

A CALCULATION OF THE MAGNETIC FIELD OF A NERVE ACTION POTENTIAL

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ABSTRACT The magnetic field outside an isolated axon is calculated using transmembrane potential data to specify the boundary conditions to a solution of Laplace's equation. It is shown that the contribution to the magnetic field from the current inside the membrane is two orders of magnitude larger than that from the external current. The contribution from current within the membrane is negligible. Comparisons are made between waveforms calculated for a crayfish lateral axon and those measured for a frog sciatic nerve. This calculation suggests that the magnetic field measured outside nerves can be used to determine their internal current without puncturing the nerve membrane.

INTRODUCTION

The electrical activity of a nerve axon has been the subject of much theoretical analysis. Theoretical work on the associated magnetic field has been limited to simple Ampere's law calculations where the nerve is treated as a current carrying line (1), or to calculations of the magnetic field of an electric dipole in a conducting half-space (2). In this paper we calculate the magnetic field of the action potential of a single nerve axon by extending a technique that determines the currents in and around the axon (3).

It has been shown that the potential differences along the outer surface of the membrane are much smaller than those across the membrane and along the inner surface of the membrane (4). We will show that outside the nerve, the contribution to the magnetic field from the current inside the nerve is two orders of magnitude larger than that from the external current, and the contribution from transmembrane current is negligible, so that a description of the total magnetic field outside the nerve can be obtained primarily from a description of the internal current. This calculation demonstrates that measurement of the external electric potential and the external magnetic field would provide information about the electrical activity inside the nerve axon, possibly to the extent of providing a noninvasive measurement of the transmembrane action potential.

CALCULATION OF THE POTENTIALS

As a first step towards obtaining the magnetic field, we need to know the current distribution in and around the activated nerve. To simplify the calculations, we will consider an infinitely long nerve with a thin membrane, of radius a , immersed in an infinite, homogeneous conducting medium. The technique used by Clark and Plonsey (3-5) is to treat the

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transmembrane action potential ϕ_m as a boundary condition and to solve Laplace's equation in cylindrical coordinates for the interior potential ϕ_i and the exterior potential ϕ_e . The transmembrane action potential is defined as

$$\phi_m = \phi_i^s - \phi_e^s, \quad (1)$$

where ϕ_e^s is ϕ_e evaluated on the outer surface of the membrane and ϕ_i^s is ϕ_i evaluated on the inner one. The continuity equation, which tells us that the current entering one side of the membrane must leave on the other side, provides us with a second boundary condition. In this case, the solution to the angularly independent Laplace's equation in cylindrical coordinates has been shown (4, 5) to be

$$\phi_e(\rho, z) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \frac{F_m(k) K_0(|k|\rho) e^{-jkz}}{\alpha(|k|a) K_0(|k|a)} dk, \quad (2)$$

$$\phi_i(\rho, z) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \frac{F_m(k) I_0(|k|\rho) e^{-jkz}}{\beta(|k|a) I_0(|k|a)} dk, \quad (3)$$

where I_0 and K_0 are the zeroth order modified Bessel's function of the first and second kind, respectively, and where $F_m(k)$ is the Fourier transform of the transmembrane potential

$$F_m(k) = \int_{-\infty}^{\infty} \phi_m e^{jkz} dz. \quad (4)$$

The other terms in the integrals are

$$\alpha(|k|a) = -[\gamma(|k|a) + 1], \quad (5)$$

$$\beta(|k|a) = 1 + \frac{1}{\gamma(|k|a)}, \quad (6)$$

$$\gamma(|k|a) = \frac{\sigma_e K_1(|k|a) I_0(|k|a)}{\sigma_i K_0(|k|a) I_1(|k|a)}, \quad (7)$$

where a is the radius of the nerve and σ_e and σ_i are the external and internal conductivities, respectively.

To simplify these integrals, the transmembrane action potential is phenomenologically fitted to the sum of three arbitrary Gaussians (4)

$$\phi_m(z) = \sum_{i=1}^3 A_i e^{-B_i^2(z-C_i)^2}, \quad (8)$$

so that we can determine the Fourier transform of $\phi_m(z)$ analytically

$$\begin{aligned} F_m(k) &= \sum_{i=1}^3 A_i \int_{-\infty}^{\infty} e^{-B_i^2(z-C_i)^2} e^{jkz} dz \\ &= \sqrt{\pi} \sum_{i=1}^3 \frac{A_i}{B_i} e^{-k^2/4B_i^2} e^{jkC_i}. \end{aligned} \quad (9)$$

The internal and external potentials can then be reduced to the form (4)

$$\phi_e(\rho, z) = \frac{1}{a\sqrt{\pi}} \sum_{i=1}^3 \frac{A_i}{B_i} \int_0^\infty \frac{K_0(y\rho/a) e^{-y^2/4a^2B_i^2}}{K_0(y) \alpha(y)} \cos [y(z - C_i)/a] dy, \quad (10)$$

$$\phi_i(\rho, z) = \frac{1}{a\sqrt{\pi}} \sum_{i=1}^3 \frac{A_i}{B_i} \int_0^\infty \frac{I_0(y\rho/a) e^{-y^2/4a^2B_i^2}}{I_0(y) \beta(y)} \cos [y(z - C_i)/a] dy, \quad (11)$$

where $y = ka$. These equations represent the potentials inside and outside the nerve in terms of a parameterization of the transmembrane action potential.

