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The Problem of Nonstationary Ion Fluxes in Excitable Membranes

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Abstract. Time-dependent electrodiffusion through a membrane is analysed within a simple model treating the boundary-layers in a consistent manner. It is shown that time-independent reversal potentials for the ion fluxes exist only under steady-state conditions. We argue that this result holds very generally. Therefore nonstationary effects like ion storage and depletion inside the membrane should not contribute to the phenomena of excitability.

Key words: Excitable membranes – Reversal potentials – Time-dependent electrodiffusion – Ion storage – Membrane transport.

1. Introduction

The starting point for most models of excitable membranes is the assumption that the membrane behaves electrically simply as a capacitance in parallel with ionic conductances and that changes in the ionic conductances are responsible for the phenomena of excitability (for a general review see Scott, 1975). In order to describe the nonmonotonic time-dependence of the (early) sodium conductance in nerve membranes one then has to invoke an activation and a blocking mechanism (not necessarily independent as in the original work of Hodgkin and Huxley, 1952). Recently, however, models have been proposed which assign a considerable ion storage capacity to the membrane and assume the sodium current to be carried primarily by ions stored within the membrane (Hoyt and Strieb, 1971; Landowne, 1972; Offner, 1972, 1975). In this way it is hoped to explain the transient nature of the sodium current in a direct manner and also to obtain better agreement with the temperature dependence of the sodium flux than the Hodgkin-Huxley model does (Landowne, 1973; Cohen and Landowne, 1974).

In the present paper no new model is proposed, but instead the problem of time-dependent electrodiffusion through a membrane is analysed in some detail. A number of relations are derived which could serve as a starting point for numerical calculations. Here the equations are used, however, to show that the existence of time-independent reversal potentials, which is one of the very basic experimental findings on excitable (and many other) tissues, implies that the diffusion is stationary. Thus concentration changes inside the membrane do not contribute appreciably to the ion fluxes and time-dependent diffusion need not be considered. Although this connection between time-independent reversal potentials and stationarity of ionic fluxes is established rigorously only for a rather specific model, we believe that it represents a general physical principle (see Sec. 2). Thus it appears that models which employ ion storage and depletion effects are in conflict with experiment or with basic physical principles.

The results of this paper can of course be applied to other types of (electrically nonexcitable) membranes and also to more complex systems. As an example we mention photoreceptor cells such as those of *Limulus* and *Balanus* where the existence of reversal potentials has been demonstrated by voltage-clamp methods (Millechia and Mauro, 1969; Mack Brown et al., 1970). Therefore the transient maximum which the receptor potential as well as the light-induced current display when turning on a long intense light stimulus cannot result from depletion of some (extracellular) compartment as has been proposed (Krischer, 1971).

2. General Considerations

In general the current $J(t)$ flowing at time t across a given part of the membrane depends on the instantaneous membrane voltage $V(t)$ as well as on the previous time course of V. Thus $J(t)$ is a *functional* of the function $V(t)$ (i.e. it includes time-dependence) and we write

$$J(t) = F[V(t)] \tag{1}$$

(square brackets denote functional relations). From voltage-clamp experiments one knows that F can be decomposed in the following manner

$$F[V] = C\frac{dV}{dt} + \sum_m F_m[V] \tag{2}$$

where the sum contains about three terms. Here C is a (nearly) constant capacity which for most biological membranes is of order 1 μF/cm^2 (Keynes, 1972) and each functional F_m has a unique "reversal potential" V_m associated with it. This means that the sign of F_m is at any instant t given by the sign of $V(t) - V_m$ so that F_m is zero whenever $V(t) = V_m$ holds.

This property can be expressed in a completely general (but not unique) way by decomposing F_m into a product of two terms

$$F_m[V] = A_m[V]\, J_m(V). \tag{3}$$

Here $J_m(V)$ is now a *function* of V with the property

$$J_m(V) \gtrless 0 \quad \text{for} \quad V - V_m \gtrless 0 \tag{4}$$

and $A_m[V]$ is a positive, bounded functional. Note that the sign of the capacitive current in Equation (2) depends only on the sign of dV/dt and therefore has definitely no reversal potential.

