

VOLUME 4 NUMBER 3 & 4 1976

Emphasizing Physical Principles in Biological Research

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Biophysics of Animal Response to an Electrostatic Field

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ABSTRACT. Numerous reports have described biological effects in animals exposed to electrostatic fields. Present equilibrium theory does not envision such effects because the bulk conductivity of biological tissue is generally held to prevent penetration of the applied electric field. Employing a two-layer mathematical model of an animal exposed to an electrostatic field we show that if the transient response of the animal is considered, then electric fields of significant strength and periodicity can occur inside the animal. We show also that the total energy available to an animal in an electrostatic field is extraordinarily small, and therefore that the biological effects associated with such exposure are not energetically driven by the applied field.

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Introduction

Interest in the biological effects associated with exposure to electrostatic fields is increasing.¹⁻⁸ Such effects are of interest for both theoretical and practical reasons. In the former instance, mathematical calculations on biological systems exposed to electrostatic fields generally lead to the conclusion that no effects are likely.⁹⁻¹¹ Consequently, there is no theoretical framework within which the biological reports may be analyzed. In the latter instance, health and safety issues arise with regard to exposure of the public to electrostatic fields.

In this paper we will analyze the response of a mathematical animal model to an imposed electrostatic field. The model permits the calculation of the energy and internal fields which arise as a consequence of exposure to an electrostatic field of arbitrary orientation for a wide variety of assumed tissue electrical parameters. Based on this analysis, we will propose a possible explanation for the existence of electrostatically induced biological effects.

Animals are composed of tissues with differing dielectric constants and conductivities. When an animal is placed in an electrostatic field, interfaces between regions characterized by differing electrical parameters become charged if they are normal to the field lines. The energy stored in the fields, the energy dissipated in the charging of interfaces, and the internal electric fields may be calculated as functions of time. If the orientation of the interfaces relative to the field lines changes periodically while the applied field remains constant, the interfaces will periodically charge and discharge.

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Energy is thereby dissipated, and corresponding internal voltage pulses are produced. Such periodic changes in interfacial orientation will occur far more frequently in horizontal (i.e., horizontal to the earth's surface) than in vertical fields.

The electrical conductivity and dielectric constant of animal tissue depends strongly on its water content. The physical model discussed below considers an animal to be composed of tissue layers with differing electrical properties. Because of the complexity of the mathematical analysis, a simple two component model is employed.

Theory

Figure 1 illustrates the physical model used for an animal placed in a rectangular enclosure with sides S_1 and S_2 . An electrostatic field is applied across S_2 . The animal's interior layer is regarded as a rectangular solid of length L with square cross-section of side W. A rectangular shell of thickness T forms an outer layer surrounding the inner layer. The animal is separated by distances W_1 and W_2 from the electrodes. Although Figure 1



Fig. 1. Two layer physical model for an animal placed in an electrostatic field. F. X. Hart & A. A. Marino Animal Response 125

illustrates the model for an horizontally applied field, the same model may be used for a vertical field if $W_1 = 0$. The inner layer, outer layer and air have dielectric constants and conductivities K_2 , G_2 ; K_1 , G_1 ; and K_0 , G_0 respectively.

Suppose that voltage step V is applied at time t = 0. The electric fields F, and the electric displacements D, are instantaneously established in the region between the plates. At t = 0, D is uniform and would remain so if all media were perfect insulators. In real media however, currents begin to flow upon application of the step. At equilibrium, the current density J is continuous. As a result of these processes, the various interfaces become charged. Energy is dissipated during the charge flow required for the attainment of equilibrium, and energy is also stored in the fields existing in the inner and outer layers.

If the applied voltage is suddenly switched off, or if the animal moves so that the charged interfaces are no longer normal to the field lines, the interfaces discharge. The energy stored in the fields decreases toward zero, and energy is dissipated during the accompanying flow of charge. Any activity of the animal which results in alternating motion of the interfaces relative to the field lines produces interfacial charging and discharging with the accompanying dissipation of energy. Such motion of the interfaces relative to the field lines occurs far more often in horizontal than in vertical fields. Hence it is assumed for simplicity that in a vertical field the interfaces remain normal to the field lines and that they retain the charges acquired during the attainment of equilibrium. In this case, significant energy may be dissipated by charge flow only during the initial period of interfacial charging.

A. Interfacial Charging. Consider interfaces normal to the field lines. Figure 2 depicts the current densities, fields, and interfacial charge densities at time t. The contributions of the front and back outer layers and the side walls to both the dissipated and stored energies can be found by using the equations derived below. Fringing of the field lines is neglected, and it is assumed that there is no net space charge present in any region.

The total voltage drop across the plates equals the sum of the voltage drops across the individual regions.

$$V = F_0(W_1 + W_2) + F_1(2T) + F_2(W)$$
(1)

where F_0 , F_1 , and F_2 are the electric fields in the air, outer, and inner layers respectively. This equation may be rewritten as

$$V = D_0(W_1 + W_2)/\gamma_0 + D_1(2T)/K_1\gamma_0 + D_2(W)/K_2\gamma_0$$
(2)

where D_0 , D_1 , and D_2 are the electric displacements in the air, outer, and inner layers respectively; γ_0 is the permittivity of free space, and $K_0 = 1$. 126 J. Biol. Phys. Volume 4. 1976 In each region, the total current density has two components: the conduction current density $J_c = GF$, and the displacement current density $J_d = dD/dt$.

$$J_0 = D_0/\beta_0 + dD_0/dt \qquad (3a)$$

$$J_1 = D_1 / \beta_1 + dD_1 / dt$$
 (3b)

$$J_2 = D_2/\beta_2 + dD_2/dt \qquad (3c)$$

where $\beta_i = K_i \gamma_0 / G_i$ is the electrical relaxation time for region i.