THE CURRENT DENSITIES

The law of Biot-Savart expresses the magnetic field as an integral of the current density, so we can use the expressions for ϕ_e and ϕ_i to calculate the current density inside and outside the nerve. The electric field in the intra- and extracellular media is the negative gradient of the potential, and the current density is proportional to the electric field via Ohm's law, i.e.,

$$\mathbf{J}(\mathbf{r}) = \sigma \mathbf{E}(\mathbf{r}) = -\sigma \nabla \phi(\mathbf{r}). \quad (12)$$

In cylindrical coordinates, this becomes

$$\mathbf{J}(\mathbf{r}) = -\sigma \left\{ \hat{\rho} \frac{\partial \phi}{\partial \rho} + \hat{k} \frac{\partial \phi}{\partial z} \right\}. \quad (13)$$

Differentiating Eqs. 10 and 11, and using expressions for the derivative of Bessel functions, we obtain expressions for the current densities inside (\mathbf{J}_i) and outside (\mathbf{J}_e) of the membrane in terms of integrals that can be evaluated numerically:

$$\begin{aligned} \mathbf{J}_i(\rho, z) = & -\frac{\sigma_e \hat{\rho}}{a^2 \sqrt{\pi}} \sum_{i=1}^3 \frac{A_i}{B_i} \int_0^\infty \frac{I_1(y\rho/a) e^{-y^2/4a^2B_i^2}}{I_0(y) \beta(y)} y \cos [y(z - C_i)/a] dy \\ & + \frac{\sigma_i \hat{k}}{a^2 \sqrt{\pi}} \sum_{i=1}^3 \frac{A_i}{B_i} \int_0^\infty \frac{I_0(y\rho/a) e^{-y^2/4a^2B_i^2}}{I_0(y) \beta(y)} y \sin [y(z - C_i)/a] dy \end{aligned} \quad (14)$$

$$\begin{aligned} \mathbf{J}_e(\rho, z) = & \frac{\sigma_e \hat{\rho}}{a^2 \sqrt{\pi}} \sum_{i=1}^3 \frac{A_i}{B_i} \int_0^\infty \frac{K_1(y\rho/a) e^{-y^2/4a^2B_i^2}}{K_0(y) \alpha(y)} y \cos [y(z - C_i)/a] dy \\ & + \frac{\sigma_0 \hat{k}}{a^2 \sqrt{\pi}} \sum_{i=1}^3 \frac{A_i}{B_i} \int_0^\infty \frac{K_0(y\rho/a) e^{-y^2/4a^2B_i^2}}{K_0(y) \alpha(y)} y \sin [y(z - C_i)/a] dy \end{aligned}$$

While we now have \mathbf{J} inside and outside the nerve, we have not yet evaluated the current within the membrane. The equation of continuity can be combined with the divergence of the electric displacement \mathbf{D} to give

$$\nabla \cdot \left(\mathbf{J} + \frac{\partial \mathbf{D}}{\partial t} \right) = 0, \quad (15)$$

where \mathbf{J} is the conduction current and $\partial \mathbf{D} / \partial t$ is termed the displacement current. At the

membrane, we must conserve the normal component of $\mathbf{J} + \partial\mathbf{D}/\partial t$. Since the conductivity of the membrane is of the order of $10^{-5} \Omega^{-1}\text{m}^{-1}$ while that of the axoplasm is $1 \Omega^{-1}\text{m}^{-1}$ (4), inside the nerve $\partial D_i^p/\partial t$ is negligible compared with J_i^p . At the inner membrane surface, Eq. 15 becomes

$$\hat{\rho} \cdot \mathbf{J}_i = \left(\mathbf{J}_m + \frac{\partial \mathbf{D}_m}{\partial t} \right) \cdot \hat{\rho}, \quad (16)$$

where $\hat{\rho}$ is the cylindrical unit vector and \mathbf{J}_i is given by Eq. 14. In the quasistatic limit (radiation effects negligible), the displacement current should not be included in the law of Biot-Savart as long as the integration includes all of the conduction currents (6). Thus, to determine the membrane conduction current using Eq. 16, we must first determine the membrane displacement current. We shall treat the membrane as a capacitor filled with a leaky dielectric with an impressed potential ϕ_m . The membrane has conductivity σ_m and electric permittivity ϵ_m . Since the radius of the nerve is much larger than the thickness of the membrane, the membrane can be described as a parallel-plate capacitor where

$$\frac{D_m^p(z)}{\epsilon_m} = \frac{\phi_m(z)}{d}, \quad (17)$$

where d is the thickness of the membrane. But we know ϕ_m , and, if the wave is nondispersive, we can relate temporal and spatial derivatives of ϕ_m to rewrite Eq. 17 as

$$\frac{\partial D_m^p}{\partial t} = -\frac{\epsilon_m u}{d} \frac{\partial \phi_m}{\partial z}, \quad (18)$$

where u is the conduction velocity. The z derivative of ϕ_m can be evaluated from the Gaussian expansion in Eq. 8, and we can solve for J_m^p , the radial component of the membrane current

$$J_m^p = J_i^p - \frac{\epsilon_m u}{d} \sum_{i=1}^3 2A_i B_i^2 (z - C_i) e^{-B_i^2(z - C_i)^2}. \quad (19)$$

