Electric field induced in cells in the human body when this is exposed to low-frequency electric fields

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A detailed analysis is carried out of the electric field induced in a cell when the body is exposed to an incident axial electric field at 50–60 Hz. It is shown that the field in a spherical cell is effectively shielded by the membrane so that the induced field in its interior is negligibly small. It is also shown that the induced electric field in a cylindrical cell (which is long compared to its radius) is the same as the axial field outside the cell. In this case, the cell membrane has no shielding effect. [S1063-651X(98)09108-9]

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I. INTRODUCTION

In his paper, Adair [1] states that the ''internal elements of a cell, such as the nucleus and the genetic material, are shielded by the resistive membrane and the fields they are subjected to are quite negligible.'' This statement applies specifically to spherical cells with a radius of 10 μm. No proof is given, but reference is made to Foster and Schwan [2]. It is the purpose of this paper to show analytically that the statement is true for small spherical cells, but incorrect for elongated cells like those found in muscle and also for long nerve cells. It is important for biophysicists and biomedical scientists to recognize this difference and not assume that the cell membrane shields the interior of all cells. This superficially paradoxical behavior is clarified in a quantitatively explicit analytical study.

II. BACKGROUND

At frequencies as low as 50–60 Hz or 10–30 kHz, all parts of the human body are conductors, i.e., $\sigma \gg \omega\epsilon$, with conductivities that range from $\sigma \sim 0.02$ to 0.85 S/m. The conductivity of the saline tissue in which the organs are embedded is $\sigma \sim 0.5$ S/m. Furthermore, the body is electrically extremely short. Accurate formulas are available for the total axial current $I_{1z}(z)$, the current density $J_{1z}(z)$, and the electric field $E_{1z}(z)$ induced in the body when this is exposed to an electromagnetic field $E_z^{\rm inc}, B_y^{\rm inc}$. These are given in Ref. [3] when the arms are in contact with the sides and the body is far from the earth or standing on it with rubber-soled shoes. Generalized formulas with the arms raised to any angle are in Ref. [4] and for the electric field induced in the individual organs in the body in Ref. [5]. These formulas provide explicit relations for $E_{1z}(z)/E_z^{\rm inc}$, where $E_{1z}(z)$ is the electric field anywhere in the body including the arms, legs, and head. The next step is to derive relations between $E_{1z}(z)$ in the saline tissues of the body and $E_{2z}(z)$ in the cells embedded in it.

III. SPHERICAL CELL

Consider first the rigorous determination of the electric field in a small spherical cell embedded in the conducting tissue with $\sigma_1 = 0.5$ S/m in which the field $E_{1z}(z)$ is maintained. The cell has a radius $b = 10^{-6}$ m. It is bounded by a thin membrane with the thickness $\delta \sim 5\times 10^{-9}$ m. The interior of the cell with radius $a = b-\delta$ consists of protoplasm with $\sigma_2 \sim 0.5$ S/m. The conductivity of the membrane in its resting state is $\sigma_m \sim 10^{-6}$ S/m. The ratio σ_m/σ_1 is the small quantity

$$\eta \equiv \frac{\sigma_m}{\sigma_1} = \frac{10^{-6}}{0.5} = 2\times 10^{-6}. \tag{1}$$

The complete solution for the electric field inside a spherical cell is given in Appendix A. The ratio of the electric field in the cell to that incident from the outside is

$$\frac{E_2(z)}{E_1(z)} = \frac{9\eta}{(2+5\eta+2\eta^2) - 2(1-2\eta+\eta^2)(a/b)^3}. \tag{2}$$

Here

$$\left(\frac{a}{b}\right)^3 = \left(\frac{b-\delta}{b}\right)^3 = \left(1-\frac{\delta}{b}\right)^3 \sim 1 - \frac{3\delta}{b} \tag{3}$$

since $\delta/b \ll 1$. With this value and $\eta \ll 1$,

$$\frac{E_2(z)}{E_1(z)} = \frac{9\eta}{9\eta + 2(1-2\eta+\eta^2)(3\delta/b)} \sim \frac{9\eta}{9\eta + (6\delta/b)} = \frac{1}{1+(2\delta/3\eta b)}. \tag{4}$$