Equations (2)-(3) form a set of four, coupled, first order differential equations which may be solved subject to the following boundary conditions.



$$D_0 - D_1 = \sigma_{01} \tag{4a}$$

Fig. 2. Electrical parameters associated with each region in the physical model. Air is denoted by 0, the outer layer by 1, and the inner layer by 2.

$$D_1 - D_2 = \sigma_{12}$$
 (4b)

$$J_0 - J_1 = -d\sigma_{01}/dt$$
 (5a)

$$\dot{J}_1 - J_2 = -d\sigma_{12}/dt$$
 (5b)

 σ_{01} and σ_{12} are respectively the charge densities at the air-outer layer and outer-inner layer interfaces near the negative plate. The corresponding interfaces near the positive plate carry charge densities equal in magnitude but opposite in sign.

Manipulation of the above expressions leads to the following second order differential equation which may be solved for σ_{01} :

$$d^{2}\sigma_{01}/dt^{2} + Qd\sigma_{01}/dt + R\sigma_{01} = S'$$
 (6)

where

$$Q = \frac{(W_1 + W_2)(1/\beta_1 + 1/\beta_2) + 2T(1/\beta_0 + 1/\beta_2)/K_1 + W(1/\beta_1 + 1/\beta_0)/K_2}{2(W_1 + W_2 + 2T/K_1 + W/K_2)}$$

$$R = \frac{(W_1 + W_2)\beta_0 + 2T\beta_1/K_1 + W\beta_2/K_2}{4\beta_0\beta_1\beta_2(W_1 + W_2 + 2T\beta_1/K_1 + W/K_2)}$$

$$S = \frac{(\beta_0 - \beta_1)\gamma_0 V}{4\beta_0\beta_1\beta_2(W_1 + W_2 + 2T/K_1 + W/K_2)}$$

The solution is

$$\sigma_{01} = S/R + H_1 e^{-P_1 t} + H_2 e^{-P_2 t}$$
(7)

where

$$P_1, P_2 = (Q + (Q^2 - 4R)^{\frac{1}{4}})/2$$
(8)

 P_1^{-1} and P_2^{-1} represent electrical relaxation times associated with the interfacial charging. Substitution of this result into equations (4) and (5) yields

$$u_{12} = (K_2/W)(-\gamma_0 V - NS/\beta_1 R) + (MP_1 - N/\beta_1)H_1 e^{-P_1 t} + (MP_2 - N/\beta_1)H_2 e^{-P_2 t}$$
(9)

where

$$M = 2\beta_1 \beta_0 (W_1 + W_2 + 2T/K_1 + W/K_2)/(\beta_1 - \beta_0)$$
(10)

$$N = \beta_1 \beta_0 (W_1 + W_2 + \beta_1 (2T/K_1 + W/K_2)/\beta_0)/(\beta_1 - \beta_0)$$
(11)

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The constants H_1 and H_2 , which arose from the solution of equation (6), may be evaluated by requiring that at t = 0, $\sigma_{01} = \sigma_a$, and $\sigma_{12} = \sigma_b$. At the instant when the field is first applied, $\sigma_a = \sigma_b = 0$. As the interfaces are repeatedly charged and discharged by the animal's motion in a horizontal field, the beginning of a new charging cycle at t = 0 may occur when there exists residual charge on the interfaces as a consequence of a preceding incomplete discharge. This situation would occur if the electrical relaxation time for discharge were not small compared to the time interval during which the discharge was taking place. In that case σ_a , $\sigma_b \neq 0$. One then obtains

$$H_{1} = [(\sigma_{b}W/K_{2} + (N/\beta_{1} - MP_{2})\sigma_{a} + \gamma_{0}V + MP_{2}S/R)]/M(P_{1} - P_{2})$$
(12a)
$$H_{2} = [(\sigma_{b}W/K_{2} + (N/\beta_{1} - MP_{1})\sigma_{a} + \gamma_{0}V + MP_{1}S/R)]/M(P_{2} - P_{1})$$
(12b)

Further manipulation of equations (4), (5), (7), and (9) leads to the following expressions for the electric fields:

$$F_0 = A_0 + B_0 e^{-P_1 t} + C_0 e^{-P_2 t}$$
(13a)

$$F_1 = A_1 + B_1 e^{-P_1 t} + C_1 e^{-P_2 t}$$
 (13b)

$$F_2 = A_2 + B_2 e^{-P_1 t} + C_2 e^{-P_2 t}$$
(13c)

where

$$A_{o} = (\beta_{o}S)/\gamma_{o}R(\beta_{o} - \beta_{1})$$
(14a)

$$\mathbf{A}_{1} = (\beta_{1} \mathbf{S}) / \mathbf{K}_{1} \gamma_{0} \mathbf{R} (\beta_{0} - \beta_{1})$$
(14b)

$$A_2 = (\beta_2 S)/K_2 \gamma_0 R(\beta_0 - \beta_1)$$
(14c)

$$B_{0} = \beta_{0}H_{1}(1 - 2P_{1}\beta_{1})/\gamma_{0}(\beta_{0} - \beta_{1})$$
(15a)