To determine the longitudinal current in the membrane, we can use the quasistatic Maxwell's equation

$$\nabla \times \mathbf{E}(\mathbf{r}) = 0. \quad (20)$$

This indicates that the axial component of \mathbf{E} at the membrane must be conserved, i.e., E_i^z and E_m^z must be equal, to yield

$$\frac{J_m^z}{J_i^z} = \frac{\sigma_m}{\sigma_i} \approx 10^{-5}. \quad (21)$$

This ratio indicates that J_m^z is negligible. Therefore, the membrane current is radial to a good approximation.

Thus far we have used the boundary condition on the membrane to determine the current through the inner surface. If we repeat our analysis of $\mathbf{J} + \partial\mathbf{D}/\partial t$ at the outer membrane wall,

we find that

$$J_i^{\rho} = J_m^{\rho} + D_m^{\rho} = J_e^{\rho} \text{ and } \frac{J_m^z}{J_e^z} = \frac{\sigma_m}{\sigma_e} \approx 10^{-5}, \quad (22)$$

confirming that the current entering the membrane leaves the membrane.

THE MAGNETIC FIELD

The magnetic field due to a current density distribution is given by the law of Biot-Savart, which involves an integral over the entire region V' where the current density is nonzero:

$$\mathbf{B}(\mathbf{r}) = \frac{\mu_0}{4\pi} \int_{V'} \frac{\mathbf{J}(\mathbf{r}') \times (\mathbf{r} - \mathbf{r}')}{|\mathbf{r} - \mathbf{r}'|^3} dV'. \quad (23)$$

If the nerve is in an infinite, homogeneous, conductive medium, V' can be broken into three regions as illustrated in Fig. 1: the region inside the nerve, V_i' , the region V_e' external to the nerve, and V_m' within the membrane. The total magnetic field, \mathbf{B}_T , can be written as the sum of the contributions of the currents in each region

$$\mathbf{B}_T(\mathbf{r}) = \frac{\mu_0}{4\pi} \left\{ \int_{V_i'} \frac{\mathbf{J}_i \times (\mathbf{r} - \mathbf{r}')}{|\mathbf{r} - \mathbf{r}'|^3} dV' + \int_{V_e'} \frac{\mathbf{J}_e \times (\mathbf{r} - \mathbf{r}')}{|\mathbf{r} - \mathbf{r}'|^3} dV' + \int_{V_m'} \frac{\mathbf{J}_m \times (\mathbf{r} - \mathbf{r}')}{|\mathbf{r} - \mathbf{r}'|^3} dV' \right\}. \quad (24)$$

Each of these integrals is of the form

$$\mathbf{I} = \int_{V'} \frac{\mathbf{J} \times (\mathbf{r} - \mathbf{r}')}{|\mathbf{r} - \mathbf{r}'|^3} dV', \quad (25)$$

which can be changed into the more convenient form involving a volume integral of the curl and a surface integral of the tangential component (7)

$$\mathbf{I} = \int_{V'} \frac{\nabla' \times \mathbf{J}}{|\mathbf{r} - \mathbf{r}'|} dV' - \oint_{S'} \frac{\hat{n} \times \mathbf{J}}{|\mathbf{r} - \mathbf{r}'|} da'. \quad (26)$$

The interpretation of this equation is that the source of the magnetic field is the curl of \mathbf{J} in the volume, and the discontinuity in \mathbf{J} at the boundaries. The medium inside and outside the axon is ohmic, and \mathbf{J} can be written as the gradient of a scalar potential. Thus \mathbf{J}_i and \mathbf{J}_e have no curl. The membrane contains the biochemical current sources, and so the current within it is not proportional to \mathbf{E} . For this reason we will perform the integration over the membrane using

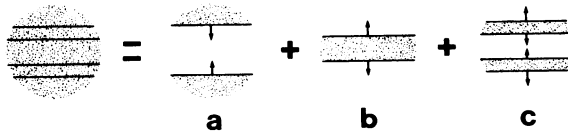


FIGURE 1 A longitudinal section of the cylindrical nerve representing the three regions: (a) V_e , outside the axon; (b) V_i , inside the axon; and (c) V_m , inside the membrane. The arrows describe the unit normal vectors to each bounding surface.

the form in Eq. 24. Thus, we have reduced the volume integral of all space to integrals over the volume and surface of the membrane.