One expects a physical basis for the mathematical decomposition (3). The simplest interpretation of Equation (3) is that $J_m(V)$ represents the current-voltage relation for a given membrane unit in a given state (e.g. an open Na^+ channel in a simple two-state model) and A_m represents the amount of membrane in this state (e.g. the number of open Na^+ channels). More generally one would assume that $A_m[V]$ is determined by the configuration of the membrane whereas $J_m(V)$ describes the current response of the mobile ions. Since $J_m(V)$ is here time-independent, i.e. effects coming from the redistribution of mobile ions are either small or sufficiently rapid to be incorporated into the capacitive current, ion storage and depletion does not contribute.

The interpretation given above is supported by the fact that the function $J_m(V)$ can often be measured (thereby making its definition unique) because it takes a time of the order of milliseconds for A_m to respond to voltage changes. Whereas in the literature the curves $J_m(V)$ are often called "instantaneous", "high-frequency" or "fully activated" $J-V$ relations, we shall refer to them as "intrinsic" $J-V$ relations. The instantaneous current will be introduced later on in a more rigorous sense.

The question now arizes if time-independent reversal potentials can exist as a universal property of excitable membranes even in the general case where the intrinsic current-voltage relations are time-dependent. Since we can see no physical reason for this to be the case we believe that diffusion inside the membrane must be stationary. In the next two sections this result is proven within a simple electrodiffusion model. The membrane is from now on considered to be in a given fixed state.

3. Poisson's Equation

Let the plane of the membrane coincide with the $y-z$ plane of a coordinate system and let the surfaces of the membrane be given by $x = \pm d$. For simplicity consider the case of a membrane which is spatially homogeneous in the $y-z$ plane so that all quantities depend on x only. A procedure for treating more realistic situations (especially that of localized channels) by the same method is shown in Appendix I. The electric potential ψ is determined by Poisson's equation

$$\frac{\partial^2 \psi}{\partial x^2} = -\frac{4\pi}{\varepsilon_0}\left(\varrho^{<}(x,t) + \varrho^{>}(x,t)\right) - \frac{4\pi}{\varepsilon_m}\left(\varrho_0(x) + \sum_i q_i\, n_i(x,t)\right). \tag{5}$$

Here $\varrho^{<}$ and $\varrho^{>}$ are the charge densities due to the boundary layers outside the membrane at $x < -d$ and $x > d$, respectively, ϱ_0 is the fixed charge distribution inside the membrane and q_i, n_i are the charge and density of the i-th ionic species inside the membrane. Also ε_0 and ε_m are the dielectric constants of the electrolyte solution (~ 80) and the membrane (~ 5). Obviously Equation (5) derives from the assumption that the various components of the system can be approximated by continuous media.

Equation (5) is to be solved subject to the boundary conditions $\psi'(-\infty) = \psi'(\infty) = 0$ and $\psi(-\infty) - \psi(\infty) = V$. These boundary conditions may be used if the conductivity of the electrolytes is large compared to that of the membrane and if the electrodes are sufficiently far from the membrane surfaces. In the following we assume these conditions to be always satisfied. In addition at $x = \pm d$ the conditions that ψ and $\varepsilon\psi'$ be continuous must be satisfied (see e.g. Landau and Lifshitz, 1960). Integrating Equation (5) from $-\infty$ to $+\infty$ one obtains the condition of overall charge neutrality

$$Q^< + Q^> + Q_0 + \int_{-d}^{d} dx \sum_i q_i n_i = 0\,. \tag{6}$$

Here the charges Q are obtained by integrating the various charge densities ϱ from $-\infty$ to $+\infty$. Equation (6) together with the continuity equation

$$q_i \frac{\partial n_i}{\partial t} + \frac{\partial j_i}{\partial x} = 0 \tag{7}$$

insures that the currents

$$j^{\lessgtr} = \sum_i j_i(\pm d) \mp \frac{dQ^{\lessgtr}}{dt} \tag{8}$$

which are measured by external electrodes are equal on both sides of the membrane[1].