$$B_{1} = \beta_{1} H_{1} (1 - 2P_{1} \beta_{0}) / K_{1} \gamma_{0} (\beta_{0} - \beta_{1})$$
(15b)

$$\mathbf{B}_{2} = (\mathbf{H}_{1}/\mathbf{K}_{2}\gamma_{0})[(1 - 2\mathbf{P}_{1}\beta_{0})\beta_{1}/(\beta_{0} - \beta_{1}) + (\mathbf{K}_{2}/\mathbf{W})(\mathbf{N}/\beta_{1} - \mathbf{M}\mathbf{P}_{1})]$$
(15c)

$$C_{0} = \beta_{0}H_{2}(1 - 2P_{2}\beta_{1})/\gamma_{0}(\beta_{0} - \beta_{1})$$
(16a)

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$$C_{1} = \beta_{1} H_{2} (1 - 2P_{2}\beta_{0}) / K_{1} \gamma_{0} (\beta_{0} - \beta_{1})$$
(16b)

$$C_{2} = (H_{2}/K_{2}\gamma_{0})[(1 - 2P_{2}\beta_{0})\beta_{1}/(\beta_{0} - \beta_{1}) + (K_{2}/W)(N/\beta_{1} - MP_{2})]$$
(16c)

The energy dissipated in the animal's inner layer during charging from time t = 0 is given by

$$E_{d2} = LW^2G_2 \int_0^t F_2^2 dt$$

Substitution of equation (13c) and integration yields

$$E_{d2} = LW^{2}G_{2}(A_{2}^{2}t + (B_{2}^{2}/2P_{1})(1 - e^{-2P_{1}t}) + (C_{2}^{2}/2P_{2})(1 - e^{-2P_{2}t}) + (2A_{2}B_{2}/P_{1})(1 - e^{-P_{1}t}) + (2A_{2}C_{2}/P_{2})(1 - e^{-P_{2}t}) + (2B_{2}C_{2}/(P_{1} + P_{2}))(1 - e^{-(P_{1}+P_{2})t}))$$
(17)

The electrostatic energy stored in the inner layer at time t is given by

$$E_{s2} = K_{2}\gamma_{0}F_{2}^{2}LW^{2}/2$$

$$E_{s2} = K_{2}\gamma_{0}LW^{2}[A_{2}^{2} + B_{2}^{2}e^{-2P_{1}t} + C_{2}^{2}e^{-2P_{2}t} + 2A_{2}B_{2}e^{-P_{1}t} + 2A_{2}C_{2}e^{-P_{2}t} + 2B_{2}C_{2}e^{-(P_{1}+P_{2})t}]/2$$
(18)

Similar expressions may be obtained for the energies dissipated and stored in the outer layer, E_{d1} and E_{s1} :

$$E_{d1} = 2TLWG_{1} [A_{1}^{2}t + (B_{1}^{2}/2P_{1})(1 - e^{-2P_{1}t}) + (C_{1}^{2}/2P_{2})(1 - e^{-2P_{2}t}) + (2A_{1}B_{1}/P_{1})(1 - e^{-P_{1}t}) + (2A_{1}C_{1}/P_{2})(1 - e^{-P_{2}t}) + (2B_{1}C_{1}/(P_{1} + P_{2}))(1 - e^{-(P_{1} + P_{2})t})]$$
(19)
$$E_{s1} = K_{1}\gamma_{0}LWT[A_{1}^{2} + B_{1}^{2}e^{-2P_{1}t} + C_{1}^{2}e^{-2P_{2}t} + 2A_{1}B_{1}e^{-P_{1}t} +$$

$$2A_1C_1e^{-P_2t} + 2B_1C_1e^{-(P_1+P_2)t}]$$
(20)

Since for vertical fields the motion of the charged interfaces relative to the field lines is being neglected, σ_a and σ_b must both be zero. Electrical equilibrium is approached for times $t \ge P_1^{-1}$, P_2^{-1} . In that case

$$F_0 + A_0 = \beta_0 S / \gamma_0 (\beta_0 - \beta_1) R$$
 (21)

$$\mathbf{F}_1 \neq \mathbf{A}_1 = \beta_1 \mathbf{S} / \mathbf{K}_1 \gamma_0 (\beta_0 - \beta_1) \mathbf{R}$$
(22)

$$\mathbf{F}_2 + \mathbf{A}_2 = \beta_2 \, \mathrm{S}/\mathrm{K}_2 \gamma_0 (\beta_0 - \beta_1) \,\mathrm{R} \tag{23}$$

The results of the derivation may be checked by noting that the correct limiting case values are obtained.

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Use of equations (15c) and (16c) to evaluate F_2 in equation (13c) is often difficult because of the complicated structure of the expressions for B_2 and C_2 . As indicated in the Appendix, evaluation of these expressions involves the subtraction of nearly equal terms. The consequent loss of precision in their evaluation may lead to spurious results for the field in the inner layer. For example, although manipulation of the exact expressions leads to the correct limiting case at t = 0, substitution of numerical values into equations (15c) and (16c) leads in some cases to negative values for small F_2 at t = 0.

