aforementioned formula is based on data taken from the bioelectric source in air (excised). This work is extended to the derivation of a formula which depends upon quantities available from *in situ* measurements. The latter formula appears to simplify to the form

$$\Phi(P) \cong \frac{1}{4\pi\sigma} \int_{S_0} \frac{J_n}{r}\, ds$$

where J_n is the normal current density flow across the surface S_0 that bounds the bioelectric source. The simplification is considered in some detail for a hypothetical action potential on a circular cylindrical axon, and is shown to be adequately substantiated for this case.

INTRODUCTION

In order to approach the problem of interpretation of recordings of bioelectric activity, as in electroencephalography, electrocardiography, electromyography, etc., a theory of the production of potentials in the surrounding passive tissue due to electrophysiological activity is necessary. If a sufficiently detailed description of the bioelectric sources can then be found, the theory permits a prediction of the results of potential measurements of various kinds. One hopes then to arrive at the ultimate goal of analysis, *i.e.* to be able to make quantitative statements concerning the biological properties of bioelectric sources, given a suitably specified (spatial and temporal) series of potential measurements.

This paper is concerned with the first goal above, namely the determination of the electric potential field due to an active nerve or muscle. We begin with a review of currently available formulations due to Lorente de Nó. Since these require data taken from excised nerve, we have extended the work to include formulas based on active sources *in situ*. Conditions which lead to a simplification of the results are discussed. In this connection, the Fourier transform technique is considered for axially symmetric circular cylindrical nerve.

Volume Conductor Potentials from Insulated Source Data. A comprehensive study of the current distribution in volume conductors resulting from nerve activity[1] was undertaken by Lorente de Nó. In order to more clearly indicate the advantages and limitations of this study, we give a brief summary of the central part of the theory. A slightly different vector approach (following Geselowitz) is used in order to simplify the presentation.

Consider, first, an arbitrary region V of finite extent which has a conductivity σ and contains current sources ω (*i.e.* $\nabla \cdot \bar{J} = \omega$), as in Fig. 1. The region external to

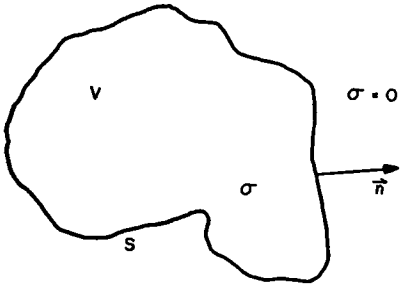

FIGURE 1 Arbitrary volume V contains all sources.

V has zero conductivity. Then within V, Poisson's equation must be satisfied by the scalar potential Φ, namely

$$\nabla^2\Phi = -\omega/\sigma \tag{1}$$

Furthermore, the fact that $\bar{n} \cdot \bar{J} = 0$ at S imposes a boundary condition that

$$\frac{\partial \Phi}{\partial n} = 0 \quad \text{on} \quad S \tag{2}$$

Now Green's theorem requires that for an arbitrary volume V bounded by the surface S

$$\int_V (\Phi \nabla^2 \psi - \psi \nabla^2 \Phi)\, dV = \int_S \left(\Phi \frac{\partial \psi}{\partial n} - \psi \frac{\partial \Phi}{\partial n} \right) dS \tag{3}$$

where Φ and ψ are any well behaved scalar functions. If we identify Φ in (3) with the potential distribution within V, and if we define

$$\psi = \frac{1}{r} = 1/\sqrt{(x - x')^2 + (y - y')^2 + (z - z')^2} \tag{4}$$

[1] The work of Lorente de Nó is specifically concerned with the bioelectric activity of nerve fibers and trunks. It should be understood, however, that the general formulations apply equally well to muscle activity. Where assumptions are made concerning the shape of the source, such results apply equally well to nerve or muscle provided they satisfy the requisite geometry.

