NUMERICAL SOLUTION OF STEADY-STATE ELECTRODIFFUSION EQUATIONS FOR A SIMPLE MEMBRANE

RICHARD A. ARNDT, JAMES D. BOND, *and* L. DAVID ROPER

From the Department of Physics, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

ABSTRACT A technique is given for obtaining numerical solutions to the steady-state electrodiffusion equations for a simple membrane. Solutions are given for several membrane boundary conditions in terms of ratios of current density to mobility for each ion type.

INTRODUCTION

Goldman (1943) solved the steady-state electrodiffusion equations for a simple membrane (homogeneous and no charge structure) with either the assumption of microscopic electroneutrality or of constant electric field. Bruner (1965 *a*, *b*; 1967) has numerically obtained solutions for special situations. He considered the solution regions on each side of the membrane and applied boundary conditions at $x = \pm\infty$. We report here a numerical method for obtaining solutions to the equations for a simple membrane for any boundary conditions at the membrane surfaces. We do not consider the solutions on each side of the membrane because ion mobilities in many biological membranes are $\sim 10^5$ times smaller than mobilities in the surrounding solutions (Cole, 1968). Later we shall alter this method for application to a dipole-layer membrane (Wei, 1969).

Our method involves expanding the ion concentrations and the electric field in Fourier series in the variable x (the position in the membrane). The series are truncated and the coefficients are obtained by an iterative matrix technique.

We give solutions for several membrane boundary conditions in terms of ratios of current density to mobility for each ion type, and we compare results for different values of the electric permittivity and membrane thickness. We find that the current-voltage curves for a biionic environment are essentially linear unless the concentration gradients are large, but considerable deviation from nonlinearity can occur in a triionic environment if the ion mobilities are considerably different.

THEORY AND NUMERICAL PROCEDURE

The steady-state electrodiffusion equations are the Nernst-Planck and Poisson equations.

The Nernst-Planck Equation (Goldman, 1943)

$$\frac{dn_k}{dx} - z_k \beta n_k E = -\frac{j_k}{z_k u_k RT} \equiv -\gamma_k, \tag{1}$$

where $n_k(x)$ is the concentration in moles per volume of ion type at position x, z_k is the valence, u_k is the mobility per unit valence (which we consider as constant across the membrane), j_k is the ion current density in the outward direction, E is the electric field in the outward direction, and $\beta = F/RT$, where F is Faraday's constant, R is the universal gas constant, and T is the absolute temperature.

The Poisson Equation (Jackson, 1962).

$$\frac{dE}{dx} = \frac{F}{\epsilon} \sum_k z_k n_k, \tag{2}$$

where ϵ is the permittivity (assumed constant across the membrane).

Equation 1 can be converted to an integral equation by integrating both sides from 0 to x:

$$n_k(x) = n_k^{(i)} - \gamma_k x + z_k \beta \int_0^x n_k(x')E(x')\, dx', \tag{3}$$

where $n_k^{(i)} \equiv n_k(0)$ is the ion concentration at the inside membrane boundary ($x = 0$). By evaluating equation 3 at the outside membrane boundary ($x = w$) we obtain an equation for the current density:

$$\gamma_k = \frac{n_k^{(i)} - n_k^{(o)}}{w} + \frac{z_k \beta}{w} \int_0^w n_k(x')E(x')\, dx', \tag{4}$$

where $n_k^{(o)} \equiv n_k(w)$ is the ion concentration at the outside boundary. Substitution of equation 4 into equation 3 yields

$$n_k(x) = \bar{n}_k(x) + f_k(x), \tag{5}$$

where

$$\bar{n}_k(x) \equiv n_k^{(i)} + \frac{n_k^{(o)} - n_k^{(i)}}{w} x,$$

and

$$f_k(x) = z_k \beta \left[\int_0^x n_k(x')E(x')\,dx' - \frac{x}{w} \int_0^w n_k(x')E(x')\,dx' \right],$$

which is the integral form of equation 1 and, in addition, contains the boundary conditions at $x = 0$ and $x = w$. Note that $f_k(0) = f_k(w) = 0$.

We assume that electroneutrality holds at the membrane boundaries; i.e., that

$$\sum_k z_k n_k^{(i)} = 0 \quad \text{and} \quad \sum_k z_k n_k^{(o)} = 0. \tag{6}$$

Perhaps some of these ions are essentially immobile in the membrane; that fact will come in later when mobilities are explicitly considered.

We shall solve numerically equations 5 and 2 simultaneously. In order to do so we expand

$$f_k(x) = \sum_{l=1}^{L} (f_k)_l \sin \frac{l\pi x}{w}, \tag{7}$$

and

$$E(x) = -\frac{V}{w} + \sum_{l=1}^{L} E_l \cos \frac{l\pi x}{w}, \tag{8}$$

where the Fourier series are truncated at some value L to be determined empirically, and V is the electric potential at $x = w$ relative to $x = 0$. The expansion functions, $\sin (l\pi x/w)$, in equation 7 vanish at $x = 0$ and $x = w$ as does $f_k(x)$. The expansion functions, $\cos (l\pi x/w)$, in equation 8 are such that $V = -\int_0^w E dx$, which is the correct relation between E and V (Jackson, 1962).