For the spherical cell, $\eta = 2\times 10^{-6}$ and $\delta/b = 5\times 10^{-9}/10^{-6} = 5\times 10^{-3}$, so that $2\delta/3\eta b = 1.67\times 10^3$. It follows that

$$\frac{E_2(z)}{E_1(z)} \sim \frac{3\eta b}{2\delta} = \frac{3\times 2\times 10^{-6}\times 10^{-6}}{2\times 5\times 10^{-9}} = 6\times 10^{-4}. \tag{5}$$

Hence, the electric field $E_2(z)$ in the protoplasm in the interior of the spherical cell is negligibly small compared to the field $E_1(z)$ in the saline tissue in which the cell is embedded. The membrane acts as an excellent shield for the interior.

IV. LONG CELL: NERVES

In addition to small approximately spherical cells, long cylindrical cells are common in the human body. When the body is exposed to an external axial electric field E_z^{inc}, an axial current $I_z(z)$ is induced in the body as shown in Ref. [3]. At 50–60 Hz, this current depends only on the length of the body and is independent of the conductivity. However, it adjusts its current density $J_{iz}(\rho,z)$ at any cross section z in accordance with the conductivities σ_i of the organs and cells in that cross section. The associated electric field is $E_{iz}(\rho,z)=J_{iz}(\rho,z)/\sigma_i$.

Consider a long cylindrical cell that extends from $z=-h$ to h. It is enclosed in a thin membrane with the thickness $\delta=7.5\times10^{-9}$ m and conductivity $\sigma_m=10^{-6}$ S/m. The outside and inside radii of the cell are $b=10^{-6}$ m and $a=b-\delta$. The entire cell is embedded in protoplasm with the conductivity $\sigma_1=0.5$ S/m. The interior of the cell has the same conductivity $\sigma_1=0.5$ S/m. It is exposed to an electric field $E_{1z}(\rho,z)$ parallel to the length of the cell. For simplicity, let it be assumed that the cell to be studied is located near the axial maximum of the current $I_z(z)$ and that $E_{1z}(\rho,z)$ is approximately constant over the length of the cell. Unlike the cylindrical surface of the cell along which the boundary conditions are straightforward, the ends of the cell present a complicated problem. Fortunately, the actual shape and structure of the end surfaces are unimportant in determining the field in the interior of the cell at moderate distances from the ends. Accordingly, the end surfaces will be assumed to be flat and to consist of the same membrane as the cylindrical sides. Because of the low conductivity of the membrane, the current in the ambient medium turns out radially near the ends to travel around instead of through the cell. Since the cross-sectional area πb^2 of the ends is small, the axial current that enters and leaves the cell through the ends is insignificant. For simplicity, it will be taken to be zero by changing the conductivity of the membrane at the ends from the small value $\sigma_m=10^{-6}$ to 0 S/m. Since the electric field incident in the cell is parallel to the cylindrical sides, this means that no current enters or leaves the cell. The only current in it is that generated by the electric field $E_{2z}(\rho,z)$ induced inside the cell.

The model used to determine the electric field in the cell is shown in Fig. 1. The total upward current in the entire body is $I_z(z)$. The current density in the vicinity of the cell is $J_{1z}(z)\sim I_z(z)/A$, where A is the cross-sectional area of the body. At all points, the scalar potential satisfies the equation

$$\nabla^2\phi=0 \tag{6}$$

and the symmetry condition $\phi(\rho,-z)=-\phi(\rho,z)$ applies. The boundary conditions are

$$\sigma_1 E_{1z}(\rho,z)=-\sigma_1\left.\frac{\partial\phi(\rho,z)}{\partial z}\right|_{z=h}=\begin{cases}0, & \rho<a\\ J_{1z}(\rho,z), & \rho>b.\end{cases} \tag{7}$$

From Eq. (B12) in Appendix B, with $\xi=\delta/\eta=\delta\sigma_1/\sigma_m$,

$$\phi_1(\rho>b,z)-\phi_2(\rho<a,z)-\xi\left.\frac{\partial\phi(\rho,z)}{\partial\rho}\right|_{\rho=a}=0,$$