where (x, y, z) is an element of V and (x', y', z') is a field point located outside of V, then (3) becomes

$$\int_V \left(\Phi \nabla^2\left(\frac{1}{r}\right) - \frac{1}{r}\nabla^2\Phi\right) dV = \int_S \left(\Phi \frac{\partial(1/r)}{\partial n} - \frac{1}{r}\frac{\partial \Phi}{\partial n}\right) dS \tag{5}$$

Now $\nabla^2(1/r) = 0$ since $r \neq 0$; also $\partial\Phi/\partial n = 0$ on S. Consequently

$$-\int_V \frac{\nabla^2\Phi}{r} dV = \frac{1}{\sigma}\int_V \frac{\omega}{r} dV = \int_S \Phi \frac{\partial(1/r)}{\partial n} dS \tag{6}$$

If the source, ω, were in an infinite region of conductivity σ, then the potential at any point, Φ_V, is given by

$$\Phi_V = \frac{1}{4\pi\sigma}\int_V \frac{\omega}{r} dV \tag{7}$$

Combining (7) with (6), and with Φ_{se} emphasizing that the surface potential is found under conditions where V is insulated (excised) from its surroundings.

$$\Phi_V = \frac{1}{4\pi}\int_S \Phi_{se} \frac{\partial(1/r)}{\partial n} dS \tag{8}$$

which is the desired result. Equation (8) relates the potential at any point in a volume conductor of infinite extent to the surface potentials that exist on any arbitrary surface S (bounding all sources) when the enclosed volume V is isolated. Thus, if S is a surface surrounding an active nerve trunk or fiber, then the potentials set up in the exterior volume conductor can be calculated from (8) provided the surface potential Φ_{se} is measured on the excised (insulated) nerve. A physical interpretation of (8) is that Φ_{se} behaves as an equivalent double layer source for potentials external to V.

A number of assumptions are implied in obtaining (8). First, it is assumed that the electrophysiological sources responsible for ω are the same whether the nerve or muscle is immersed in an infinite volume conductor or is excised. This requirement must be fulfilled in order that ω in (6) and (7) be identical. In addition, we have assumed the conductivity within and outside of V to be the same, and implied, furthermore, that it is a constant (*i.e.* that the medium is uniform, isotropic, and linear). Finally, in application to a practical problem, the external region is assumed extensive enough so that it may be considered infinite. A discussion of some of these questions can be found in Lorente de Nó, Benjamin *et al.*, and Schwan. The effect of finite external dimensions can sometimes be considered by the method of images (Plonsey) or by inclusion of suitable equivalent surface sources.

When S is a circular cylindrical surface and where axial symmetry is satisfied (*e.g.* the surface surrounding a nerve trunk or axon as an approximation), then a function $\Phi(x,y,z)$ can be defined as

$$\Phi(x,y,z) = \Phi_{se}(z) \tag{9}$$

for (x,y,z) in V. That is, Φ is taken to be uniform over the cross-section and takes on the value at the surface of the nerve (excised). Of course, Φ is simply a mathematical abstraction and represents a real potential only on S. But with Φ defined above, the divergence theorem can be used to transform (8) as follows:

$$\Phi_V = \frac{1}{4\pi}\int_S \Phi_{se}\frac{\partial}{\partial n}\left(\frac{1}{r}\right)dS = \frac{1}{4\pi}\int_S \Phi\nabla\left(\frac{1}{r}\right)\cdot dS = \frac{1}{4\pi}\int_V \nabla\cdot\left[\Phi\nabla\left(\frac{1}{r}\right)\right]dV \qquad (10)$$