The expansion coefficients $(f_k)_l$ in equation 7 are obtained in the Appendix:

$$(f_k)_l = (A_k^{-1})_{lm}(y_k)_m\,; \tag{9}$$

the complicated expressions for $(y_k)_m$ and $(A_k)_{ml}$ are given in the Appendix (equations A 1 and A 2). Equation 9 gives the ionic concentrations for a given input field, E^{in}, at some stage of the iteration. From the f_k's the output field, E^{out}, as shown in the Appendix (equation A 3), can be determined by

$$E_m^{\text{out}} = -\frac{Fw}{\epsilon \pi m} \sum_k z_k (f_k)_m. \tag{10}$$

Now, incrementing the input field by an amount Δ will produce a change in the output field; we want to pick an increment Δ to change the input field to make it equal to the new output field. That is, we start with values for E_m^{in}, then calculate E_m^{out} by equations 9 and 10, and then solve for the vector $\underline{\Delta}$ by means of the equations

$$E_m^{\text{in}} + \Delta_m = E_m^{\text{out}} + \sum_l \frac{\partial E_m^{\text{out}}}{\partial E_l^{\text{in}}} \Delta_l, \tag{11}$$

where $\partial E_m^{\text{out}}/\partial E_l^{\text{in}}$ is obtained as indicated in the Appendix. This gives us a new input field, $E_m^{\text{in}} + \Delta_m$, and we go through the procedure again.

The numerical procedure is as follows:

(*a*) Start with some electric field distribution (say, constant E) and calculate the ion concentrations by equations 9, 7, and 5.

(*b*) Calculate $\underline{\Delta}$ by equation 11.

(*c*) Change E^{in} by $\underline{\Delta}$ and go back to step 1 until

$$\chi^2 = \sum_l (E_l^{\text{in}} - E_l^{\text{out}})^2$$

is less than some small value.

(*d*) Calculate γ_k from equation 1.

TABLE I

ION ENVIRONMENT FOR OUR NUMERICAL CALCULATIONS.

Concentrations are in mmoles per liter. The membrane thickness w is taken as 100 A and the electric permittivity is $10\epsilon_0$.

Ion number	1		2	
Ion valance	$z = 1$		$z = -1$	
Figure	Inside conc.	Outside conc.	Inside conc.	Outside conc.
1 A	50	50	50	50
1 B	100	100	100	100
2	50	100	50	100
3	1	1000	1	1000

Ion number	1		2	
Ion valence	$z = 2$		$z = -1$	
Figure	Inside conc.	Outside conc.	Inside conc.	Outside conc.
4 A	50	50	100	100
4 B	100	100	200	200
5	50	100	100	200

Ion number	1		2		3	
Ion valence	$z = 1$		$z = 1$		$z = -1$	
Figure	Inside conc.	Outside conc.	Inside conc.	Outside conc.	Inside conc.	Outside conc.
6	100	100	100	100	200	200
7	50	100	50	100	100	200
8	50	460	400	10	450	470

APPLICATION

We have applied the numerical procedure given above to a simple membrane with several ion environments. The situations used are given in Table I. In Figs. 1–8 the quantity

$$\Gamma_k \equiv \frac{j_k}{u_k} = z_k RT\gamma_k$$

is plotted for $T = 293.2°K$, where the unit for the current density j_k is milliamperes per square centimeter and the unit for the mobility u_i is centimeter angstroms per millivolt seconds. We use $w = 100$ A for the membrane thickness and 10 terms in equations 7 and 8. Inclusion of more terms did not significantly change the result.

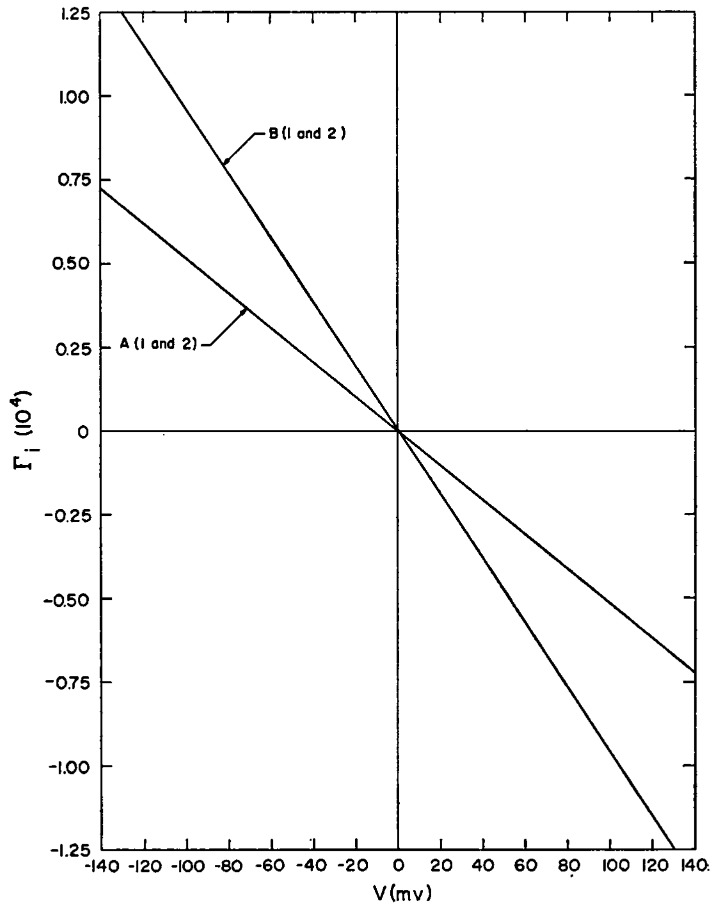

FIGURE 1 Current density/mobility in (ma-mv-sec)/cm³-A. See Table I for ion valences and concentrations. Here the constant electric field solution is the exact solution (Arndt, Bond, and Roper, 1970).