The complexity discussed above originates in the decision to solve equations (2) – (5) for σ_{01} . D_2 is then expressed as the difference between D_1 and σ_{12} which are themselves functions of σ_{01} . A simpler expression for D_2 can be obtained by solving equations (2) – (5) for σ_{12} and then using $D_2 = \beta_1 \beta_2 (2d\sigma_{12}/dt + \sigma_{12}/\beta_1)/(\beta_1 - \beta_2)$ to find D_2 subject to the conditions that as t + 0, $\sigma_{12} + \sigma_b$, and $D_2 + D_{20}$ where $D_{20} = \gamma_0 V/(W_1 + W_2 + 2T/K_1 + W/K_2)$. This approach yields

$$A_2 = \beta_2 S' / K_2 \gamma_0 (\beta_1 - \beta_2) R \qquad (24a)$$

$$B_{2} = \beta_{2}H_{3}(1 - 2P_{1}\beta_{1})/K_{2}\gamma_{0}(\beta_{1} - \beta_{2})$$
(24b)

$$C_{2} = \beta_{2} H_{4} (1 - 2P_{2}\beta_{1}) / K_{2} \gamma_{0} (\beta_{1} - \beta_{2})$$
(24c)

where

$$S' = (\beta_1 - \beta_2)S/(\beta_0 - \beta_1)$$

$$H_3 = [(\beta_1 - \beta_2)D_{20}/\beta_2 - 2P_2\beta_1S'/R - o_b(1 - 2P_2\beta_1)]/2\beta_1(P_2 - P_1)$$

$$H_4 = [(\beta_1 - \beta_2)D_{20}/\beta_2 - 2P_1\beta_1S'/R - o_b(1 - 2P_1\beta_1)]/2\beta_1(P_1 - P_2)$$

Equations (24a) - (24c) yield the correct limiting behavior, with no loss of precision in their numerical evaluation. The inner layer field can be found using these expressions.

B. Interfacial Discharging. In a horizontal field, the animal may turn so that its charged interfaces are suddenly no longer normal to the field lines. Energy is dissipated in the charge flow which accompanies the resulting discharge. The energy stored in the fields decreases towards zero. Suppose that the discharge begins at time t' = 0, with charge densities σ_{c} and σ_{d} residing on the air-outer and outer-inner layer interfaces respectively. Equations (2) - (5) still apply, but with V = 0. Since S = 0, equation (6) becomes

$$d^2 \sigma'_{01} / dt'^2 + Q d\sigma'_{01} / dt' + R \sigma'_{01} = 0$$

whose solution is

$$\sigma'_{01} = H_5 e^{-P_1 t'} + H_6 e^{-P_2 t'}$$
(25)

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where P_1 and P_2 are given by equation (8). Substitution of this result into equations (4) and (5) yields

$$\sigma'_{12} = (K_2/W)[H_5 e^{-P_1 t'}(MP_1 - N/\beta_1) + H_6 e^{-P_2 t'}(MP_2 - N/\beta_1)]$$
(26)

where M and N are given by equations (10) and (11). H_5 and H_6 are evaluated by recalling that $\sigma'_{01} \rightarrow \sigma_c$, and $\sigma'_{12} \rightarrow \sigma_d$, as $t' \rightarrow 0$. One thus obtains

$$H_{5} = [(N/\beta_{1} - MP_{2})\sigma_{c} + W\sigma_{d}/K_{2}]/M(P_{1} - P_{2})$$
$$H_{6} = [(N/\beta_{1} - MP_{1})\sigma_{c} + W\sigma_{d}/K_{2}]/M(P_{2} - P_{1})$$

The electric fields in the air, outer, and inner layers at time t' after the interfaces begin to discharge are given by

$$F'_{0} = B'_{0}e^{-P_{1}t'} + C'_{0}e^{-P_{2}t'}$$
(27a)

$$F'_1 = B'_1 e^{-P_1 t'} + C'_1 e^{-P_2 t'}$$
 (27b)

$$F'_2 = B'_2 e^{-P_1 t'} + C'_2 e^{-P_2 t'}$$
 (27c)

where

$$\begin{split} B'_{0} &= \beta_{0} H_{5} (1 - 2P_{1}\beta_{1}) / \gamma_{0} (\beta_{0} - \beta_{1}) \\ B'_{1} &= \beta_{1} H_{5} (1 - 2P_{1}\beta_{0}) / K_{1} \gamma_{0} (\beta_{0} - \beta_{1}) \\ C'_{0} &= \beta_{0} H_{6} (1 - 2P_{2}\beta_{1}) / \gamma_{0} (\beta_{0} - \beta_{1}) \\ C'_{1} &= \beta_{1} H_{6} (1 - 2P_{2}\beta_{0}) / K_{1} \gamma_{0} (\beta_{0} - \beta_{1}) \end{split}$$

To avoid spurious results for the inner layer fields, an approach similar to that which led to equations (24b) and (24c) must be again used. At time t' after discharge,

$$\sigma'_{12} = H_7 e^{-P_1 t'} + H_8 e^{-P_2 t'}$$
$$D'_2 = \beta_1 \beta_2 (2d\sigma'_{12}/dt' + \sigma'_{12}/\beta_1)/(\beta_1 - \beta_2)$$