Since, in general $\nabla\cdot\psi\mathbf{A} = \psi\nabla\cdot\mathbf{A} + \nabla\psi\cdot\mathbf{A}$, the last term in (10) yields

$$\Phi_V = \frac{1}{4\pi}\int \frac{\partial\Phi}{\partial z}\frac{\partial(1/r)}{\partial z}\,dV \qquad (11)$$

if one utilizes $\nabla^2(1/r) = 0$ and the properties of Φ given by (9). If (11) is now integrated by parts (with respect to z), then

$$\Phi_V = \frac{1}{4\pi}\int_{A_2}\left(\frac{\partial\Phi}{\partial z}\frac{1}{r}\right)dA - \frac{1}{4\pi}\int_{A_1}\left(\frac{\partial\Phi}{\partial z}\frac{1}{r}\right)dA - \frac{1}{4\pi}\int_V \frac{\partial^2\Phi}{\partial z^2}\frac{1}{r}\,dV \qquad (12)$$

where the surfaces A_1 and A_2 are the end (cap) surfaces of the cylinder, and dA is an element of cross-sectional area. In this form, the sources are dual to surface and volume charge density sources of electrostatics.

Specialization to One-Dimensional Form. An electric circuit representation of a uniform nerve trunk or of a single fiber, which is cylindrical and axially symmetric, is shown in Fig. 2. In this schematic r_e is the "external" resistance while r_i is the "internal" resistance per unit length. The shunt element Y represents passive and active elements both linear and non-linear. In the usual interpretation of Fig. 2,

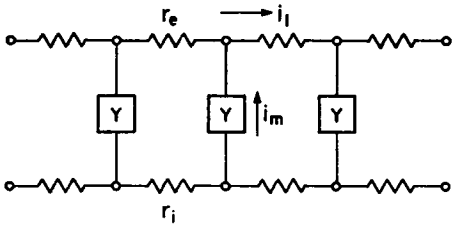

FIGURE 2 Lumped circuit representation of axon.

the potential along the resistance r_e is considered to be the actual surface potential Φ_{se} along the excised nerve. From the circuit, one can confirm that

$$\partial\Phi_{se}/\partial z = -i_i r_e \qquad (13a)$$

$$\partial i_i/\partial z = i_m \qquad (13b)$$

where i_i is the net effective external longitudinal current and i_m is the effective transverse current. Combining (13a) and (13b) leads to

$$\partial^2\Phi_{se}/\partial z^2 = -i_m r_e \qquad (14)$$

For a length of nerve that completely contains the action potential, no contribution from A_1 and A_2 in (12) occurs; consequently, if (14) is utilized, we get

$$\Phi_V = \frac{r_e}{4\pi} \int_V \frac{i_m}{r} \, dV \tag{15}$$

which expresses the potential in the infinite volume in terms of quantities obtained from the isolated nerve. Now in (15) the expression for volume conductor potentials takes on a particularly simple form, as noted by Lorente de Nó. For the single axon, i_m can be identified with the transmembrane current, while for the nerve trunk i_m is the algebraic sum of membrane currents of the individual fibers that does not go into axial current flow in the interstitial space within the trunk. If the external current density were uniformly distributed over a cross-section of area C, then for a conductivity of σ,

$$\Phi_V = \frac{1}{4\pi\sigma C} \int_V \frac{i_m}{r} \, dV \tag{16}$$

The above results are valid only for excised nerve and, furthermore, require the shape of the nerve to be cylindrical and the excitation axially symmetric.

Volume Conductor Potentials from in Situ Parameters. The formulation of Lorente de Nó given by (8) and its subsequent transformation to expressions as in (16) all involve quantities to be measured on an excised nerve. There are numerous situations where the data is available only for the nerve *in situ*. For example, the Hodgkin-Huxley theory for the squid axon yields solutions for *in situ* conditions. We turn our attention, therefore, to a derivation of appropriate formulas which relate the potentials in volume conductors to *in situ* bioelectric source conditions.