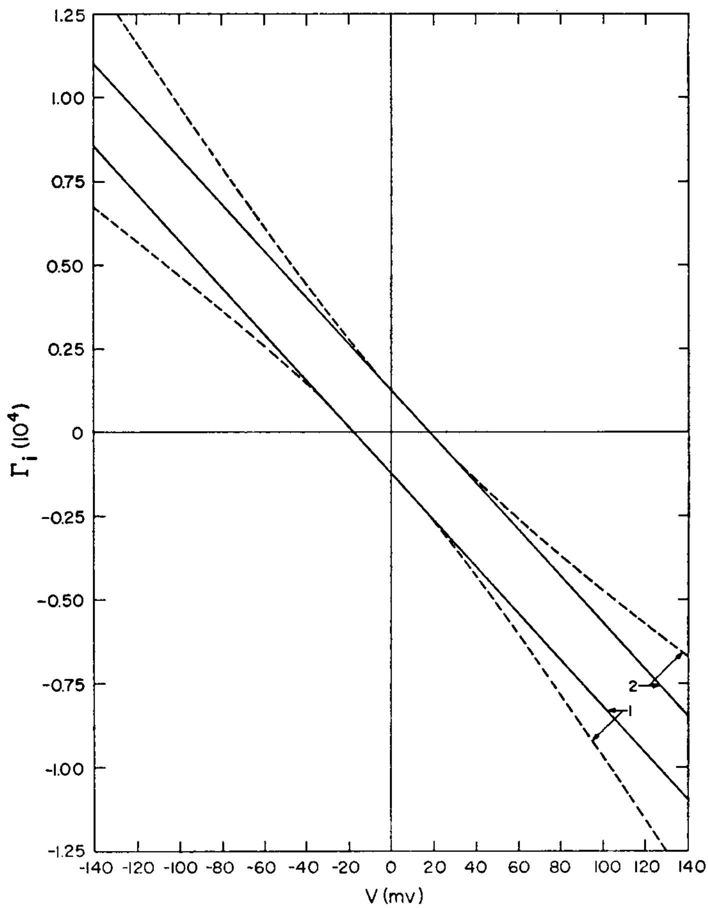

FIGURE 2 Current density/mobility in (ma-mv-sec)/cm^3-A. See Table I for ion concentrations. The constant electric field solution (dashed) is also shown.

In some of the figures the constant electric field solution is also given for comparison.

In Table II we compare the coefficients, currents, electric fields, and concentrations for different numbers of terms in the Fourier series. It appears that the electric field coefficients and the concentration coefficients each form two absolutely convergent series, one with the odd terms and one with the even terms [excluding the first term for $(f_{-})_m$].

Since no one really knows what the permittivity of biological membranes is, in Table III we compare solutions for $\epsilon = 5\epsilon_0$ and $\epsilon = 10\epsilon_0$. The difference in the currents is small.

Likewise, in Table IV we compare solutions for different membrane thicknesses: $w = 75$ and 100 A.

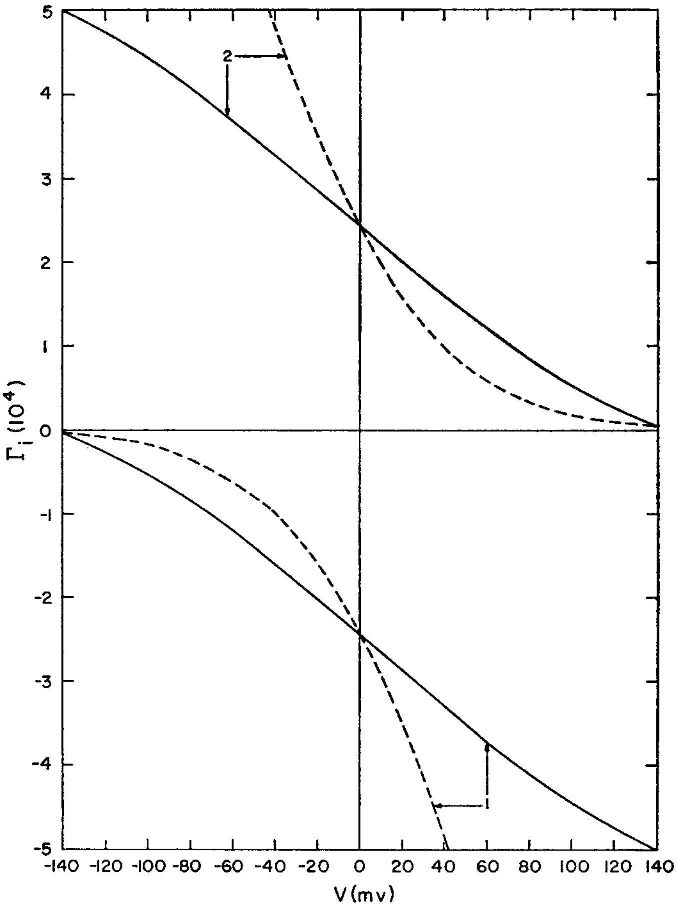

FIGURE 3 Current density/mobility in (ma-mv-sec)/cm³-A. See Table I for ion concentrations. The constant electric field solutions (dashed) is also shown.

The number of iterations required to obtain a solution ($\chi^2 < 10^{-6}$) varied between one and three depending on the starting point.

To fit experimental $J(V)$ data for simple membranes one need only vary the u_k's in

$$J(V) = \sum_k u_k \Gamma_k(V),$$

where $\Gamma_k(V)$ is taken from our figures, until the best fit is obtained. If a particular free ion is essentially immobile through the membrane, its mobility would turn out to be very small.