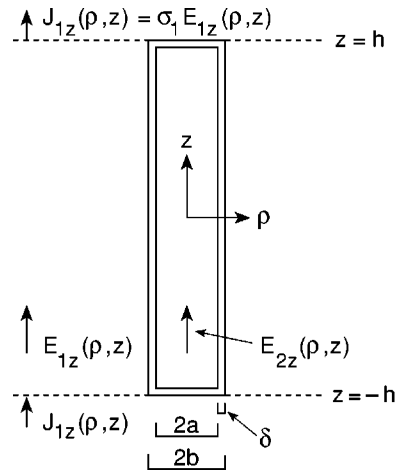

FIG. 1. A long cell (length $2h$, outside radius b, inside radius a, and membrane thickness δ) immersed in a conducting medium with current density $J_{1z}(\rho,z)$ and electric field $E_{1z}(\rho,z)=J_{1z}(\rho,z)/\sigma_1$.

$$-h\leqslant z\leqslant h, \tag{8}$$

$$-E_{1z}(b,z)=\left.\frac{\partial\phi_1(\rho,z)}{\partial\rho}\right|_{\rho=b}=\left.\frac{\partial\phi_2(\rho,z)}{\partial\rho}\right|_{\rho=a}=-E_{2z}(a,z). \tag{9}$$

At distances $\rho\gg b$, Eq. (7) gives

$$\frac{\partial\phi_1(\rho,z)}{\partial z}=-E_{1z}(\rho,z) \tag{10}$$

or

$$\phi_1(\rho,z)=-zE_{1z}(\rho,z). \tag{11}$$

V. SOLUTION FOR THE SCALAR POTENTIAL

The condition (11) at large distances suggests the introduction of the function $\psi(\rho,z)$ defined as

$$\psi(\rho,z)=\begin{cases}\phi(\rho,z), & \rho<a\\ \phi(\rho,z)+zE_{1z}(\rho,z), & \rho>b.\end{cases} \tag{12}$$

It follows that

$$\frac{\partial\psi(\rho,\pm h)}{\partial z}=0 \quad \text{for all } \rho \tag{13}$$

and

$$\nabla^2\psi(\rho,z)=0. \tag{14}$$

A solution will be sought in terms of a Fourier series. The symmetry condition $\phi(\rho,-z)=-\phi(\rho,z)$ indicates the form $\sin(\pi kz/2h)$ when k is a positive integer and the factor 2 in the denominator follows from Eq. (13), which requires the period $4h$. Application of Eq. (13) gives

$$\left.\cos\frac{\pi kz}{2h}\right|_{z=h}=0 \quad \text{or} \quad \cos\frac{\pi k}{2}=0. \tag{15}$$

This means that k is odd, i.e., $k=2n+1$. With

$$k_n \equiv \frac{(2n+1)\pi}{2h}, \tag{16}$$

the Fourier sine series is

$$\psi(\rho,z)=\sum_{n=0}^{\infty} f_n(k_n\rho)\sin k_n z. \tag{17}$$

In the cylindrical coordinates ρ,z and with rotational symmetry, Eq. (14) gives

$$\left\{\frac{\partial^2}{\partial\rho^2}+\frac{1}{\rho}\frac{\partial}{\partial\rho}+\frac{\partial^2}{\partial z^2}\right\}\psi(\rho,z)=0, \tag{18}$$

so that

$$\left\{\frac{\partial^2}{\partial\rho^2}+\frac{1}{\rho}\frac{\partial}{\partial\rho}-k_n^2\right\}f_n(k_n\rho)=0. \tag{19}$$

The solution of Eq. (19) is

$$f_n(k_n\rho)=\begin{cases}\text{const}\times I_0(k_n\rho), & \rho<a\\ \text{const}\times K_0(k_n\rho), & \rho>b,\end{cases} \tag{20}$$

where I and K are the modified Bessel functions. Now let

$$c_n=\frac{d}{d(k_n\rho)}f_n(k_n\rho)\big|_{\rho=b\sim a}. \tag{21}$$

This is continuous at $\rho=b\sim a$. It follows that

$$f_n(k_n\rho)=\begin{cases}c_n\dfrac{I_0(k_n\rho)}{I_0'(k_na)}, & \rho<a\\[2ex] c_n\dfrac{K_0(k_n\rho)}{K_0'(k_nb)}, & \rho>b.\end{cases} \tag{22}$$