We begin by considering, as in Fig. 3, a bioelectric source contained in a volume conductor V of conductivity σ and of infinite extent. The surface S_0 is any surface surrounding the source, while S_∞ designates the surface at infinity. Consider an

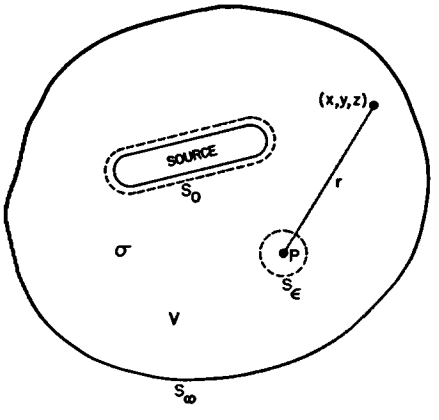

FIGURE 3 Nerve in infinite conductor.

arbitrary point $P(x',y',z')$ external to S_0 and let an element of integration be defined by the unprimed variables (x,y,z).

Now if we surround P by a very small spherical surface of radius ϵ, whose surface is designated S_ϵ, and let the region bounded by S_∞, S_0, and S_ϵ be designated $(V-\epsilon)$, then in the latter region Green's theorem (3) becomes

$$\int_{V-\epsilon}(\Phi\nabla^2\psi - \psi\nabla^2\Phi)\,dV = \int_{S_\epsilon}\left(\Phi\frac{\partial\psi}{\partial n} - \psi\frac{\partial\Phi}{\partial n}\right)dS + \int_{S_\epsilon}\left(\Phi\frac{\partial\psi}{\partial n} - \psi\frac{\partial\Phi}{\partial n}\right)dS + \int_{S\infty}\left(\Phi\frac{\partial\psi}{\partial n} - \psi\frac{\partial\Phi}{\partial n}\right)dS \qquad (17)$$

We now let Φ be the desired solution, *i.e.* $\nabla^2\Phi = -\omega/\sigma$, while ψ is defined as in (4).

The behavior of Φ and ψ at infinity is that they diminish at least as $1/r^2$ and $1/r$, respectively. Consequently, if we think of the surface at infinity as a spherical surface of radius $R \to \infty$, then the integrals over S_∞ go to zero as $0(1/R^2)$. (See Stratton.)

Substituting (1) and (4) into the remaining terms of (17) leaves

$$\int_{V-\epsilon}\Phi\nabla^2\left(\frac{1}{r}\right)dV + \frac{1}{\sigma}\int_{V-\epsilon}\frac{\omega}{r}\,dV = \int_{S_\epsilon}\Phi\nabla\left(\frac{1}{r}\right)\cdot dS - \int_{S_\epsilon}\frac{\partial\Phi}{\partial n}\frac{1}{r}\,dS + \int_{S_\epsilon}\Phi\nabla\left(\frac{1}{r}\right)\cdot dS - \int_{S_\epsilon}\frac{\partial\Phi}{\partial n}\frac{1}{r}\,dS \qquad (18)$$

Since $r \neq 0$ in the region $V-\epsilon$, then $\nabla^2(1/r) = 0$ and the first integral in the expression above vanishes. In the integral over S_ϵ, $\nabla\Phi$ is well behaved on the vanishingly small spherical surface of radius $r = \epsilon \to 0$ so that it may be removed from the integral evaluated at the point. Then we see that

$$\lim_{r\to 0}\int_{S_\epsilon}\frac{\partial\Phi}{\partial n}\frac{1}{r}\,dS = \lim_{r\to 0}\int_{S_\epsilon}\frac{\nabla\Phi\cdot dS}{r} = \lim_{r\to 0}\nabla\Phi\cdot\int_{S_\epsilon}\frac{dS}{r} \qquad (19)$$

Since the area varies as r^2 the magnitude of the last integral vanishes at least as $0(r)$. Actually this integral is identically zero as is clear from symmetry. The same procedure when applied to the remaining integral over S_ϵ yields

$$\lim_{r\to 0}\Phi\Big|_P\int_{S_\epsilon}\nabla\left(\frac{1}{r}\right)\cdot dS = \lim_{r\to 0}\Phi(P)\times\frac{4\pi r^2}{r^2} = 4\pi\Phi(P) \qquad (20)$$