The constants H_7 and H_8 are found by requiring that as $t' \cdot 0$, $\sigma'_{12} + \sigma_0$, and $D'_2 + D'_{20}$, where D'_{20} is the electric displacement in the inner layer at the instant when the discharge begins. In this way one finds

$$B_{2} = \beta_{2}H_{7}(1 - 2P_{1}\beta_{1})/K_{2}\gamma_{0}(\beta_{1} - \beta_{2})$$

$$C'_{2} = \beta_{2}H_{8}(1 - 2P_{2}\beta_{1})/K_{2}\gamma_{0}(\beta_{1} - \beta_{2})$$
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If E'_{d1} and E'_{d2} represent the energies dissipated in the outer and inner layers respectively during the discharge from t' = 0 to t', then

$$E'_{d1} = 2LWTG_{1} [(B'_{1}{}^{2}/2P_{1})(1 - e^{-2P_{1}t'}) + (C'_{1}{}^{2}/2P_{2})(1 - e^{-2P_{2}t'}) (28) + (2B'_{1}C'_{1}/(P_{1} + P_{2}))(1 - e^{-(P_{1} + P_{2})t'})] E'_{d2} = LW^{2}G_{2} [(B'_{2}{}^{2}/2P_{1})(1 - e^{-2P_{1}t'}) + (C'_{2}{}^{2}/2P_{2})(1 - e^{-2P_{2}t'}) (29) + (2B'_{2}C'_{2}/(P_{1} + P_{2}))(1 - e^{-(P_{1} + P_{2})t'})]$$

Similarly, if E'_{s1} and E'_{s2} represent the energies stored in the electrostatic fields still present at time t' in the outer and inner layers respectively, then

$$E'_{s1} = K_1 \gamma_0 LWT(B'_1 e^{-2P_1 t'} + C'_1 e^{-2P_2 t'} + 2B'_1 C'_1 e^{-(P_1 + P_2)t'}) (30)$$

$$\mathbf{E}_{s2}' = \mathbf{K}_{2} \gamma_{0} \mathbf{L} \mathbf{W}^{2} (\mathbf{B}_{2}'^{2} e^{-2P_{1}t'} + \mathbf{C}_{2}'^{2} e^{-2P_{2}t'} + 2\mathbf{B}_{2}' \mathbf{C}_{2}' e^{-(P_{1}+P_{2})t'})/2 \quad (31)$$

C. Behavioral Model. To obtain an estimate for the amount of energy available to an animal as it moves in a horizontal field, consider the following behavioral pattern. The animal is initially placed in corner (1) of the enclosure illustrated in Figure 3: $\sigma_a = \sigma_b = 0$. At t = 0, the voltage is applied and the animal begins to walk at a speed v toward corner (2). Interfaces parallel to side A gradually become charged with time constants P_1^{-1} and P_2^{-1} . The energies dissipated and stored during charging are given by equations (17) - (20). Upon reaching corner (2) the animal turns sharply and walks toward corner (3) at the same speed. Interfaces parallel to side A then begin to discharge. The corresponding energies are given by equations (28) - (31). In addition, interfaces parallel to side B become charged with energies given by equations (17) - (20). This process continues as the animal walks around the perimeter of the enclosure. The charge densities residing on interfaces parallel to sides A and B as the animal turns each corner depend on the electrical relaxation times as well as the time intervals during which charging and discharging occur (S_1 /v and S_{2}/v). An HP-2000F computer has been programmed to calculate the cumulative energy dissipated in the animal as it walks around the enclosure n times.

Results

To apply the two layer physical model described above, we must select values for the dielectric constants and conductivities of the inner and outer layers. Unfortunately, such values are difficult to measure and consequently there is a paucity of such data in the literature. Some values have been reported at very low frequencies (12-14), but their reliability is questionable

because of electrode polarization phenomena and variable tissue moisture content. We have therefore assumed a wide range of possible combinations of the electrical properties of each layer. Specifically, we have considered values of K_1 in the range 80 - 8 × 10⁶, K_2 in the range 10 - 7 × 10⁵, G_1 in the range 0.02 - 1.0 mho/m, and G_2 in the range 0.01 - 0.10 mho/m. Twenty-four combinations were analyzed, and in each case the dielectric constant and conductivity of air were assumed to be 1 and 5 × 10⁻¹⁴ mho/m respectively.

The model was applied to the case of a mouse $(6 \times 2 \text{ cm})$ housed in a typical plastic mouse cage $(37 \times 20 \times 17 \text{ cm})$ across which 1000 volts was applied, resulting in an equilibrium electric field in the air of 5.5 kV/m in the vertical case and 6.7 kV/m in the horizontal case.



Fig. 3. Top view of an animal walking around the periphery of the cage while subject to a horizontal electrostatic field. A denotes the animal's side surface, B denotes the front surface.

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Figures 4 and 5 illustrate the electric field and energy dissipated in the outer layer for six choices of outer layer electrical parameters, with the inner layer characterized by $K_2 = 7 \times 10^5$ and $G_2 = 0.01$ mho/m. For times $t < P_1^{-1}, P_2^{-1}$, the electric field is determined by the dielectric constant of the outer layer; for times $t > P_1^{-1}, P_2^{-1}$, the effects of only one time constant, which depends solely on the electrical properties of the outer layer, are apparent. Figure 5 indicates that the cumulative energy dissipated is determined by the



Fig. 4. Outer layer electric fields for an inner layer characterized by $K_2 = 7 \times 10^5$, $G_2 = 0.01$ mho/m. The outer layer parameters corresponding to each curve are: a, $K_1 = 80$ and $G_1 = 1$ mho/m; b, 80 and 0.33; c, 8 $\times 10^5$ and 0.2; d, 8 $\times 10^6$ and 0.2; e, 8 $\times 10^5$ and 0.02; f, 8 $\times 10^5$ and 0.02.