By evaluating the expression

$$\int_{-\infty}^{\infty} dx \int_{-\infty}^{x} dx' \frac{\partial^2 \psi}{\partial x'^2} \tag{9}$$

one deduces from Equation (5) the relation

$$Q^< + \frac{\varepsilon_m}{8\pi d}(V^< - V^>) = \frac{\varepsilon_m}{8\pi d} V - \int_{-d}^{d} \frac{dx}{2d} \int_{-d}^{x} dx' \left(\varrho_0 + \sum_i q_i n_i\right). \tag{10}$$

Here $V^<$ and $V^>$ are the potential drops occuring inside the boundary layers. In Appendix II it is shown that $V^{\lessgtr}$ can in fact be neglected in Equation (10). Now inserting $Q^<$ into Equation (8) yields the following expression for the external current

$$j = j^{\lessgtr} = \frac{\varepsilon_m}{8\pi d} \frac{dV}{dt} + \sum_i \langle j_i \rangle\,. \tag{11}$$

The bracket denotes the spatial average, i.e.

$$\langle f \rangle = \int_{-d}^{d} \frac{dx}{2d} f(x) \tag{12}$$

for any function $f(x)$. The first term on the RHS of (11) represents the capacitive current.

4. Electrodiffusion Theory

Using simple electrodiffusion theory we next provide expressions for the current-voltage relation in the steady-state limit (slow voltage changes) and in the instanta-

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[1] Contributions connected with changes in the surface charges of the electrodes themselves are of course not accounted for in Equation (8)

neous limit (rapid voltage changes). It will turn out that whenever n_i changes in time the two expressions differ and no time-independent reversal potential exists.

The currents j_i are driven by the gradients of the electrochemical potentials g_i. Thus we write

$$j_i = -\, q_i\, \mu_i(x)\, n_i(x)\, \frac{dg_i(x)}{dx}\,, \tag{13}$$

where μ_i is the mobility of the i-the ionic species. For low density of mobile ions inside the membrane one has

$$g_i = kT \ln n_i + w_i(x) + q_i\, \psi(x) \tag{14}$$

where k is Boltzmann's constant, T the temperature and w_i the activation energy. Equation (14) is probably not a very good approximation for many excitable membranes but has the advantage of allowing simple calculations. Outside the membrane the electrochemical potentials are nearly constant and given by

$$\begin{aligned} g_i^< &= kT \ln n_i^< + q_i\, V \quad \text{for} \quad x < -d \\ g_i^> &= kT \ln n_i^> \qquad\qquad \text{for} \quad x > d\,. \end{aligned} \tag{15}$$

Here $n_i^<$ and $n_i^>$ are the ionic densities far away from the membrane at $x = -\infty$ and $x = +\infty$, respectively. We have set $\psi(\infty) = 0$.

First consider the steady state where the current j_i^{stat} is constant [see Eq. (7)]. Equation (13) together with (14) now is an ordinary first-order differential equation which can be solved for $n_i(x)$. Imposing the boundary condition (15) at $x = -d$ yields

$$n_i(x) = (\mu_i\, \zeta_i)^{-1} \left[n_i^>\, e^{q_i(V - V_i)/kT} - \frac{j_i^{\text{stat}}}{q_i\, kT} \int_{-d}^{x} dx'\, \zeta_i(x') \right], \tag{16}$$

where

$$\zeta_i(x) = \mu_i^{-1}(x) \exp\,(w_i(x) + q_i\, \psi(x))/kT \tag{17}$$

$$V_i = \frac{\mathrm{kT}}{q_i} \ln \frac{n_i^>}{n_i^<} \tag{18}$$

Imposing the boundary condition (15) at $x = d$ yields

$$j_i^{\text{stat}} = q_i\, kT\, n_i^>\, (2\, d\, \langle \zeta_i \rangle)^{-1}\, (e^{q_i(V - V_i)/kT} - 1)\,. \tag{19}$$