However, the Bessel functions are insensitive to variations in argument of the order $k_n\delta$ so that b can be replaced by a. The application of the membrane condition (8) yields c_n. In terms of $\psi(\rho,z)$ as defined in Eq. (12), this is

$$\psi(b,z)-\psi(a,z)-\xi\frac{\partial\psi(\rho,z)}{\partial\rho}\bigg|_{\rho=a}=zE_{1z}(\rho,z). \tag{23}$$

It is now necessary to express the right-hand side in a series corresponding to Eq. (17) for $\psi(\rho,z)$. This is accomplished by noting that the coefficients are

$$\begin{aligned}\frac{1}{2h}\int_{-2h}^{2h}dz\ z\ \sin k_nz&=\frac{1}{h}\int_{-h}^{h}dz\ z\ \sin k_nz\\&=\frac{4h}{[(2n+1)\pi]^2}\sin k_nz\big|_{-h}^{h}\\&=\frac{(-1)^n8h}{[(2n+1)\pi]^2}.\end{aligned} \tag{24}$$

Hence

$$z=\sum_{n=0}^{\infty}\frac{(-1)^n8h}{[(2n+1)\pi]^2}\sin k_nz. \tag{25}$$

With this value, Eq. (23) gives

$$c_n\left[\frac{K_0(k_na)}{K_0'(k_na)}-\frac{I_0(k_na)}{I_0'(k_na)}-\xi k_n\right]=\frac{(-1)^n8h}{[(2n+1)\pi]^2}E_{1z}(\rho,z). \tag{26}$$

With the Wronskian formula $I_0'(z)K_0(z)-I_0(z)K_0'(z)=1/z$, Eq. (26) becomes

$$c_n\left[\frac{1}{k_naI_0'(k_na)K_0'(k_na)}-\xi k_n\right]=\frac{(-1)^n8h}{[(2n+1)\pi]^2}E_{1z}(\rho,z). \tag{27}$$

Since $I_0'=I_1$ and $K_0'=-K_1$, the final result is

$$c_n=-\frac{\dfrac{(-1)^n4a}{(2n+1)\pi}E_{1z}(\rho,z)I_1(k_na)K_1(k_na)}{1+\xi ak_n^2I_1(k_na)K_1(k_na)}. \tag{28}$$

With this, the scalar potential $\phi(\rho,z)$ is

$$\phi(\rho,z)=\begin{cases}-\displaystyle\sum_{n=0}^{\infty}\frac{\dfrac{(-1)^n4a}{(2n+1)\pi}E_{1z}(\rho,z)K_1(k_na)I_0(k_n\rho)\sin k_nz}{1+\xi ak_n^2I_1(k_na)K_1(k_na)}, & \rho<a\\[4ex] -E_{1z}(\rho,z)\left[z-\displaystyle\sum_{n=0}^{\infty}\frac{\dfrac{(-1)^n4a}{(2n+1)\pi}I_1(k_na)K_0(k_n\rho)\sin k_nz}{1+\xi ak_n^2I_1(k_na)K_1(k_na)}\right], & \rho>b.\end{cases} \tag{29}$$

VI. ELECTRIC FIELD INSIDE THE CELL

The electric field inside the cell $\rho<a$ is given by

$$E_{2z}(\rho,z)=-\frac{\partial\phi(\rho,z)}{\partial z},\quad \rho<a, \tag{30}$$

with $\phi(\rho,z)$ given by Eq. (29). This gives

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=\sum_{n=0}^{\infty}\frac{\frac{(-1)^n 2a}{h}K_1(k_na)I_0(k_n\rho)\cos k_nz}{1+\xi ak_n^2I_1(k_na)K_1(k_na)},\quad \rho<a. \tag{31}$$

When $\rho<a$, $k_n\rho$ is very small so that $I_0(k_n\rho)\sim 1$. Similarly, the small-argument formulas for I_1 and K_1 can be used. These are $I_1(k_na)\sim k_na/2$ and $K_1(k_na)\sim 1/k_na$. Hence