CONCLUSION

We have developed a numerical technique for solving the Nernst-Planck and Poisson equations simultaneously for a simple membrane. Less complicated methods were

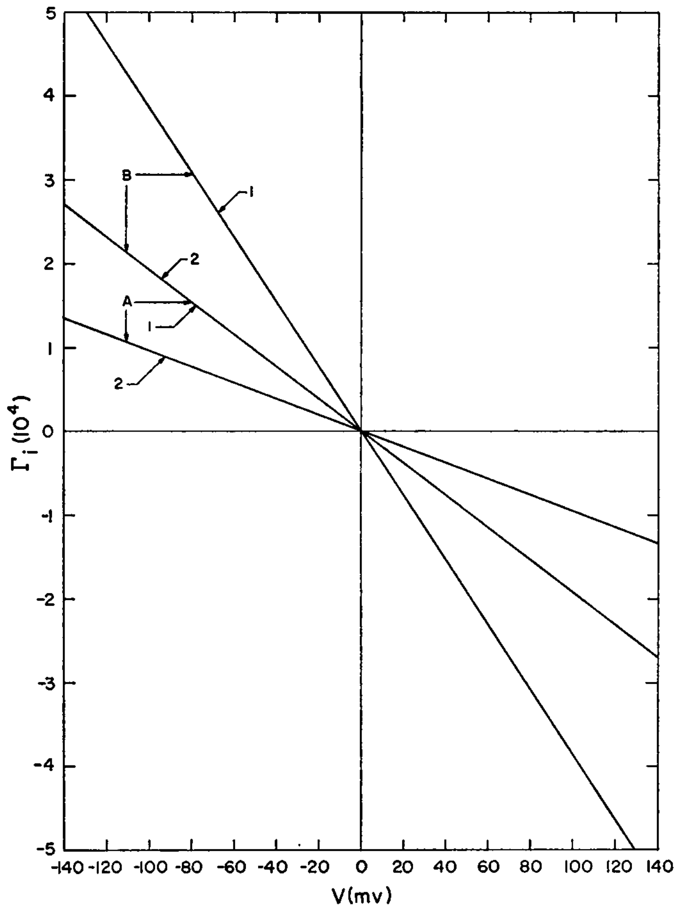

FIGURE 4 Current density/mobility in (ma-mv-sec)/cm^3-A. See Table I for ion concentrations. Here the constant electric field solution is the exact solution (Arndt, Bond, and Roper, 1970).

tried but failed, because of various numerical difficulties. With the method given here the ratio j_k/u_k for each ion can be calculated for a given ion environment and a given membrane thickness. We have done so here for thickness w = 100 A, electric permittivity $\epsilon = 10\epsilon_0 = 0.0553\ e/(\text{volt–A})$, and several ion environments (Table I) and have presented the results in graph form. We would be glad to do the calculation for other values for thickness, electric permittivity, and ion environments upon request.

Some interesting results are:

(*a*) For a biionic environment (Figs. 1–5), the current is essentially linear with the potential unless the concentration gradient is large (Fig. 3).

(*b*) For a triionic environment (Figs. 6–8), the current-potential curve can be considerably nonlinear (Fig. 8), depending on the ion mobility differences.

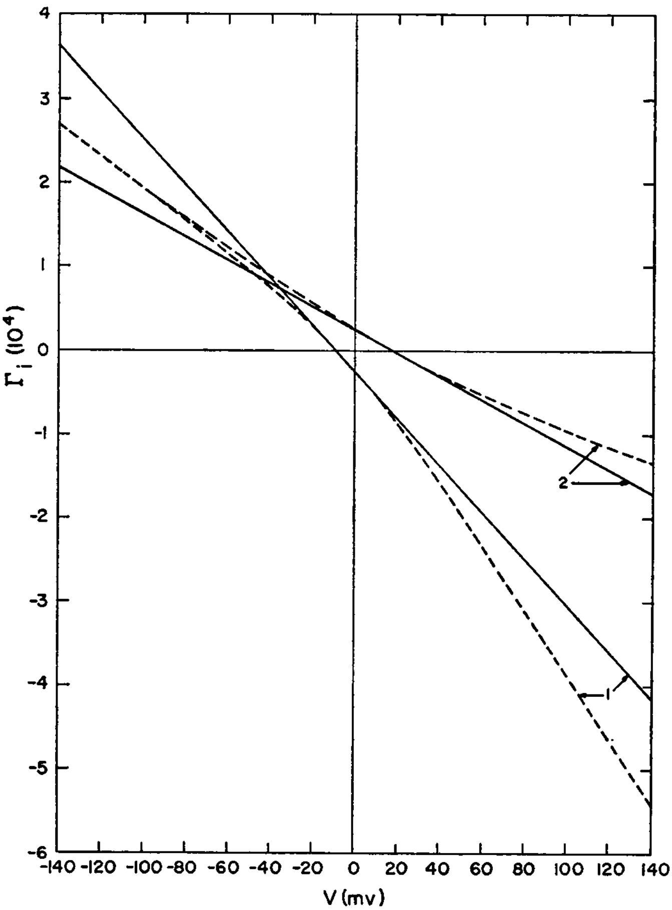

FIGURE 5 Current density/mobility in (ma-mv-sec)/cm^3-A. See Table I for ion concentrations. The constant electric field solution (dashed) is also shown.

APPENDIX

Concentration Coefficients

An equation for the expansion coefficients, $(f_k)_l$, in equation 7 can be obtained by multiplying both sides of the equation by sin $(m\pi x/w)$ and integrating between $x = 0$ and $x = w$. The result is

$$(f_k)_m = \frac{2}{w}\int_0^w \sin\frac{m\pi x}{w} f_k(x)\, dx.$$

Since $f_k(0) = f_k(w) = 0$, integration by parts gives

$$(f_k)_m = \frac{2}{m\pi}\int_0^w \cos\frac{m\pi x}{w}\frac{df_k(x)}{dx}\, dx.$$

