AN EXTENSION OF THE SOLID ANGLE POTENTIAL FORMULATION FOR AN ACTIVE CELL

ROBERT PLONSEY

From the Bioengineering Group, Case Institute of Technology, Cleveland

ABSTRACT A formula is derived which extends the solid angle potential formulation for an active cell in a volume conductor to the case of unequal internal and external conductivities.

INTRODUCTION

The potential set up by an active cell in a volume conductor of infinite extent can be formulated in terms of the solid angle subtended at the field point by each active area element of the membrane. A derivation and discussion can be found, for example, in Ruch and Fulton [1]. Existing results depend on an assumption of equal conductivity of the intra- and extracellular medium. We present here an analysis for the more likely condition that the aforementioned conductivities differ.

APPLICATION OF GREEN'S THEOREM

Fig. 1 illustrates a single cell lying in a volume conductor. The external surface is S_o and the internal membrane surface is S_i. We let $P(x', y', z')$ be an arbitrary field point in the external medium and $r = \sqrt{(x - x')^2 + (y - y')^2 + (z - z')^2}$ be the distance from it to an arbitrary internal point (x, y, z). We now apply Green's theorem to the volume V_i bounded by S_i, namely

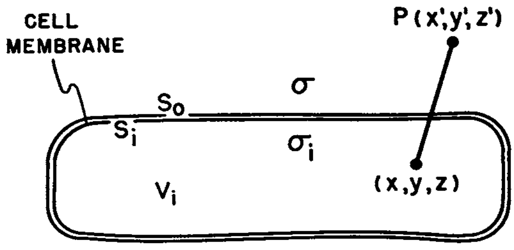

FIGURE 1 Single cell in a volume conductor of infinite extent.

$$\int_{V_i} [\Phi \nabla^2 \psi - \psi \nabla^2 \Phi] \, dV = \int_{S_i} [\Phi \, \partial\psi/\partial n - \psi \, \partial\Phi/\partial n] \, dS \tag{1}$$

and choose the scalar function $\psi = 1/r$ and Φ_i equal to the potential field in V_i. The field Φ_i arises from sources within the membrane under either resting or active conditions. Since r cannot go to zero by virtue of P being outside the region of integration, we have $\nabla^2(1/r) = 0$. Also since no sources exist within V_i (the axoplasm is assumed to be a passive conductor) $\nabla^2\Phi_i = 0$. Consequently

$$\int_{S_i} \Phi_i \frac{\partial(1/r)}{\partial n} \, dS = \int_{S_i} \frac{1}{r} \frac{\partial \Phi_i}{\partial n} \, dS \tag{2}$$

We can replace

$$-\frac{\partial \Phi_i}{\partial n}\bigg|_{S_i} = \frac{I_m}{\sigma_i} \tag{3}$$

where σ_i is the conductivity in the axoplasm and I_m is the outward membrane current density. From equations (2) and (3), we have

$$\int_{S_i} \Phi_i \frac{\partial(1/r)}{\partial n} \, dS = -\frac{1}{\sigma_i} \int_{S_i} \frac{I_m}{r} \, dS$$

If we multiply both sides by $\sigma_i/4\pi\sigma$ then we obtain

$$\frac{1}{4\pi\sigma} \int_{S_i} \frac{I_m}{r} \, dS = -\frac{1}{4\pi} \frac{\sigma_i}{\sigma} \int_{S_i} \Phi_i \frac{\partial(1/r)}{\partial n} \, dS \tag{4}$$

Green's theorem is now applied to the external region. In this case we choose $\Phi = \Phi_o$, where Φ_o is the external potential field due to the bioelectric sources, while $\psi = 1/r$ as before. The following result is obtained, [2]

$$\Phi_o(P) = -\frac{1}{4\pi} \int_{S_o} \frac{1}{r} \frac{\partial \Phi_o}{\partial n} \, dS + \frac{1}{4\pi} \int_{S_o} \Phi_{S_o} \frac{\partial}{\partial n} \left(\frac{1}{r}\right) dS \tag{5}$$

where $\Phi_o\,(P)$ is the potential at the point $P(x', y', z')$ (see Fig. 1). The sign given in this equation assumes the positive normal taken outward from V_i and corresponds to the direction given in equation (2). The additional term, as compared with equation (2), is a consequence of the singularity of $\nabla^2(1/r)$ at P, which now lies in the region of integration. Since the membrane is very thin, we may assume negligible longitudinal current in which case the transverse current must be continuous. That is

$$-\frac{\partial \Phi_o}{\partial n}\bigg|_{S_o} = \frac{I_m}{\sigma} \tag{6}$$

where I_m is the same as that in equation (3) and σ is the external conductivity. Using equation (6) and adding equations (4) and (5) yields the following expression for the potential $\Phi_o(P)$,

$$\Phi_o(P) = \frac{1}{4\pi\sigma}\left[\int_{S_o} \frac{I_m}{r}\, dS - \int_{S_i} \frac{I_m}{r}\, dS\right] - \frac{1}{4\pi}\left[\frac{\sigma_i}{\sigma}\int_{S_i} \Phi_i \frac{\partial(1/r)}{\partial n}\, dS - \int_{S_o} \Phi_o \frac{\partial(1/r)}{\partial n}\, dS\right] \tag{7}$$