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=\frac{4}{\pi}\sum_{n=0}^{\infty}\frac{(-1)^n\cos k_nz}{(2n+1)\left[1+\frac{1}{2}\xi ak_n^2\right]}. \tag{32}$$

With

$$\beta\equiv\frac{\pi^2}{8}\frac{\xi a}{h^2}, \tag{33}$$

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=\frac{2}{\pi}\sum_{n=-\infty}^{\infty}\frac{(-1)^n e^{ik_nz}}{(2n+1)[1+\beta(2n+1)^2]}. \tag{34}$$

The evaluation of this sum can be carried out with the help of the following contour integral, which is evaluated over a large circle in the complex plane:

$$\frac{1}{2\pi i}\oint dz\frac{e^{ik_nz}}{z(1+4\beta z^2)\cos\pi z}=-\sum_{n=-\infty}^{\infty}\frac{(-1)^n(2/\pi)e^{ik_nz}}{(2n+1)[1+\beta(2n+1)^2]}+1-\frac{\cosh(\pi z/2\sqrt{\beta}h)}{\cosh(\pi/2\sqrt{\beta})}=0. \tag{35}$$

It follows with Eq. (34) that

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=1-\frac{\cosh(\pi z/2\sqrt{\beta}h)}{\cosh(\pi/2\sqrt{\beta})}. \tag{36}$$

At the center of the cell $z=0$ and with β given by Eq. (33) and $\xi=\delta\sigma_1/\sigma_m=7.5\times10^{-9}\times0.5/10^{-6}=3.75\times10^{-3}$ m, it follows that

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=1-\operatorname{sech}\frac{\pi}{2\sqrt{\beta}}=1-\operatorname{sech}\left(h\sqrt{\frac{2}{\xi a}}\right)=1-\operatorname{sech}\left(h\sqrt{\frac{2\sigma_m}{a\delta\sigma_1}}\right). \tag{37}$$

This is the final formula for the ratio of the electric field $E_{2z}(\rho,z)$ in the interior $\rho<a$ and near the center $z=0$ of a long cell and the incident field $E_{1z}(\rho,z)$ in the ambient medium with the conductivity σ_1. The membrane has the thickness δ and the conductivity σ_m.

Consider a cell with the half-length $h=0.25$ m and radius $a=10^{-6}$ m, enclosed in a membrane with $\delta=7.5\times10^{-9}$ m and $\sigma_m=10^{-6}$ S/m. The conductivity outside and inside the cell is $\sigma_1=0.5$ S/m. With these values,

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=1-\operatorname{sech}\left(0.25\sqrt{\frac{2\times10^{-6}}{10^{-6}\times7.5\times10^{-9}\times0.5}}\right)=1-\operatorname{sech}(0.25\times2.3\times10^4)=1-\operatorname{sech}(5.8\times10^3)\sim1. \tag{38}$$

For a short cylindrical cell with $h=a=10^{-6}$ m,

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=1-\operatorname{sech}(10^{-6}\times2.3\times10^4)=1-0.9997\sim0. \tag{39}$$

When the cell has a half-length $h=250a=2.5\times10^{-4}$ m,

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=1-\operatorname{sech}(2.5\times10^{-4}\times2.3\times10^4)=1-\operatorname{sech}5.75=0.99. \tag{40}$$

Thus the electric field inside the cell is the same as that outside for cells with lengths $2h>0.5$ mm. For cells with lengths comparable to or less than the diameter, the electric field inside is essentially zero and the membrane acts as a perfect shield.

The numerical calculations up to this point have been restricted to unmyelinated cells with thin membranes and small diameters. However, the formulas apply equally to all types of long nerves cells, including the myelinated ones that have much thicker membranes and larger diameters. Specifically, for a myelinated cell with $\delta\sim200\times10^{-9}$ m and $a=10^{-5}$ m, Eq. (37) gives

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=1-\operatorname{sech}\left(h\sqrt{\frac{2\times10^{-6}}{10^{-5}\times2\times10^{-7}\times0.5}}\right)=1-\operatorname{sech}(1.4\times10^3)h. \tag{41}$$

With $h=0.025$ m$=2.5$ cm,

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=1-\operatorname{sech}35.4=1-8.8\times10^{-16}=1. \tag{42}$$

With $h=250a=2.5\times10^{-3}$ m$=2.5$ mm,

$$\frac{E_{2z}(\rho,z)}{E_{1z}(\rho,z)}=1-\operatorname{sech}3.54=1-0.058\sim0.94. \tag{43}$$

Thus the electric field inside the myelinated cell is the same as outside when $2h>5$ mm. This is ten times the length for the unmyelinated cell, but is no significant restriction for the long cells of interest here.