$$\mathbf{B}_T(\mathbf{r}) = \frac{\mu_0}{4\pi} \left\{ \int_{V'_m} \frac{\mathbf{J}_m \times (\mathbf{r} - \mathbf{r}')}{|\mathbf{r} - \mathbf{r}'|^3} dV' + \oint_{S'_e} \frac{\mathbf{J}_e \times \hat{n}}{|\mathbf{r} - \mathbf{r}'|} da' + \oint_{S'_i} \frac{\mathbf{J}_i \times \hat{n}}{|\mathbf{r} - \mathbf{r}'|} da' \right\}. \quad (27)$$

Since \mathbf{J}_e and \mathbf{J}_i go to zero at infinite z , the two surface integrals do not have to be closed on the z axis. This assumption is justified only for action potentials whose spatial extent is shorter than the length of the nerve, and is the reason we consider an infinitely long nerve.

Since we have obtained integral expressions for the magnetic field in terms of the current densities, and the current densities in terms of modified Bessel's functions and the Gaussian parameters of the action potential, the problem is essentially solved. What remains is the evaluation of the integrals.

The contribution to the magnetic field from the current along the outer membrane wall, \mathbf{B}_e , is given by the second term in Eq. 27. The current density is symmetric about the z axis, so we can write

$$\mathbf{J}_e(\rho, z) = J_e^x(\rho, z)\hat{\rho} + J_e^z(\rho, z)\hat{k}. \quad (28)$$

For the outer region, Fig. 1 shows the direction of \hat{n} to be

$$\hat{n} = -\hat{\rho}. \quad (29)$$

Evaluation of both the current density at the membrane ($\rho = a$) and the cross product yields

$$\mathbf{B}_e = -\frac{\mu_0}{4\pi} \int_{S'_e} \frac{\hat{\theta}' J_e^z(a, z') d\alpha'}{|\mathbf{r} - \mathbf{r}'|}. \quad (30)$$

The integral is more tractable if we use the fixed Cartesian unit vectors

$$\hat{\theta}' = -\sin(\theta')\hat{i} + \cos(\theta')\hat{j}. \quad (31)$$

The field must be independent of θ , hence we will evaluate it at θ equal to zero, where

$$|\mathbf{r} - \mathbf{r}'| = [\rho^2 + a^2 + (z - z')^2 - 2a\rho \cos(\theta')]^{1/2}. \quad (32)$$

We can now write \mathbf{B}_e in the more explicit form

$$\mathbf{B}_e = -\frac{\mu_0}{4\pi} a \left\{ -\hat{i} \int_{z_1}^{z_2} J_e^z(z') \int_0^{2\pi} \frac{\sin(\theta') d\theta' dz'}{[\rho^2 + a^2 + (z - z')^2 - 2a\rho \cos(\theta')]^{1/2}} + \hat{j} \int_{z_1}^{z_2} J_e^z(z') \int_0^{2\pi} \frac{\cos(\theta') d\theta' dz'}{(\rho^2 + a^2 + (z - z')^2 - 2a\rho \cos(\theta'))^{1/2}} \right\}. \quad (33)$$

The first integral is an odd function over the range of integration, and it vanishes. The θ' integration in the remaining integral is

$$I = \int_0^{2\pi} \frac{\cos(\theta') d\theta'}{[\rho^2 + a^2 + (z - z')^2 - 2a\rho \cos(\theta')]^{1/2}} \quad (34)$$

This integral can be evaluated in terms of the complete elliptic integrals (8)

$$F(K^2) = \int_0^{2\pi} \frac{d\phi}{[1 - K^2 \sin^2(\phi)]^{1/2}}, \quad (35)$$

$$E(K^2) = \int_0^{2\pi} [1 - K^2 \sin^2(\phi)]^{1/2} d\phi, \quad (36)$$

where

$$K^2 = \frac{4a\rho}{(a + \rho)^2 + (z - z')^2}. \quad (37)$$

These definitions and a change in variables $\theta' = \pi + 2\phi$ allow us to identify I as the sum of the two tabulated functions $F(K^2)$ and $E(K^2)$

$$I = \frac{2}{(a\rho)^{1/2}K} \{(2 - K^2)F(K^2) - 2E(K^2)\}. \quad (38)$$

The contribution of the external current density to the total magnetic field is thus

$$\mathbf{B}_e = -\frac{\hat{\theta}\mu_0}{2\pi} \left(\frac{a}{\rho}\right)^{1/2} \int_{z_1}^{z_2} J_e^z(z') \left\{ \frac{(2 - K^2)F(K^2) - 2E(K^2)}{K} \right\} dz', \quad (39)$$

where we have used the fact that for a θ of zero

$$\hat{j} = \hat{\theta}. \quad (40)$$

This process can be repeated to determine the contribution \mathbf{B}_i from the interior of the axon, given by the third term of Eq. 27. Fig. 1 shows \hat{n} to be the same as $\hat{\rho}$. Writing \mathbf{J}_i as the sum of a radial and longitudinal part and evaluating the cross product as was done for the exterior current, we obtain the expression

$$\mathbf{B}_i = \frac{\mu_0}{4\pi} \int_{s_i} \frac{\hat{\theta}' J_i^z(a, z') da'}{|\mathbf{r} - \mathbf{r}'|}. \quad (41)$$