In the limit $\epsilon \to 0$, $(V-\epsilon) \to V$, and we get finally

$$\Phi(P) = \frac{1}{4\pi\sigma}\int_V\frac{\omega}{r}\,dV + \frac{1}{4\pi}\int_{S_0}\frac{\partial\Phi}{\partial n}\frac{1}{r}\,dS - \frac{1}{4\pi}\int_{S_0}\Phi\nabla\left(\frac{1}{r}\right)\cdot dS \qquad (21)$$

The above result and the derivation is a standard one in electromagnetic theory (Stratton) and is included here for completeness.

For the case where S_0 encloses all sources, as for example where S_0 contains a single axon or nerve trunk, then $\omega = 0$. In addition, we have

$$J_n = \sigma\partial\Phi/\partial n \qquad (22)$$

where J_n is the normal component of current density flowing out of S_0. Equation (21) now becomes

$$\Phi(P) = \frac{1}{4\pi\sigma}\int_{S_e}\frac{J_n}{r}\,dS + \frac{1}{4\pi}\int_{S_e}\Phi_e\nabla\left(\frac{1}{r}\right)\cdot d \tag{23}$$

where dS has been reversed so that it is an outward normal from S_0. In this form, J_n behaves like a current source surface density while Φ_e is the magnitude of a double layer potential source.

Cylindrical Nerves with Axial Symmetry—(Infinite Volume Conductor). If S_0 in Fig. 3 is the external surface of a single axon, then J_n in (23) is identical to the transmembrane current density. Equation (23) would be equally satisfactory if S_0 is chosen to be a surface some distance beyond the actual axon surface, but in this case J_n can no longer be identified as the membrane current density. For a cylindrical trunk that is bounded by S_0, J_n is the actual current density crossing into the surrounding volume conductor. For the same nerve, the numerical value of J_n will differ depending on whether the nerve is excised or in a volume conductor (as well as depending on the choice of S_0 in the latter case).

We may repeat the formal mathematical transformation of (8) into (12) with respect to the second integral in (23). If, in addition, the action potential is assumed to lie completely within the nerve, the contribution from the end surfaces is zero with the result that

$$\Phi(P) = \frac{1}{4\pi\sigma}\int_{S_e}\frac{J_n}{r}\,dS - \frac{1}{4\pi}\int_{V_e}\frac{\partial^2\Phi}{\partial z^2}\frac{1}{r}\,dV \tag{24}$$

In (24) Φ is defined by (9) except that Φ_e replaces Φ_{se}, where Φ_e refers to the *in situ* surface potential.

If the equivalent circuit of Fig. 2 could be applied, then we have

$$\frac{\partial^2\Phi_e}{\partial z^2} = -i_n r_e \tag{25}$$

where i_n is the net normal current outflow from S_0 per unit length (related to J_n by a transformation of current per unit area to current per unit length). For field points whose distance from the axis is large compared with the diameter of S_0, r in (24) is approximately constant in the integration over a cross-section. Consequently both integrals in (24) go over into the following line integrals where a is the radius:

$$\Phi(P) \simeq \frac{1}{4\pi\sigma}\int_z\frac{i_n}{r}\,dz + \frac{1}{4\pi}\int_z\frac{i_n\pi a^2 r_e}{r}\,dz \tag{26}$$

If the internal axial current is assumed uniform, then its resistance will be

$$r_i \simeq \frac{1}{\sigma_i\pi a^2}$$

for an internal conductivity σ_i. For the nerve trunk, the cross-sectional area available

is less than πa^2 so that r_i is then larger in value. Then (26) can be written

$$\Phi(P) = \left[1 + \frac{r_e}{r_i(\sigma_i/\sigma)}\right] \frac{1}{4\pi\sigma} \int_Z \frac{i_n}{r}\, dz \tag{27}$$