The simple formula (37) is independent of the distance z from the center of the cell. However, it is not applicable to points near the ends, owing to the approximations made in the boundary condition on the end surfaces. It can be assumed that a reasonable estimate of distances from the end where it should not be used in a long cell is when $h-z \leqslant 10^{-4}$ m$=0.1$ mm for an unmyelinated cell and when $h-z \leqslant 1$ mm for a myelinated cell.

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APPENDIX A: ANALYTICAL FORMULATION AND SOLUTION FOR THE ELECTRIC FIELD IN A SPHERICAL CELL

Consider a spherical cell with inner radius a and outer radius $b=a+\delta$, where δ is the thickness of the cell wall or membrane. The conductivity of the saline fluid outside the cell (region 1) is $\sigma_1=0.5$ S/m. The conductivity of the protoplasm in the interior of the cell (region 2) is $\sigma_2=\sigma_1=0.5$ S/m. The conductivity of the membrane is $\sigma_m=10^{-6}$ S/m. Let

$$\eta \equiv \sigma_m/\sigma_1 = 2\times 10^{-6}. \tag{A1}$$

Since the frequency is low, the electric field can be determined from the scalar potential $\phi \equiv \phi(r,\theta)$:

$$\mathbf{E} = -\nabla\phi, \quad \nabla^2\phi = 0. \tag{A2}$$

The boundary conditions between region 2 ($r<a$) and region m ($a<r<b$) and between region m and region 1 ($r>b$) are

$$E_{2r} = \eta E_{mr}, \quad \phi_2 = \phi_m \quad (r=a), \tag{A3a}$$

$$\eta E_{mr} = E_{1r}, \quad \phi_m = \phi_1 \quad (r=b). \tag{A3b}$$

Far from the cell,

$$\mathbf{E} \to \hat{\mathbf{z}} E_{1z}^{\text{inc}}, \quad \phi \to -zE_{1z}^{\text{inc}} = -r\cos\theta\, E_{1z}^{\text{inc}} \quad (r\to\infty). \tag{A4}$$

Since the spherical cell is rotationally symmetric and the incident electric field is reasonably constant at the location of the cell, the spherical coordinates r,θ can be used and

$$\phi = \phi(r,\theta) = f(r)\cos\theta. \tag{A5}$$

The differential equation for $\phi(r,\theta)$ is

$$\nabla^2\phi(r,\theta) = \frac{1}{r^2\sin\theta}\frac{\partial}{\partial\theta}\left(\sin\theta\frac{\partial\phi}{\partial\theta}\right) + \frac{1}{r^2}\frac{\partial}{\partial r}\left(r^2\frac{\partial\phi}{\partial r}\right) = 0. \tag{A6}$$

With Eq. (A5), this is readily transformed into

$$\cos\theta\left(\frac{\partial^2 f}{\partial r^2} + \frac{2}{r}\frac{\partial f}{\partial r} - \frac{2}{r^2}f\right) = 0. \tag{A7}$$

This has the solution

$$f = f(r) = C_1 r + C_2/r^2, \tag{A8}$$

where C_1 and C_2 are constants to be determined from the boundary conditions $f_2(r)=f_m(r)$ at $r=a$, $f_m(r)=f_1(r)$ at $r=b$, and $f(r)\to -rE_{1z}^{\text{inc}}$ at $r\to\infty$.