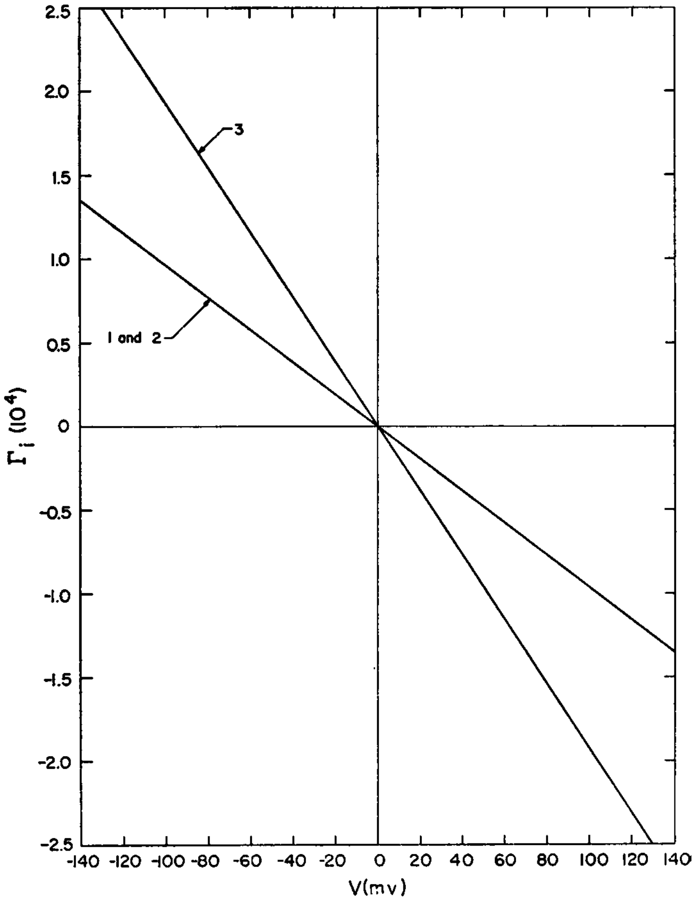

FIGURE 6 Current density/mobility in (ma-mv-sec)/cm^3-A. See Table I for ion concentrations. Here the constant electric field solution is the exact solution (Arndt, Bond, and Roper, 1970).

But,

$$\frac{df_k}{dx} = \beta z_k \left[\frac{d}{dx} \int_0^x n_k(x')E(x')\, dx' - \frac{1}{w} \int_0^w n_k(x')E(x')\, dx' \right]$$
$$= \beta z_k \left[n_k(x)E(x) - \frac{1}{w} \int_0^w n_k(x')E(x')\, dx' \right].$$

Therefore,

$$(f_k)_m = \frac{2\beta z_k}{m\pi} \int_0^w \cos \frac{m\pi x}{w}\, n_k(x)E(x)\, dx,$$

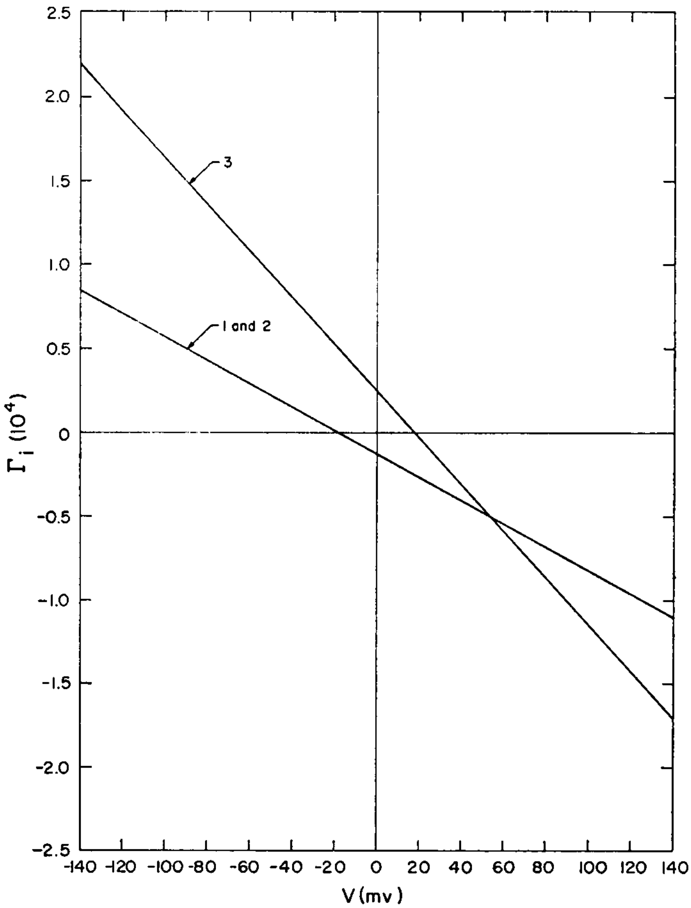

FIGURE 7 Current density/mobility in (ma-mv-sec)/cm³-A. See Table I for ion concentrations. The constant electric field solution is not shown.

since

$$\int_0^w \cos \frac{m\pi x}{w} \, dx = 0.$$

Substituting in from equations 5 and 7 we get

$$(f_k)_m = \frac{2\beta z_k}{m\pi} \int_0^w \cos \frac{m\pi x}{w} E(x) \left[\bar{n}_k(x) + \sum_l (f_k)_l \sin \frac{l\pi x}{w} dx \right].$$