Since $\sigma_i \approx \sigma$ and $r_e \ll r_i$, the second term in (27), hence (26) can be ignored leaving

$$\Phi(P) \simeq \frac{1}{4\pi\sigma} \int_Z \frac{i_n}{r}\, dz \tag{28}$$

It is interesting to note the similarity of (28) to (16). Of course, (16) applies only to the excised nerve where $C \ll \pi a^2$. However, (28) shows that when C becomes very large (becoming infinite), it is as if the correct value to insert for C in (16) is then $C = \pi a^2$.

The result expressed by (28) suggests that even for non-cylindrical nerves the second term in (23) may be negligible compared to the first. Such a conclusion is also suggested by the following crude argument. Because the external region is so extensive and of a conductivity comparable to axoplasm, variations in Φ_e are relatively small. Thus, in the work of Hodgkin and Huxley the cable network of Fig. 2 is utilized but with r_e set equal to zero. As a second example, Taylor, Moore, and Cole find that neglecting potential variations in the external sea water causes no more than a 5 per cent error in the computation of characteristic length. Now if Φ_e can be taken to be a constant, the second integral in (23) can be transformed using the divergence theorem and we obtain the result that

$$\frac{\Phi_e}{4\pi} \int_{S_e} \nabla\left(\frac{1}{r}\right) \cdot dS = \frac{\Phi_e}{4\pi} \int_V \nabla^2\left(\frac{1}{r}\right) dV = 0 \tag{29}$$

since $\nabla^2(1/r) = 0$. Under these circumstances the second term in (23) can truly be neglected. The argument here is weak since it is not certain that when Φ_e takes on true values (not precisely constant) that the second integral in (23) will indeed be small compared to the first, but such a conclusion is plausible.

Infinite Axon Example. The use of Fig. 2 to represent a nerve in an infinite volume conductor involves an unsatisfactory approximation of external quantities. Specifically, the current density in the external cross-section is far from uniform and it is no longer true that the surface potential along the nerve and the net axial current are related by (13*a*).[2] The previous demonstration may be qualitatively satisfactory but it is not completely convincing.

We circumvent this difficulty by proceeding to compare the terms J_n and $\partial^2\Phi/\partial z^2$ of (24) directly. This can be done since specification of Φ_e determines both J_n and $\partial^2\Phi/\partial z^2$. Unfortunately, the determination of these quantities is too complicated to

[2] At the very least (13*a*) requires the radial dependence of axial current density in the external media to be independent of z, a condition that is not fulfilled.

consider in general, consequently we proceed to a specific example and its numerical evaluation.

In order to make the mathematical analysis more tractable, we assume the nerve to be circular cylindrical and of infinite extent. We will take a to be the radius of any circular cross-section of the nerve and z to be the distance from an origin taken in the middle of the nerve fibre. The conductivity of the external media is taken as σ. The result should be entirely satisfactory for our purposes, particularly for the case where the action potential lies completely between the ends of the nerve. We assume that axial symmetry ($\partial/\partial\phi = 0$) and the potential over the surface, $\Phi_s(z)$, are known. The general form of the solution to Laplace's equation in cylindrical co-ordinates that has an appropriate behavior for $a \leq r \leq \infty$ is

$$[A(\Gamma)\, d\Gamma]\, K_0(\Gamma r) e^{-i\Gamma z}$$

where $[A(\Gamma)d\Gamma]$ is an undetermined coefficient, Γ is a separation constant (eigenvalue), and K_0 the modified Bessel function. Because the region is infinite all real values of Γ are permissible, consequently a general solution to the potential at an arbitrary point (r, z) is

$$\Phi(r, z) = \int_{-\infty}^{\infty} A(\Gamma)\, K_0(\Gamma r) e^{-i\Gamma z}\, d\Gamma \tag{30}$$