In the three regions, $f(r)$ must have the forms

$$\begin{aligned} f_2(r) &= A_2 r, \quad r<a \\ f_m(r) &= A_m' r + A_m''/r^2, \quad a<r<b \\ f_1(r) &= -rE_{1z}^{\text{inc}} + A_1/r^2, \quad r>b. \end{aligned} \tag{A9}$$

The conditions for determining the four constants A_2, A_m', A_m'', A_1 are obtained from Eqs. (A3a) and (A3b) with $E(r,\theta) = -[\partial f(r)/\partial r]\cos\theta$. They are

$$f_2(a) = f_m(a), \quad \frac{\partial f_2(r)}{\partial r} = \eta\frac{\partial f_m(r)}{\partial r} \quad (r=a), \tag{A10a}$$

$$f_m(b) = f_1(b), \quad \eta\frac{\partial f_m(r)}{\partial r} = \frac{\partial f_1(r)}{\partial r} \quad (r=b). \tag{A10b}$$

With $f(r)$ as given in Eq. (A9), the four relations are, for $r=a$,

$$\begin{aligned} A_2 a &= A_m' a + A_m''/a^2, \\ A_2 &= \eta(A_m' - 2A_m''/a^3), \end{aligned} \tag{A11a}$$

and for $r=b$,

$$\begin{aligned} A_m' b + A_m''/b^2 &= -bE_{1z}^{\text{inc}} + A_1/b^2, \\ \eta(A_m' - 2A_m''/b^3) &= -E_{1z}^{\text{inc}} - 2A_1/b^3. \end{aligned} \tag{A11b}$$

The solution of these equations for A_2, which determines the field inside the cell ($r<a$), is

$$A_2 = D^{-1}\begin{vmatrix} 0 & -1 & -1/a^3 & 0 \\ 0 & -\eta & 2\eta/a^3 & 0 \\ -E_{1z}^{\text{inc}} & 1 & 1/b^3 & -1/b^3 \\ -E_{1z}^{\text{inc}} & \eta & -2\eta/b^3 & 2/b^3 \end{vmatrix}, \tag{A12}$$

where

$$D = \begin{vmatrix} 1 & -1 & -1/a^3 & 0 \\ 1 & -\eta & 2\eta/a^3 & 0 \\ 0 & 1 & 1/b^3 & -1/b^3 \\ 0 & \eta & -2\eta/b^3 & 2/b^3 \end{vmatrix}. \tag{A13}$$

The evaluation of the matrices gives

$$D = \frac{1}{b^3}\left[\frac{2}{b^3}(\eta-1)^2 - \frac{1}{a^3}(2\eta^2 + 5\eta + 2)\right] \tag{A14}$$

and

$$A_2=\frac{E_{1z}^{\text{inc}}}{D}\frac{9\eta}{a^3b^3}. \qquad \text{(A15)}$$

It follows that

$$A_2=E_{1z}^{\text{inc}}\left[\frac{9\eta}{2(a^3/b^3)(\eta-1)^2-(2\eta^2+5\eta+2)}\right]. \qquad \text{(A16)}$$

When Eq. (A16) is substituted in Eq. (A9) with Eq. (A5), the potential ϕ_2 in the spherical cell is obtained explicitly. It is

$$\phi_2=A_2 r\cos\theta=A_2 z, \qquad \text{(A17)}$$

with A_2 given by Eq. (A16). The electric field $E_2(z)$ in the spherical cell is obtained with Eq. (A2).

APPENDIX B: BOUNDARY CONDITIONS

Since the membrane of a cell is extremely thin with $\delta \sim 7.5\times10^{-9}$ m and a very poor conductor with $\sigma_m \sim 10^{-6}$ S/m, the boundary conditions relating the electric field on the outer surfaces to that on the inner surface have an interesting form. This is best shown for a one-dimensional model in which the membrane with its conductivity σ_m is a thin sheet defined by the coordinates: $0\leqslant x\leqslant\delta$. The regions $x\leqslant 0$ and $x\geqslant\delta$ are characterized by the conductivity $\sigma_1 = 0.5$ S/m. At the low frequencies and electrically small dimensions involved, the electric field can be derived from the scalar potential ϕ in the form $\mathbf{E}=-\nabla\phi$, where ϕ satisfies Laplace's equation $\nabla^2\phi=0$. In the one-dimensional case,

$$E_x=-\frac{\partial\phi}{\partial x},\quad \frac{\partial^2\phi}{\partial x^2}=0. \qquad \text{(B1)}$$

The solution of the second equation is

$$\phi(x)=\begin{cases}A_1x+B_1, & x<0\\ A_2x+B_2, & 0<x<\delta\\ A_3x+B_3, & x>\delta.\end{cases} \qquad \text{(B2)}$$