For a given ion type (index k) this is a matrix equation for the coefficients $(f_k)_l$. In matrix notation the solution to this equation is

$$\underline{f_k} = A_k^{-1} \underline{y_k};$$

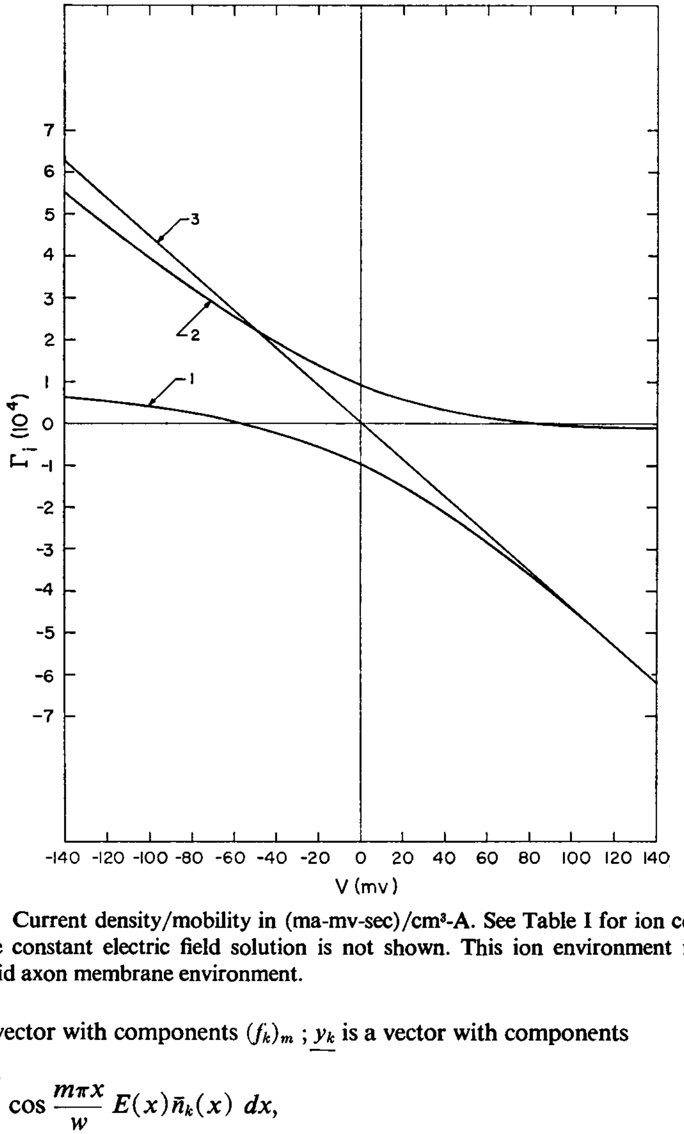

FIGURE 8 Current density/mobility in (ma-mv-sec)/cm³-A. See Table I for ion concentrations. The constant electric field solution is not shown. This ion environment is similar to the squid axon membrane environment.

where $\underline{f_k}$ is a vector with components $(f_k)_m$; $\underline{y_k}$ is a vector with components

$$
\begin{aligned}
(y_k)_m &= \int_0^w \cos\frac{m\pi x}{w}\, E(x)\bar{n}_k(x)\; dx, \\
&= \frac{w}{\pi}\int_0^\pi \cos my\left(-\frac{V}{w} + \sum_l E_l \cos ly\right)\left[n_k^{(i)} + (n_k^{(o)} - n_k^{(i)})\,\frac{y}{\pi}\right] dy \\
&= \frac{V}{\pi^2 m^2}\,(n_k^{(o)} - n_k^{(i)})[1 - (-1)^m] + \frac{1}{2}\, n_k^{(i)} w E_m \\
&\quad + \frac{w}{\pi^2}\,(n_k^{(o)} - n_k^{(i)}) \sum_l E_l \left\{\frac{\pi^2}{4}\,\delta_{lm} - \frac{l^2 + m^2}{(l^2 - m^2)^2}\right. \\
&\qquad\qquad \left. \cdot[1 - (-1)^{m+l}]\bar{\delta}_{lm}\right\}, \qquad (\text{A } 1)
\end{aligned}
$$

TABLE II

COMPARISON OF COEFFICIENTS, CURRENTS, CONCENTRATIONS, AND ELECTRIC FIELDS FOR DIFFERENT NUMBERS OF TERMS IN THE FOURIER SERIES (EQUATIONS 7 AND 8) FOR THE BIIONIC SYSTEM OF FIG. 2.

(See Table I for boundary concentrations and membrane parameters.) The membrane potential is −140 mv.

A. Electric field

Number of terms	2	4	6	8	10	12	14	Fourier coeff.
	0.3779	0.3806	0.3813	0.3815	0.3816	0.3817	0.3817	m = 1, E_m
	0.0510	0.0559	0.0562	0.0562	0.0562	0.0563	0.0563	2
		0.0444	0.0444	0.0445	0.0444	0.0444	0.0444	3
		0.0108	0.0118	0.0118	0.0118	0.0118	0.0118	4
			0.0131	0.0131	0.0131	0.0131	0.0131	5
			0.0036	0.0039	0.0039	0.0039	0.0039	6
				0.0052	0.0052	0.0052	0.0052	7
				0.0015	0.0016	0.0016	0.0016	8
					0.0024	0.0024	0.0024	9
					0.0007	0.0007	0.0007	10
						0.0013	0.0013	11
						0.0004	0.0004	12
							0.0007	13
							0.0002	14
				Current density/mobility				
Γ_+	8469	8444	8438	8435.5	8434.5	8433.8	8433.5	
Γ_-	11007	10996	10994	10992.8	10992.4	10992.2	10992.1	
				Concentrations and electric field at midpoint (50 A)				
n_+(mmoles/liter) =	74.12	74.17	74.08	74.11	74.08	74.09	74.08	
n_-(mmoles/liter) =	75.21	74.88	74.98	74.91	74.94	74.91	74.93	
E(mv/A) =	1.349	1.355	1.352	1.353	1.353	1.353	1.353	