The evaluation of this integral proceeds in the same manner to produce

$$\mathbf{B}_i = \frac{\hat{\theta}\mu_0}{2\pi} \left(\frac{a}{\rho}\right)^{1/2} \int_{z_1}^{z_2} J_i^z(z') \left\{ \frac{(2 - K^2)F(K^2) - 2E(K^2)}{K} \right\} dz', \quad (42)$$

Thus we have \mathbf{B}_i and \mathbf{B}_e in terms of integrals involving the tangential component of the current density at the inner and outer membrane surfaces.

To complete the evaluation of Eq. 27 we must consider the integral over the membrane volume

$$\mathbf{B}_m = \frac{\mu_0}{4\pi} \int_{V'_m} \frac{\mathbf{J}_m \times (\mathbf{r} - \mathbf{r}')}{|\mathbf{r} - \mathbf{r}'|^3} dV'. \quad (43)$$

It was demonstrated earlier that the membrane current density is radial to a good approximation

$$\mathbf{J}_m(\rho, z) = J_m^{\rho}(z)\hat{\rho}. \quad (44)$$

We will evaluate \mathbf{B}_m for a θ of zero

$$(\mathbf{r} - \mathbf{r}') = [\rho - \rho' \cos(\theta')] \hat{i} - \rho' \sin(\theta') \hat{j} + (z - z') \hat{k}. \quad (45)$$

The cross product in Eq. 43 is

$$\mathbf{J}_m \times (\mathbf{r} - \mathbf{r}') = J_m^\rho(z') [\hat{i}(z - z') \sin(\theta') - \hat{j}(z - z') \cos(\theta') - \hat{k}\rho \sin(\theta')]. \quad (46)$$

When this expression is substituted in Eq. 43, the terms with a $\sin(\theta')$ are odd functions and integrate to zero:

$$\mathbf{B}_m = -\frac{\mu_0 \hat{j}}{4\pi} \int_a^{a+d} \int_{z_1}^{z_2} J_m^\rho(z') (z - z') \int_0^{2\pi} \frac{\rho' \cos(\theta') d\rho' d\theta' dz'}{[\rho^2 + \rho'^2 + (z - z')^2 - 2\rho\rho' \cos(\theta')]^{3/2}}. \quad (47)$$

Since $J_m^\rho(z)$ is independent of ρ , and because the membrane thickness d is infinitesimal, the ρ integral simply contributes a factor of d . The integral over θ' can be rewritten in terms of elliptic integrals (10) to yield \mathbf{B}_m , the contribution of the radial membrane current to the total magnetic field

$$\mathbf{B}_m = -\frac{\hat{\theta}\mu_0}{8\pi} \left(\frac{a}{\rho^3}\right)^{1/2} d \int_{z_1}^{z_2} J_m^\rho(z) (z - z') K \left[\frac{(2 - K^2)E(K^2)}{(1 - K^2)} - 2F(K^2) \right]. \quad (48)$$

The total field is obtained by adding Eqs. 39, 42, and 48. At this point we have simplified Eq. 27 as far as is analytically possible. To continue we must resort to a particular example and proceed numerically.

CALCULATION OF THE MAGNETIC FIELD FOR A CRAYFISH LATERAL AXON

Having derived general expressions for \mathbf{B} and \mathbf{J} and reduced them as far as possible analytically, we now proceed to calculate the fields for the specific case of the crayfish lateral axon. Clark and Plonsey (4) fit the three Gaussians in Eq. 8 to transmembrane potential data from Watanabe and Grundfest (9). The parameters describing the nerve and the transmembrane potential are

$$\begin{array}{lll} a = 6 \times 10^{-5} \text{ m} & d = 13.7 \times 10^{-9} \text{ m} & u = 10.6 \text{ ms}^{-1} \\ \sigma_0 = 5 \Omega^{-1} \text{ m}^{-1} & \epsilon_m = 6.195 \times 10^{-12} \text{ C}^2 \text{ N}^{-1} \text{ m}^2 & \\ \sigma_i = 1 \Omega^{-1} \text{ m}^{-1} & \sigma_m = 10^5 \Omega^{-1} \text{ m}^{-1} & \\ A_1 = 0.051 \text{ V} & B_1 = 800 \text{ m}^{-1} & C_1 = 0.0054 \text{ m} \\ A_2 = 0.072 \text{ V} & B_2 = 533 \text{ m}^{-1} & C_2 = 0.0066 \text{ m} \\ A_3 = 0.018 \text{ V} & B_3 = 333 \text{ m}^{-1} & C_3 = 0.0086 \text{ m} \end{array} \quad (49)$$