The boundary conditions are as follows: $\phi(x)$ is everywhere continuous (this corresponds to continuity for the tangential component of the electric field) and

$$\sigma_1\left(\frac{\partial\phi}{\partial x}\right)_{x=0^-}=\sigma_m\left(\frac{\partial\phi}{\partial x}\right)_{x=0^+},$$
$$\sigma_m\left(\frac{\partial\phi}{\partial x}\right)_{x=\delta^-}=\sigma_1\left(\frac{\partial\phi}{\partial x}\right)_{x=\delta^+}. \qquad \text{(B3)}$$

These are the boundary conditions for the normal component of the electric field. When these conditions are applied to Eq. (B2), with $\eta=\sigma_m/\sigma_1$, the results are

$$B_1=B_2,\quad A_1=\eta A_2, \qquad \text{(B4)}$$

$$A_2\delta+B_2=A_3\delta+B_3,\quad \eta A_2=A_3. \qquad \text{(B5)}$$

With $A_2=A_1/\eta$, $A_3=A_1$, and $B_2=B_1$, it follows that

$$\frac{\delta}{\eta}A_1+B_1=A_1\delta+B_3 \ \text{ or } \ B_3-B_1=\delta\left(\frac{1}{\eta}-1\right)A_1. \qquad \text{(B6)}$$

Let

$$\xi\equiv\delta\left(\frac{1}{\eta}-1\right)\sim\frac{\delta}{\eta}\quad \text{since}\quad \frac{1}{\eta}=0.5\times10^6\gg1. \qquad \text{(B7)}$$

With $\delta=7.5\times10^{-9}$ m and $\eta=2\times10^{-6}$,

$$\xi=3.75\times10^{-3}\ \text{m}. \qquad \text{(B8)}$$

With Eq. (B6), Eq. (B2) gives

$$\phi(\delta^+)-\phi(0^-)\equiv A_1\delta+B_3-B_1=A_1\left(\delta+\frac{\delta}{\eta}-\delta\right)=\frac{A_1\delta}{\eta}. \qquad \text{(B9)}$$

From Eq. (B2), $A_1=(\partial\phi/\partial x)_{x=0^-}$ and $A_3=(\partial\phi/\partial x)_{x=\delta^+}$. It follows that Eq. (B9) becomes

$$\phi(\delta^+)-\phi(0^-)=\frac{\delta}{\eta}\left(\frac{\partial\phi}{\partial x}\right)_{x=0^-}=\xi\left(\frac{\partial\phi}{\partial x}\right)_{x=0^-}. \qquad \text{(B10)}$$

Since $A_3=A_1$,

$$\left(\frac{\partial\phi}{\partial x}\right)_{x=\delta^+}=\left(\frac{\partial\phi}{\partial x}\right)_{x=0^-}. \qquad \text{(B11)}$$

In terms of the outward normal to a cylindrical region, the boundary conditions that connect the conducting region on one side of the membrane with that on the other side are

$$\phi_+-\phi_-=\xi\frac{\partial\phi}{\partial\rho},\quad \left(\frac{\partial\phi}{\partial\rho}\right)_+=\left(\frac{\partial\phi}{\partial\rho}\right)_-. \qquad \text{(B12)}$$

Here $\xi=3.75\times10^{-3}$ m. Note that Eq. (B12) relates the scalar potential and its normal derivative outside the cell directly to these quantities inside the cell. The membrane is involved only in the factor ξ.

In applying these conditions to a long cylindrical cell with a radius $b=10^{-6}$ m, it is interesting to note that the derivative $\partial\phi/\partial\rho$ is taken at $\rho=b$ and $\rho=a=b-\delta$. This means that $\partial\rho$ is a small change in ρ at $\rho=b=10^{-6}$ m. In other words, $\partial\rho$ has a magnitude smaller than b. In the first condition in Eq. (B12), the right-hand side has the factor $\xi = 1/267$ multiplied by a factor greater than $(1/\partial\rho)_{\rho\sim b}\sim10^5$. Clearly, the potential difference $\phi_+-\phi_-$ is a large quantity.

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