We require satisfaction of the following boundary condition, namely

$$\Phi(a, z) = \Phi_s(z) = \int_{-\infty}^{\infty} A(\Gamma)\, K_0(\Gamma a) e^{-i\Gamma z}\, d\Gamma \tag{31}$$

Taking the inverse Fourier transform gives

$$A(\Gamma)\, K_0(\Gamma a) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \Phi_s(z) e^{i\Gamma z}\, dz \tag{32}$$

Hence

$$\Phi(r, z) = \int_{-\infty}^{\infty} \left[\frac{\int_{-\infty}^{\infty} \Phi_s(z) e^{i\Gamma z}\, dz}{2\pi\, K_0(\Gamma a)} \right] K_0(\Gamma r) e^{-i\Gamma z}\, d\Gamma$$

$$\Phi(r, z) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \Phi_s(\zeta) e^{i\Gamma\zeta}\, d\zeta\, \frac{K_0(\Gamma r)}{K_0(\Gamma a)} e^{-i\Gamma z}\, d\Gamma \tag{33}$$

The change of variable to ζ in (33) is to assist in identifying the true parameter z which exists on both sides of the equation. We define

$$F(\Gamma) = \int_{-\infty}^{\infty} \Phi_s(\zeta) e^{i\Gamma\zeta}\, d\zeta \tag{34}$$

so that $F(\Gamma)$ is the Fourier transform of the given surface potential distribution.

We consider field points which are at a distance from the nerve that is large compared with the radius of the latter. Then (24) can be written

$$\Phi(P) = \frac{1}{4\pi}\int_z \left[2\pi a \frac{\partial \Phi}{\partial r}\Big|_{a}\right]\frac{1}{r}\,dz - \frac{1}{4\pi}\int_z \left[\pi a^2 \frac{\partial^2 \Phi}{\partial z^2}\Big|_{r=a}\right]\frac{1}{r}\,dz \tag{35}$$

Thus we wish to compare the relative magnitudes[8] of $I_1(z)$ and $I_2(z)$ defined as

$$I_1(z) = \frac{a}{2}\frac{\partial \Phi}{\partial r}\Big|_{r=a} = -\frac{a}{4\pi}\int_{-\infty}^{\infty} F(\Gamma)\Gamma \frac{K_1(\Gamma a)}{K_0(\Gamma a)} e^{-i\Gamma z}\,d\Gamma \tag{36}$$

$$I_2(z) = \frac{a^2}{4}\frac{\partial^2 \Phi}{\partial z^2}\Big|_{r=a} = -\frac{a^2}{8\pi}\int_{-\infty}^{\infty} \Gamma^2 F(\Gamma) e^{i\Gamma z}\,d\Gamma = \frac{a^2}{4}\frac{\partial^2 \Phi_e(z)}{\partial z^2} \tag{37}$$

The integral formulations in (36) and (37) follow directly from (33) and (34) by carrying out the indicated differentiation under the integral sign.

Specific conditions were chosen to correspond to typical squid axon data. We take $a = 0.02$ cm, velocity of propagation of 20 m/sec., and a monophasic action potential duration of 1 msec. The spatial extent of the propagated action potential is then approximately 2 cm. To simplify the computation, the action potential was approximated by the equation

$$\Phi_{se}(z) = Ae^{-4z^2} \tag{38}$$

where z is in centimeters and $\Phi_{se}(z)$ is the monophasic action potential of the axon in air. Equation (38) yields a normalized action potential looking like a normal Gaussian curve dropping to 0.018 at $z = \pm 1$ cm, whereas a true action potential would be unsymmetrical with a rise time much shorter than the decay. However, this approximation yields a significant computational simplification; for the purpose of establishing the relative strength of $I_1(z)$ and $I_2(z)$, the error should not be too serious.