B. Positive ion coefficients $(f_+)_m$

Number of terms	2	4	6	8	10	12	14	Fourier Coeff.
	−0.8752	−0.9896	−1.0223	−1.0336	−1.0402	−1.0429	−1.0444	m = 1, $(f_+)_m$
	0.0404	−0.1117	−0.1418	−0.1525	−0.1572	−0.1595	−0.1609	2
		−0.1596	−0.1748	−0.1794	−0.1813	−0.1822	−0.1827	3
		0.0084	−0.0286	−0.0358	−0.0386	−0.0398	−0.0405	4
			−0.0734	−0.0777	−0.0791	−0.0796	−0.0799	5
			0.0020	−0.0117	−0.0143	−0.0153	−0.0159	6
C. Negative ion coeff. $(f_-)_m$								
14	0.0085			−0.0405	−0.0422	−0.0427	−0.0429	7
13	0.0163			0.0006	−0.0054	−0.0066	−0.0071	8
12	0.0117	0.0129			−0.0244	−0.0251	−0.0254	9
11	0.0240	0.0245			0.0003	−0.0027	−0.0033	10
10	0.0179	0.0186	0.0206			−0.0156	−0.0160	11
9	0.0373	0.0377	0.0387			0.0001	−0.0015	12
8	0.0293	0.0299	0.0312	0.0351			−0.0105	13
7	0.0616	0.0620	0.0627	0.0647			0.0001	14
6	0.0514	0.0521	0.0532	0.0560	0.0648			
5	0.1084	0.1088	0.1095	0.1111	0.1157			
4	0.0959	0.0966	0.0980	0.1008	0.1080	0.1335		
3	0.2015	0.2020	0.2029	0.2048	0.2093	0.2238		
2	0.1633	0.1645	0.1669	0.1715	0.1819	0.2105	0.3340	
$(f_-)_m$, m = 1	0.0554	0.0568	0.0594	0.0646	0.0763	0.1070	0.2134	
Fourier coeff.	14	12	10	8	6	4	2	Number of terms

TABLE III

COMPARISON OF COEFFICIENTS, CURRENTS, CONCENTRATIONS, AND ELECTRIC FIELDS FOR DIFFERENT VALUES OF THE ELECTRIC PERMITTIVITY FOR THE BIIONIC SYSTEM OF FIG. 2.

(See Table I for boundary concentrations and membrane parameters.) The membrane potential is −140 mv.

ϵ	E_m		$(f_+)_m$		$(f_-)_m$	
m	$5\epsilon_0$	$10\epsilon_0$	$5\epsilon_0$	$10\epsilon_0$	$5\epsilon_0$	$10\epsilon_0$
1	0.3854	0.3816	−0.5496	−1.0402	0.0056	0.0594
2	0.0610	0.0562	−0.0986	−0.1572	0.0770	0.1669
3	0.0487	0.0444	−0.1049	−0.1813	0.1056	0.2029
4	0.0145	0.0118	−0.0298	−0 0386	0.0536	0.0980
5	0.0158	0.0131	−0.0500	−0.0791	0.0635	0.1095
6	0.0054	0.0039	−0.0137	−0.0143	0.0328	0.0532
7	0.0069	0.0052	−0.0290	−0.0422	0.0401	0.0627
8	0.0024	0.0016	−0.0067	−0.0054	0.0211	0.0312
9	0.0035	0.0024	−0.0180	−0.0244	0.0268	0.0387
10	0.0011	0.0007	−0.0014	−0.0003	0.0145	0.0206

ϵ	Γ_+	Γ_-	
$5\epsilon_0$	8475	10978	
$10\epsilon_0$	8434	10992	
At 50 A			
ϵ	n_+	n_-	E
	mmoles/ liter	moles/ liter)	mv/A
$5\epsilon_0$	74.52	74.95	1.349
$10\epsilon_0$	74.08	74.94	1.353

TABLE IV

COMPARISON OF COEFFICIENTS, CURRENTS, CONCENTRATIONS, AND ELECTRIC FIELDS FOR DIFFERENT VALUES OF THE MEMBRANE THICKNESS FOR THE BIIONIC SYSTEM OF FIG. 2.

(See Table I for boundary concentrations and membrane parameters.) The membrane potential is −140 mv.

$w(A)$	E_m		$(f_+)_m$		$(f_-)_m$	
m	75	100	75	100	75	100
1	0.5008	0.3816	−1.7267	−1.0402	0.1971	0.0594
2	0.0665	0.0562	−0.1993	−0.1572	0.3120	0.1669
3	0.0524	0.0444	−0.2691	−0.1813	0.3348	0.2029
4	0.0122	0.0118	−0.0343	−0.0386	0.1528	0.0980
5	0.0139	0.0131	−0.1070	−0.0791	0.1608	0.1095
6	0.0036	0.0039	−0.0084	−0.0143	0.0743	0.0532
7	0.0051	0.0052	−0.0529	−0.0422	0.0844	0.0627
8	0.0014	0.0016	−0.0012	−0.0054	0.0405	0.0312
9	0.0023	0.0024	−0.0292	−0.0244	0.0489	0.0387
10	0.0006	0.0007	−0.0030	0.0003	0.0260	0.0206

$w(A)$	Γ_+	Γ_-	
75	11172	14691	
100	8434	10992	
At midpoint			
w(A)	n_+	n_-	E
	mmoles/ liter	*mmoles/ liter*	mv/A
75	73.80	75.31	1.801
100	74.08	74.94	1.353

where we have used equations 5 and 8, have evaluated the integrals, δ_{ml} is the usual Kronecker delta

$$\left(\delta_{lm} = \begin{cases} 1 & \text{for} \quad l = m \\ 0 & \text{for} \quad l \neq m \end{cases}\right),$$

and we define an anti-delta

$$\bar{\delta}_{lm} = \begin{cases} 0 & \text{for} \quad l = m \\ 1 & \text{for} \quad l \neq m \end{cases};$$

and A_k is a matrix with elements

$$(A_k)_{ml} = \frac{m\pi}{2\beta z_k}\delta_{ml} - \int_0^w \cos\frac{m\pi x}{w}\sin\frac{l\pi x}{w}E(x)\,dx$$

$$= \frac{m\pi}{2\beta z_k}\delta_{ml} - \frac{w}{\pi}\int_0^\pi \cos my \sin ly\left(-\frac{V}{w} + \sum_r E_r \cos ry\right)dy$$

$$= \frac{m\pi}{2\beta z_k}\delta_{ml} + \frac{Vl}{\pi(l^2 - m^2)}[1 - (-1)^{l+m}]\bar{\delta}_{ml}$$

$$- \frac{lw}{\pi}\sum_r E_r \frac{l^2 - m^2 - r^2}{[l^2 - (m+r)^2][l^2 - (m-r)^2]}[1 - (-1)^{l+m+r}]. \quad (\text{A } 2)$$

Of course, one needs the E_m coefficients to obtain f_k.