To calculate the magnetic field, the current densities must be evaluated from the expressions already derived. The integrals in Eq. 14 for the current density at the membrane surfaces converge fast enough so that the upper infinite limit can be replaced by 0.3 with <1%

error. The axial current densities at the surfaces become

$$J_i^z(a, z) = \frac{\sigma_i}{a^2 \sqrt{\pi}} \sum_{i=1}^3 \frac{A_i}{B_i} \int_0^{0.3} \frac{e^{-y^2/4a^2 B_i^2}}{\beta(y)} y \sin [y(z - C_1)/a] dy,$$

$$J_e^z(a, z) = \frac{\sigma_e}{a^2 \sqrt{\pi}} \sum_{i=1}^3 \frac{A_i}{B_i} \int_0^{0.3} \frac{e^{-y^2/4a^2 B_i^2}}{\alpha(y)} y \sin [y(z - C_1)/a] dy. \quad (50)$$

The transmembrane current density is listed in Eq. 19.

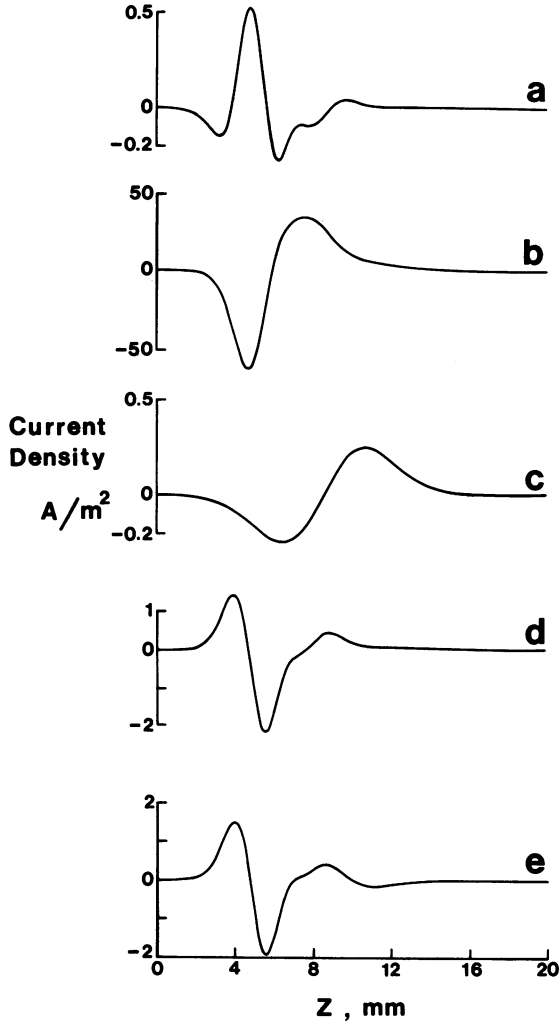


FIGURE 2 The calculated current densities, as a function of z , for a crayfish lateral axon in an unbounded, homogeneous conductor. (a) Axial current density along the outer membrane surface. (b) The axial current density along the inner membrane surface. (c) The radial displacement current density crossing the membrane. (d) The current density striking the membrane from the inside. (e) The transmembrane current density. Note the differing vertical scales.

The integrals were evaluated by a midpoint approximation with three thousand intervals. The Bessel's functions were evaluated by subroutines in the IMSL library (11). The current densities are graphed in Fig. 2. The potentials have been evaluated by Clark and Plonsey (4) and the derivatives of their potential graphs agree with our currents.

The magnetic fields can be calculated once the current densities are known as functions of z . Fig. 3 shows B_i , B_e , and B_T as functions of z at a distance of 1.2×10^{-4} m (twice the nerve radius) from the nerve center. B_e is two orders of magnitude smaller than B_i . B_m is nine orders of magnitude smaller than B_e and is not shown. There are several reasons for this large range in magnitudes. First, the large difference between the internal and membrane conductivities provides a large tangential discontinuity in J at inner membrane surface as the primarily axial internal current transverses the membrane as a radial current. This tangential discontinuity is equivalent to a large curl in J and thus is a strong source of magnetic field. Second, the external current flows in an unbounded external medium. Because of the cylindrical symmetry of the problem, Ampere's law requires that the magnetic field at a distance ρ from the nerve be determined by the current flowing within ρ ; the current beyond ρ makes no contribution. For a ρ close to the nerve, essentially all of the external current is beyond ρ , the