Fig. 5. Energy dissipated in the outer layer for an inner layer characterized by $K_2' = 7 \times 10^5$, $G_2 = 0.01$ mho/m. The curves are lettered as in Figure 4. F. X. Hart & A. A. Marino Animal Response 135

dielectric constant of the outer layer, and that it decreases as K_1 increases. The time during which energy flow is appreciable is of course determined by the relaxation time governing the behavior of the outer layer field.

Figures 6 and 7 depict the electric field and energy dissipated in the inner layer for the same six choices of outer layer electrical parameters, with the inner layer characterized by $K_2 = 7 \times 10^5$, and $G_2 = 0.01$ and 0.1 mho/m. Note that the inner layer field is the same for all choices of outer layer electrical parameters. Thus, the energy dissipated must also be the same for



Fig. 6. Inner layer electric fields. For curve a, $K_2 = 7 \times 10^5$, $G_2 = 0.1$ mho/m. For curve b, $K_2 = 7 \times 10^5$, $G_2 = 0.01$ mho/m. Since the outer and inner layer fields are decoupled, the inner layer fields are identical for all six sets of outer layer parameters shown in Figure 4, and are represented by the same curve.



Fig. 7. Energy dissipated in the inner layer. The curves are lettered as in Figure 6. 136 J. Biol. Phys. Volume 4, 1976

each case. The outer and inner layers are therefore decoupled. The temporal variation of the fields in each layer is governed by the electrical parameters of that layer.

Note that the dissipated energies are quite small — at most 1.84×10^{-11} joules — and for large t depend only on the dielectric constant of the layer in question. Although the stored energies are not presented graphically, the maximum stored energy for these cases is also on the order of 10^{-11} joules. Nevertheless, use of the literature values for tissue electrical parameters leads to fields on the order of tens to hundreds of microvolts/cm existing in the tissue for times on the order of microseconds to milliseconds.

Similar results are obtained for the other choices of inner layer parameters: $K_1 = 10$; $G_2 = 0.1$ and 0.01 mho/m. It should be noted that smaller "knees" appear in the inner layer fields for these two sets of inner layer parameters. These small pertubations are due to a weak coupling of the inner and outer layers which occurs with large differences in the dielectric constant of these layers. Since the field pertubations are weak, they make no significant contribution to the dissipated energy.

A commonly employed model of biological systems exposed to electric fields is that of a bulk region of high conductivity surrounded by a shell of insulating material. When applied to an individual cell, the two regions correspond to the cell cytoplasm and cell membrane respectively. When applied to an animal, the internal milieu is characterized as a region of high conductivity as a consequence of vascularization and the presence of interstitial fluids, and the skin is viewed as an insulating layer. We have considered this model for the assumptions listed in Figures 8 and 9. The figures illustrate the electric field and energy dissipated in the animal's interior for a very thin (10^{-2} cm) outer layer characterized by K₁ = 10, and $G_1 = 0.1$ mho/m. The inner and outer layers are again essentially decoupled. The response of the interior is determined by its own electrical properties. For small t the field is determined by its dielectric constant, for large t by its conductivity. The cumulative energy dissipated depends only on the dielectric constant. This energy is again small (about 10⁻¹¹ joules), while fields on the order of ten microvolts/cm can exist for times on the order of microseconds to milliseconds. Essentially the same results are obtained with a larger dielectric constant (7×10^5) for the outer layer. Variations in the thickness of the skin layer do not lead to significantly different values.

Several representative sets of values for the electrical parameters characterizing the inner and outer layers were chosen for the calculation of the cumulative energy dissipated as the animal walks twice around the periphery of the enclosure $(37 \times 17. \text{ cm})$, at a speed of 10 cm/sec. The potential of 1000 volts is applied across the shorter side. The results of the calculation



Fig. 8. Interior electric fields for a very thin (10^{-2} cm) outer layer characterized by $K_1 = 10, G_1 = 0.1 \text{ mho/m}$. The interior parameters corresponding to these curves are: a, $K_2 = 80$ and $G_1 = 1 \text{ mho/m}$; b, 80 and 0.33; c, 8 x 10^6 and 0.2; d, 8 x 10^6 and 0.02.



Fig. 9. Energy dissipated in the interior for a very thin (10^{-2} cm) outer layer characterized by $K_1 = 10$, $G_1 = 0.1$ mho/m. The curves are lettered as in Figure 8. 138 J. Biol. Phys. Volume 4, 1976

are presented in Table 1. The first six sets of values are selected from the model in which the outer and inner layers have equal thicknesses, and the last three are chosen from the thin outer layer model. The cumulative energy dissipated listed in the last column is the sum of the energies dissipated in the inner and outer layers as the animal traverses eight sides. As previously noted, the dissipated energy is independent of the conductivity and varies inversely with the dielectric constant of the medium. In the first six sets, the cumulative energy dissipated is thus determined primarily by the layer with the lower dielectric constant. This energy is essentially the same for the first five sets where it is determined primarily by K_2 . Only in the fifth set, where K_1 is also relatively small, is there a contribution from the outer layer. This energy is smallest in the sixth set, where both dielectric constants are large. In the last three sets, the dissipated energy is determined mainly by the interior since the volume of the outer layer is very small.

Of particular interest are the small values obtained for the dissipated energy. If a daily schedule of activity in which the animal makes 200 circuits is assumed and the values of the fifth set are used, the energy is small in comparison with its daily food intake (on the order of 100,000 joules).