Electric Field Coefficients

Poisson's equation, equation 2, and equation 8 combine to give

$$\frac{F}{\epsilon}\sum_k z_k n_k(x) = -\frac{\pi}{w}\sum_l lE_l \sin\frac{l\pi x}{w}.$$

But, according to equation 5

$$\sum_k z_k n_k(x) = \beta\left[\int_0^x \eta(x')E(x')\,dx' - \frac{x}{w}\int_0^w \eta(x')E(x')\,dx'\right] = \sum_k z_k f_k(x),$$

where $\eta(x) \equiv \sum_k z_k^2 n_k(x)$, because

$$\sum_k z_k \bar{n}_k(x) = \sum_k z_k n_k^{(i)} + \frac{x}{w}\left(\sum_k z_k n_k^{(o)} - \sum_k z_k n_k^{(i)}\right) = 0$$

by equation 6. Therefore,

$$\sum_l lE_l \sin\frac{l\pi x}{w} = -\frac{F\beta w}{\epsilon\pi}\left[\int_0^x \eta E\,dx' - \frac{x}{w}\int_0^w \eta E\,dx'\right].$$

The expansion coefficients, E_l, can be obtained by multiplying both sides of this equation by $\sin(m\pi x/w)$ and integrating between $x = 0$ and $x = w$. Then

$$\frac{w}{2}mE_m = -\frac{F\beta w}{\epsilon\pi}\left[\int_0^w \sin\frac{m\pi x}{w}\int_0^x \eta(x')E(x')\,dx'\,dx\right.$$

$$\left. - \frac{1}{w}\int_0^w \eta(x')E(x')\,dx'\int_0^w x\sin\frac{m\pi x}{w}\,dx\right]$$

$$= -\frac{F\beta w}{\epsilon\pi}\left[\int_0^w \eta(x')E(x')\int_{x'}^w \sin\frac{m\pi x}{w}\,dx\,dx'\right.$$

$$\left. + \frac{(-1)^m w}{m\pi}\int_0^w \eta(x')E(x')\,dx'\right],$$

where we have used

$$\int_0^w \int_0^x g(x', x)\, dx'\, dx = \int_0^w \int_{x'}^w g(x', x)\, dx\, dx',$$

a standard relation for an arbitrary integrand $g(x', x)$ in the first double integral and an integral table (or integration by parts) in the second double integral. The integral involving $\sin (m\pi x/w)$ can be evaluated to give

$$E_m = -\frac{2F\beta w}{\epsilon\pi^2 m^2} \int_0^w \cos \frac{m\pi x}{w}\, \eta(x) E(x)\, dx.$$

Now substitute equation 8 for $E(x)$:

$$\frac{m^2\pi^2\epsilon}{2F\beta w} E_m = \frac{V}{w} \int_0^w \cos \frac{m\pi x}{w}\, \eta(x)\, dx - \sum_l E_l \int_0^w \cos \frac{m\pi x}{w} \cos \frac{l\pi x}{x}\, \eta(x)\, dx.$$

This equation can be considered as an equation for obtaining an output electric field, represented by $E_m{}^{\text{out}}$, for some given input field, represented by $E_l{}^{\text{in}}$. [Note that $\eta(x)$ is a function of $E_l{}^{\text{in}}$.] We use the numerical method of finite differencing to find $\partial E_m{}^{\text{out}}/\partial E_l{}^{\text{in}}$ from this equation.

Poisson's equation can also be formulated as

$$\frac{F}{\epsilon} \sum_k z_k n_k(x) = \frac{F}{\epsilon} \sum_k z_k f_k(x) = \frac{F}{\epsilon} \sum_k z_k \sum_l (f_k)_l \sin \frac{l\pi x}{w} = -\frac{\pi}{w} \sum_l l E_l \sin \frac{l\pi x}{w},$$

or

$$E_m{}^{\text{out}} = -\frac{Fw}{\epsilon\pi m} \sum_k z_k (f_k)_m, \qquad \text{(A 3)}$$

where the $(f_k)_m$ are obtained from an input field, E^{in}, by equation (A 1).

Received for publication 14 July 1970 and in revised form 16 September 1970.

REFERENCES

ARNDT, R. A., J. D. BOND, and L. D. ROPER. 1970. *Biophys. J.* **10**:1149.
BRUNER, L. J. 1965 *a*. *Biophys. J.* **5**:867.
BRUNER, L. J. 1965 *b*. *Biophys. J.* **5**:887.
BRUNER, L. J. 1967. *Biophys. J.* **7**:947.
COLE, K. S. 1968. Membranes, Ions and Impulses. University of California Press, Berkeley. 186.
GOLDMAN, D. E. 1943. *J. Gen. Physiol.* **27**:37.
JACKSON, J. D. 1962. Classical Electrodynamics. John Wiley and Sons, Inc., New York. 12, 133.
WEI, L. Y. 1969. *Bull. Math. Biophys.* **31**:39.