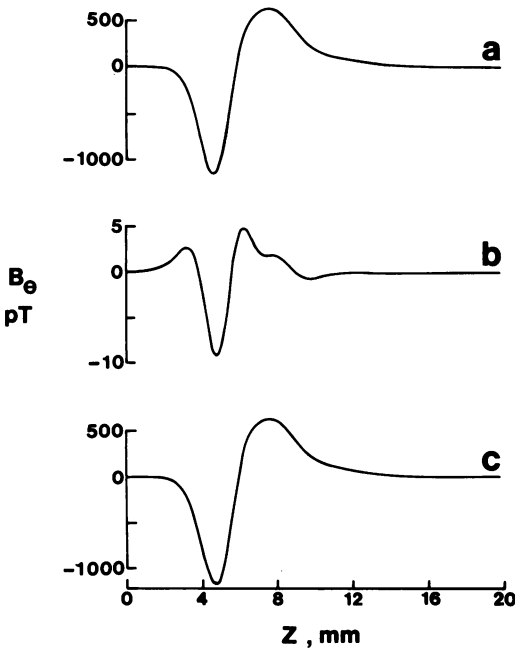


FIGURE 3

FIGURE 3 The contributions from the regions V_i and V_e in Fig. 1 to the magnetic field encircling the nerve at a distance of $2a$ (1.2×10^{-4} m) as a function of z . The contribution from interior current is shown in *a*, that from external current is shown in *b*. The magnetic field from the membrane currents is negligible. The total magnetic field is the sum of these and is shown in *c*. Note the differing vertical scales.

FIGURE 4 (a) A plot of the peak-to-peak width W of the magnetic field waveform as a function of the radial distance R from the nerve. (b) A plot of the absolute value of the ratio of the height of the upper peak B_{\max} to the height of the lower peak B_{\min} as a function of the radial distance R from the center of the nerve.

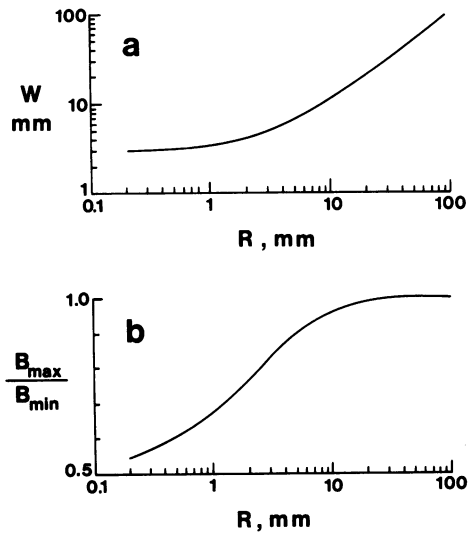


FIGURE 4

external current provides a negligible contribution to \mathbf{B}_T , and the magnitude of \mathbf{B}_T decreases as $(1/\rho)$. Further from the nerve, an increasing fraction of the external current exists within ρ and produces a magnetic field that partially cancels that of the current inside the nerve. As a result, the magnetic field falls off more steeply with increasing distance, eventually as $(1/\rho^3)$. Even so, the internal current maintains its dominance. While the membrane current is large, it provides a negligible contribution to the magnetic field because a uniform radial current produces no magnetic field. The axial dependence of this radial membrane current determines the curl of \mathbf{J} within the membrane, but the membrane is so thin that this provides an infinitesimal contribution.

Fig. 4 *a* is a plot of the peak-to-peak width of the magnetic waveform as a function of the radial distance. From this graph we see that the spreading of the waveform starts slowly. At 5 mm from the center and beyond the width increases linearly with distance, R , from the nerve. Fig. 4 *b* is a plot of the absolute value of the ratio of the peak height of the smaller peak to that of the larger. This gives us an indication of the symmetry of the wave. Here it is seen that beyond 5 mm the wave is symmetric. Both graphs indicate that many details of the nerve impulse structure are lost beyond this distance. The distance will be determined by the spatial extent of the nerve action potential.

Fig. 5 shows the radial dependence of \mathbf{B}_T and \mathbf{B}_e . The plot is of the peak-to-peak height in order to avoid the effect of a shift in peak location with increasing distance. We see that for distances <1 mm, \mathbf{B}_T falls as $1/\rho$, consistent with Ampere's law, and beyond 10 mm it falls as the radial distance cubed, consistent with the nerve being a quadrupolar electrical current source. The external current field \mathbf{B}_e is two orders of magnitude smaller than the field due to the internal current at all distances. Thus the total external magnetic field near the nerve is an indirect measurement of the internal currents, and, in Eq. 24, only the integration of \mathbf{J} over the inside of the nerve need be considered in calculating \mathbf{B}_T to an accuracy of 1%. If this equation can be inverted into an integration over \mathbf{B}_T to find \mathbf{J}_i , then measurements of \mathbf{B} and ϕ_e will provide a noninvasive technique for finding \mathbf{J}_i and ϕ_m .