The electric field and energy dissipated in the front and back end faces are determined by the electrical parameters characterizing the medium. Essentially the same results are obtained as for the outer-inner layer

Set	K 1	G1 (mho/m)	K2	G2 (mho/m)	W (cm)	T (cm)	Cumulative Energy Dissipated (joules)
1	8×10 ⁶	0.2	10	0.01	0.67	0.67	9.04×10 ⁻⁹
2	8×10 ⁶	0.02	10	0.01	0.67	0.67	9.04×10 ⁻⁹
3	8×10 ⁵	0.2	10	0.01	0.67	0.67	9.04×10 -9
4	8×10 ⁶	0.2	10	0.1	0.67	0.67	9.04×10 ⁻⁹
5	80	1	10	0.01	0.67	0.67	9.37×10 ⁻⁹
6	8×10 ⁶	0.2	7×10 ⁵	0.01	0.67	0.67	1.40×10 ⁻¹³
7	10	0.1	8×10 ⁶	0.2	2	10-2	1.08×10^{-10}
8	10	0.1	80	0.33	2	10 ⁻²	3.20×10 -9
9	7×10 ⁵	0.01	80	0.33	2	10-2	3.09×10 ⁹

TABLE 1 Cumulative Energy Dissipated in a Horizontal Field

calculations. Since there is only one interface (air-end face), only one time constant appears. The dissipated energies are comparable to those discussed above and are thus small relative to the energy value of the daily food intake.

Discussion

The results of the calculations as illustrated in Figures 4 -9 appear much simpler than might be expected from the complexity of equations (13), (17) and (19). In the Appendix it is shown that for $\beta_0 \ge \beta_1, \beta_2$ the fields in each region are characterized by only one time constant which depends on the electrical properties of the region. It is further shown that the cumulative energy dissipated depends only on the dielectric constant of the region.

Within the framework of the model which is analyzed here, the total energy available to an animal exposed to an electrostatic field is extraordinarily small. Even if more complex multi-interfacial models are considered however, the total energy available remains quite negligible in comparison with metabolic energy consumption. Thus it is concluded that the biological effects associated with exposure to electrostatic fields are informational in origin. That is, the electrostatic field controls or triggers the observed effect, but does not drive it energetically.

The calculations reveal the existence of significant electric fields in the animal for times on the order of microseconds to milliseconds (Figures 4, 6 and 8). An animal exposed to a horizontal field will be subjected far more frequently to the field transients as compared to an animal exposed to a vertical field. Such a differential may be responsible for the directionally dependent biological effects observed recently (1).

Any reasonable generalization or variation of the model employed, such as a multi-interfacial model or a model in which the electrical constants of each layer are allowed to vary from point to point, will also predict the existence of significant electric fields for times on the order of microseconds to milliseconds. Thus the apparent inconsistency between the reports of electrostatically induced biological effects on the one hand, and the theoretical arguments against the existence of such effects on the other hand, may find its resolution in a consideration of the transient response of the system. That is, normal animal experimentation ordinarily does not require that the animal under study remain motionless. Our calculations show that any periodic motion of the animal relative to the applied field will produce transient periodic electric fields within the animal of significant strength. Such fields may be responsible for the observed biological effects (1-8).

Appendix

For all the models discussed in this paper $\beta_0 = 177$ seconds and $\beta_1, \beta_2 < 3.54 \times 10^{-3}$ seconds. The air gap between the electrodes is much greater than the thickness of either the inner or outer layer for all models. In the limit $\beta_0 \ge \beta_1, \beta_2$, and $(W_1 + W_2) \ge 2T/K_1, W/K_2$

$$Q + (\beta_{2} + \beta_{1})/2\beta_{1}\beta_{2}$$

$$R + 1/4\beta_{1}\beta_{2}$$

$$S + \gamma_{0}V/4\beta_{1}\beta_{2}(W_{1} + W_{2})$$

$$S/R + \gamma_{0}V/(W_{1} + W_{2})$$

$$M + -2\beta_{1}(W_{1} + W_{2})$$

$$N + -\beta_{1}(W_{1} + W_{2})$$

$$P_{1}, P_{2} + \frac{(\beta_{2} + \beta_{1}) \mp (\beta_{2}^{2} - 2\beta_{1}\beta_{2} + \beta_{1}^{2})^{4}}{4\beta_{1}\beta_{2}}$$

Thus for $\beta_2 > \beta_1$, $P_1 + \frac{1}{2}\beta_2$ and $P_2 + \frac{1}{2}\beta_1$, whereas for $\beta_1 > \beta_2$, $P_1 + \frac{1}{2}\beta_1$ and $P_2 + \frac{1}{2}\beta_2$. In determining the electric field and energy dissipated in each region as functions of time, it is assumed that $\sigma_a = \sigma_b = 0$. Thus for $\beta_2 > \beta_1$, $H_1 + 0$ and $H_2 + -\gamma_0 V/(W_1 + W_2)$, whereas for $\beta_1 > \beta_2$, $H_1 + -\gamma_0 V/(W_1 + W_2)$ and $H_2 + 0$. One thus obtains

$$A_0 \neq S/\gamma_0 R \neq V/(W_1 + W_2)$$

$$A_1 \neq \beta_1 S/\beta_0 K_1 \gamma_0 R \neq VG_0/G_1(W_1 + W_2)$$

$$A_2 \neq \beta_2 S/\beta_0 K_2 \gamma_0 R \neq VG_0/G_2(W_1 + W_2)$$

Since $H_1 + 0$ for $\beta_2 > \beta_1$, B_1 , $B_0 + 0$. For $\beta_1 > \beta_2$, $B_0 + 0$ and $B_1 + V/K_1(W_1 + W_2)$. Since $H_2 + 0$ for $\beta_1 > \beta_2$, C_0 , $C_1 + 0$. For $\beta_2 > \beta_1$, $C_0 + 0$ and $C_1 + V/K_1(W_1 + W_2)$.