We shall consider field points whose distance to the membrane is large compared to the membrane thickness m_d. Since m_d is actually extremely small, this is not a significant restriction. Under this circumstance, the integrals in the first bracket can be combined into a double layer representation. Also, the integrals in the second bracket may both be integrated over a mean surface S which lies between S_o and S_i. Equation (7) then takes on the following form (where the positive surface normal is outward from the cell, *i.e.*, from S),

$$\Phi_o(P) = \frac{1}{4\pi\sigma}\int_S m_d I_m \nabla\left(\frac{1}{r}\right)\cdot d\mathbf{S} - \frac{1}{4\pi}\int_S \left(\frac{\sigma_i}{\sigma}\Phi_i - \Phi_o\right)\nabla\left(\frac{1}{r}\right)\cdot d\mathbf{S} \tag{8}$$

The quantity

$$-\nabla\left(\frac{1}{r}\right)\cdot d\mathbf{S} = \frac{\mathbf{a}_r\cdot d\mathbf{S}}{r^2} \tag{9}$$

corresponds to the solid angle subtended at P by a surface element dS. If we designate this quantity by $d\Omega$ then equation (8) can be expressed as

$$\Phi_o(P) = \frac{1}{4\pi}\int_S \left[\frac{\sigma_i}{\sigma}\Phi_i - \Phi_o - \frac{m_d I_m}{\sigma}\right] d\Omega \tag{10}$$

A sketch of the above parameters is given in Fig. 2.

Equation (10) can be simplified since the third term is ordinarily negligible.[1]

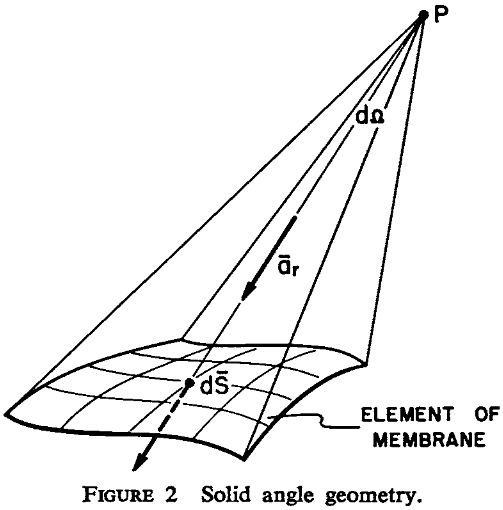

FIGURE 2 Solid angle geometry.

[1] The fact that the integral of I_m over the surface is zero (a consequence of its solenoidal nature) is of no help here since the integral is with respect to the solid angle.

To show this we first note that the contribution to $\Phi_o(P)$ comes only from variations in the integrand over S; constant terms evaluate to zero. Assuming the external potential, Φ_o, to vary relatively little we can consider the first two terms to have a range of about 5 to 100 mv. For a membrane of 100 A thickness, 1 ma/cm^2 maximum current density, and with σ equal to 0.05 mho/cm, the third term evaluates to 2×10^{-5} mv a completely negligible quantity. Thus, as an excellent approximation,

$$\Phi(P) \simeq \frac{1}{4\pi} \int_S \left(\frac{\sigma_i}{\sigma} \Phi_i - \Phi_o\right) d\Omega \tag{11}$$

When $\sigma_i = \sigma$, this result reduces to that conventionally obtained.[2]

A further approximation, which is somewhat crude, is based on Φ_o being relatively constant so that its contribution is small. In this case, we can take it to be a zero reference and get

$$\Phi(P) \simeq \frac{1}{4\pi} \frac{\sigma_i}{\sigma} \int_S \Phi_i \, d\Omega \tag{12}$$

and Φ_i is identified as the transmembrane potential.

Considering the solid angle formulation itself, its utility comes about when the surface can be divided into a small number of sections on each of which the integrand is essentially constant. Then the net potential is the sum of several terms, each of which depends on its respective solid angle. The computation of potential at any point is readily accomplished by noting the values of solid angle subtended. In this way, a ready picture of the potential field can be achieved.

CONCLUSIONS

The results given by equations (11) and (12) permit the extension of solid angle potential expressions to the case where the internal and external cellular conductivities are unequal. Typical values for internal and external conductivities for the squid giant axon [3] are $\sigma = 0.05$ mho/cm and $\sigma_i = 0.025$ mho/cm so that the derived forms are of practical importance. To the extent that equation (12) is valid, it is seen that the inequality of σ_i and σ affect the potential variation by means of the multiplicative ratio σ_i/σ.

The aforementioned derivation also shows the approximations that lead to forms

---

[2] However, it should be noted that the conventional derivation, as in Ruch and Fulton [1], imply static or resting (zero current) conditions. For that case equations (3) and (6) do not apply. However an independent derivation yields

$$\Phi_S = \frac{1}{4\pi} \int_S \Phi_i \, d\Omega$$

and appropriately does not depend on the conductivities. The zero current case is actually a trivial one since the potential field is a constant in the external and internal medium.

such as in equation (10) (continuity of transmembrane current) and that further approximations are necessary to obtain equations (11) and (12).

The work described in this paper was supported in full by the Public Health Service through National Institutes of Health Grants GM 08569, GM 12203, and 1T1 GM 1090-01A1.

Received for publication, February 15, 1965.

REFERENCES

[1] Ruch, T., and Fulton, J. F., Medical Physiology and Biophysics, Philadelphia, W. B. Saunders Co., 1960, 86.

[2] Plonsey, R., Volume conductor fields of action currents, *Biophysic. J.*, 1964, **4**, 317, see equation (21).

[3] Tasaki, I., Conduction of the nerve impulse *in* Handbook of Physiology, Section I: Neurophysiology, American Physiological Society, Washington, D. C., 1960, **1**.