COMPARISON OF CALCULATED AND MEASURED MAGNETIC FIELDS

Experimental verification of this calculation will require simultaneous recording of the magnetic field and the transmembrane potential for a single nerve axon. While these measurements are yet to be made, preliminary data (12, 13) recorded from frog sciatic nerves are in qualitative agreement with this calculation. Fig. 6 *a* shows magnetic field data recorded at an effective distance of 1.3 mm in an 800–1100 Hz bandwidth. The peak signal corresponds to 60 pT. Fig. 6 *b* shows this same data corrected (13) for the bandpass characteristics of the magnetometer system. This waveform was smoothed during processing. Note that the corrections remove the spurious overshoot late in the waveform in Fig. 6 *a*. Fig. 6 *c* shows the axial electric potential gradient at the outer surface of the nerve as recorded by a pair of electrodes separated by 5.3 mm. Both measurements were made with the nerve immersed in amphibian Ringer's solution. By Ohm's law, the external, axial potential gradient will be proportional to the external axial current density. Comparison of Fig. 6 *b* with Fig. 3 *c* shows that the theoretical and experimental magnetic waveforms are similar. Comparison of Fig. 6 *c* with Fig. 2 *a* shows that the electric waveforms are also similar, and each resembles the derivative of the corresponding magnetic field. Since the sciatic nerve is a bundle of nerve

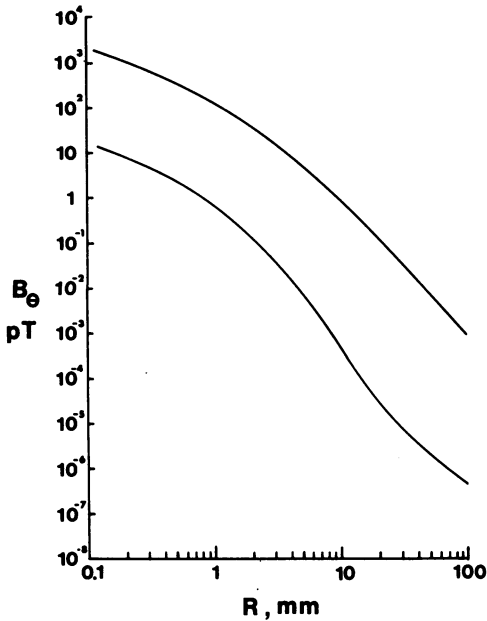


FIGURE 5

FIGURE 5 A graph of the peak-to-peak height of B_T (upper curve) and B_r (lower curve) as a function of the radial distance R from the nerve.

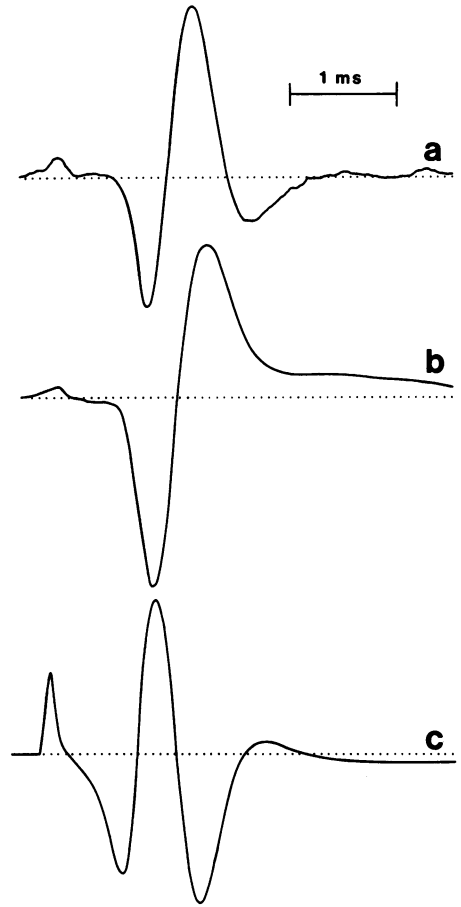


FIGURE 6

FIGURE 6 (a) A recording of the magnetic field at an effective distance of 1.3 mm from an isolated frog sciatic nerve immersed in Ringer's solution. Adapted from reference 12. The first, small peak is stimulus artifact. (Average of 1,024 responses.) (b) The waveform of *a* corrected for the bandpass characteristics of the magnetometer system. Note the absence of the spurious overshoot late in the signal. Adapted from reference 13. (c) The electric potential gradient along the outer surface of the sciatic nerve at the location of the magnetometer pick-up coil. Adapted from reference 12. (Average of 512 responses.)

fibers, whereas the calculation is for a single axon, quantitative comparison is not possible. However, this does indicate the promise for magnetic measurements of nerve function.

CONCLUSION

In this paper we have utilized a technique for calculating the potential outside an activated nerve axon from transmembrane potential data to obtain the current densities required to calculate the magnetic field of a nerve. The technique was applied to a transmembrane potential found in the literature. The magnetic field waveform and radial dependence were

plotted. It has been established that the currents outside the nerve and through the membrane make a negligible contribution to the total field. It has been found that to observe the details of the waveform predicted by the model, measurements of B for the crayfish lateral axon should be made within 5 mm of the nerve center. Comparisons of the calculated magnetic field and external current waveforms with those measured in the frog provide a preliminary experimental confirmation of the ability of the magnetic field to provide a noninvasive measurement of the internal currents in a nerve.

The authors are grateful to John Barach and John Freeman for their comments and suggestions.

This research has been supported in part by grants from the Research Corporation and the Vanderbilt University Research Council.

Received for publication 8 January 1980 and in revised form 17 May 1980.

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