Evaluation of the expressions for B_2 and C_2 is more complicated. For $\beta_2 > \beta_1$, one finds that

$$B_{2} + (H_{1}/K_{2}\gamma_{0})(-\beta_{1}/\beta_{2} + (K_{2}/W)(W_{1} + W_{2})(\beta_{1}/\beta_{2} - 1))$$

$$C_{2} + -H_{2}/K_{2}\gamma_{0} + V/K_{2}(W_{1} + W_{2})$$

One would expect that $B_2 + 0$, since $H_1 + 0$. However $H_1 + 0$ as the difference of two nearly equal terms. Loss of precision in the subtraction by the computer can yield a very small, but nonzero result for H_1 , which

in turn leads to a non-negligible value for B_2 when multiplied by the second term in the above expression. A similar problem arises in the evaluation of C_2 when $\beta_1 > \beta_2$. To overcome these difficulties in the numerical evaluation of the coefficients B_2 and C_2 , it was necessary to re-express them in equations (24b) and (24c). Using those equations, one finds that in the same limits

$$H_3 + \gamma_0 V(\beta_1 - \beta_2)/2\beta_1 \beta_2 (W_1 + W_2)(P_2 - P_1)$$

and

$$H_4 + \gamma_0 V(\beta_1 - \beta_2)/2\beta_1 \beta_2 (W_1 + W_2)(P_1 - P_2)$$

For $\beta_2 > \beta_1$, $H_3 + -\gamma_0 V/(W_1 + W_2)$. Thus $B_2 + V/K_2 (W_1 + W_2)$ and $C_2 + 0$. For $\beta_1 > \beta_2$, $H_4 + -\gamma_0 V/(W_1 + W_2)$. Thus $B_2 + 0$ and $C_2 + V/K_2 (W_1 + W_2)$. The expressions for the fields in each region then reduce to

$$F_0 \rightarrow A_0 \rightarrow V/(W_1 + W_2)$$

For $\beta_2 > \beta_1$

$$F_{1} + A_{1} + C_{1}e^{-P_{2}t} + (V/(W_{1} + W_{2}))(G_{0}/G_{1} + (1/K_{1})e^{-t/2\beta_{1}})$$

$$F_{2} + A_{2} + B_{2}e^{-P_{1}t} + (V/(W_{1} + W_{2}))(G_{0}/G_{2} + (1/K_{2})e^{-t/2\beta_{2}})$$
For $\beta_{1} > \beta_{2}$

$$F_{1} \neq A_{1} + B_{1}e^{-P_{1}t} \neq (V/(W_{1} + W_{2}))(G_{0}/G_{1} + (1/K_{1})e^{-t/2\beta_{1}})$$

$$F_{2} \neq A_{2} + B_{2}e^{-P_{2}t} \neq (V/(W_{1} + W_{2}))(G_{0}/G_{2} + (1/K_{2})e^{-t/2\beta_{2}})$$

Note that the same expressions are obtained for F_1 and F_2 whether $\beta_2 > \beta_1$, or $\beta_1 > \beta_2$. The electrical response of each region is characterized by a time constant which depends only on the electrical parameters of that region. The inner and outer layers are essentially decoupled. The second time constant which appears in Figure 8 is due to terms on the order of β_1/β_0 or β_2/β_0 .

Since the A coefficients are small in comparison to the B and C coefficients, the energy dissipation given by equations (17) and (19) will be determined by the B or C terms. Thus for $\beta_2 > \beta_1$, as $t + \infty$

$$E_{d2} + LW^{2}G_{2}B_{2}^{2}/2P_{1} + (LW^{2}\gamma_{0}/K_{2})(V/(W_{1} + W_{2}))^{2}$$

$$E_{d1} + 2LWTG_{1}C_{1}^{2}/2P_{2} + (2LWT\gamma_{0}/K_{1})(V/(W_{1} + W_{2}))^{2}$$

For $\beta_1 > \beta_2$, as $t \cdot \infty$

$$E_{d2} + LW^{2}G_{2}C_{2}^{2}/2P_{2} + (LW^{2}\gamma_{0}/K_{2})(V/(W_{1} + W_{2}))^{2}$$

$$E_{d1} + 2LWTG_{1}B_{1}^{2}/2P_{1} + (2LWT\gamma_{0}/K_{1})(V/(W_{1} + W_{2}))^{2}$$
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The cumulative energy dissipated thus depends only on the dielectric constant of the region and varies inversely with it.

A similar analysis applied to the discharge process indicates that for $\beta_2 > \beta_1$, both H_5 , $H_7 \neq 0$, $H_6 \neq \sigma_c$, $H_8 \neq \sigma_d$. While for $\beta_1 > \beta_2$, H_6 , $H_8 \neq 0$, $H_5 \neq \sigma_c$, $H_7 \neq \sigma_d$. Since $\sigma_c \gg \sigma_d$, the energy dissipated in the outer layer during discharge is much greater than that dissipated in the inner layer if the dielectric constants of the two media are comparable.

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