Based on (9) and (12), the surface potential of the axon in an infinite conductor, $\Phi_s(z)$, is clearly proportional to $\partial^2 \Phi_{se}/\partial z^2$. Thus we have

$$\Phi_s(z) = Bd^2(e^{-4z^2})/dz^2 = B(64z^2 - 8)e^{-4z^2} \tag{39}$$

where B is a new constant. The surface potential will have the expected triphasic form, and a normalized surface potential will have the form of a Gaussian second derivative being equal to -1 at $z = 0$, zero at $z = \pm\sqrt{2}/4 = 0.354$, and having a maximum (0.44626) at $z = \pm\sqrt{6}/4 = 0.612$. One special advantage of the analytic expression of (39) is that $F(\Gamma)$ can be readily found from (34).

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[8] Strictly, the comparison is between $\int I_1/r\,dz$ and $\int I_2/r\,dz$. However, the functional form of I_1 and I_2 are fairly similar so that a comparison of their relative magnitudes is sufficient. In any event, this question can be reexamined once the functions $I_1(z)$ and $I_2(z)$ are found.

After a change in variable and taking advantage of the symmetry we finally get

$$I_1(z) = 17{,}600 \int_0^{0.85} y^2 e^{-156 \cdot 2y^2} \left\{ \frac{1 - \frac{y^2}{2}\left[\ln\left(\frac{1}{y}\right) + \frac{1}{2}\right]}{\left[\ln\left(\frac{1}{y}\right) + 0.116\right]\left[1 + \frac{y^2}{4}\right]} \right\} \cos(50yz)\, dy \qquad (40)$$

where the amplitude constant B has been set equal to unity. The upper limit of the integral in (40) was chosen to include all essential contributions to $I_1(z)$. The quantity in the braces is an approximation (series form) to the Bessel functions which is accurate to within 2½ per cent. The value of $I_2(z)$ is obtained directly from (39), although it was also evaluated, as a check, by the Fourier integral of (37). Its evaluation and that of (40) were accomplished on a digital computer and the results are plotted in Fig. 4. The magnitude of I_1 is clearly dominant over

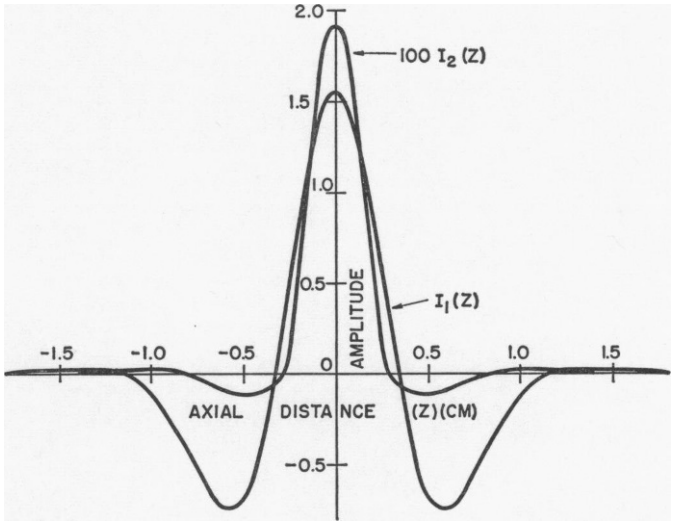

FIGURE 4 Quantities $I_1(z)$ and $I_2(z)$ (see text) for hypothetical action potential.

I_2, thus substantiating the result expressed by (28). It is also of interest to note that the form of the membrane current of the axon in an infinite media (from (36) this is clearly proportional to $-I_1$) is similar to that for the nerve in air, as might be anticipated.

The author wishes to thank Dr. David G. Fleming, Associate Professor of Bioengineering at Case Institute of Technology, for his helpful assistance and discussion of this paper. This investigation was supported in whole by the Public Health Service Research Grant RG 08569, from the National Institutes of Health.

Received for publication, August 14, 1963.

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