The electric potential is to be determined selfconsistently from Poisson's equation. Note that the spatial average in Equation (11) can now be omitted. One sees that j_i^{stat} reverses sign at the Nernst potential V_i. The differential steady-state conductance is given by

$$\frac{dj_i^{\text{stat}}}{dV} = \frac{q_i^2}{\langle \zeta_i \rangle} \left[\frac{n_i^>}{2\, d}\, e^{q_i(V - V_i)/kT} - \frac{j_i^{\text{stat}}}{q_i\, kT} \left\langle \frac{d\psi}{dV}\, \zeta_i \right\rangle \right]. \tag{20}$$

Second consider the instantaneous response of the system when changing the voltage suddenly from V to $V + \Delta V$. One may assume the electrolyte solutions to be in equilibrium instantaneously. At the beginning the densities n_i inside the membrane are unchanged so that the instantaneous change of the electrochemical potential is simply

$$\Delta g_i = q_i \, \Delta \psi = q_i \, \Delta V \frac{d - x}{2\,d} \,. \tag{21}$$

To obtain the last expression we have again neglected $V^<$ and $V^>$ (see Appendix II). From Equation (13) the instantaneous current change, which is related linearly to ΔV, is given by

$$\Delta j_i^{\text{inst}} / \Delta V = q_i^2 \, \mu_i \, n_i / 2\,d \,. \tag{22}$$

Inserting Equation (16) yields for the externally measured spatial average

$$\langle \Delta j_i^{\text{inst}} \rangle / \Delta V = q_i^2 \int_{-d}^{d} \frac{dx}{2\,d} \, \zeta_i^{-1}(x) \left[\frac{n_i^>}{2\,d} e^{q_i(V - V_i)/kT} - \frac{j_i^{\text{stat}}}{q_i kT} \int_{-d}^{x} \frac{dx'}{2\,d} \, \zeta_i(x') \right] . \tag{23}$$

Obviously the expressions in Equation (20) and (23) are in general different so that the instantaneous and the steady-state J–V relations are indeed not identical. Moreover the Nernst potential is in general not a time-independent reversal potential since otherwise the expressions would have to agree at least for $V = V_i$. This, however, is not the case as can be seen in the following way: For $V = V_i$ Equations (16), (20) and (23) reduce to

$$n_i(x) = (\mu_i \, \zeta_i)^{-1} \, n_i^> , \tag{24}$$

$$dj_i^{\text{stat}} / dV = (q_i^2 \, n_i^> / 2\,d) \, \langle \zeta_i \rangle^{-1} , \tag{25}$$

$$\langle \Delta j_i^{\text{inst}} \rangle / \Delta V = (q_i^2 \, n_i^> / 2\,d) \, \langle \zeta_i^{-1} \rangle \,. \tag{26}$$

From the Schwarz inequality (see e.g., Morse and Feshbach, 1953) one knows that for any two functions f and g the relation

$$\langle f \rangle \, \langle g \rangle \geqslant \langle (f g)^{1/2} \rangle^2 \tag{27}$$

holds. The equality sign holds if and only if g is proportional to f. Choosing $f = \zeta_i$ and $g = \zeta_i^{-1}$ one has $f\,g = 1$ and therefore

$$\langle \Delta j_i^{\text{inst}} \rangle / \Delta V \geqslant dj_i^{\text{stat}} / dV \,. \tag{28}$$

The equality sign holds if and only if ζ_i is proportional to ζ_i^{-1}, i.e., if ζ_i is a constant independent of x. From (24) and (22) one then notes that $\mu_i n_i$ and Δj_i^{inst} are also independent of x. Therefore $\partial n_i / \partial t = 0$ [Eq. (7)] and no ion storage or depletion occurs.

A very simple example is obtained by assuming that the mobile ion densities inside the membrane are so small that their influence on the electric potential can be neglected. Assuming in addition that fixed charges exist only near the surface one has (Kramer, 1975)

$$\psi = (V^- - V) \frac{x - d}{2\,d} - V^+ \frac{x + d}{2\,d} \,. \tag{29}$$

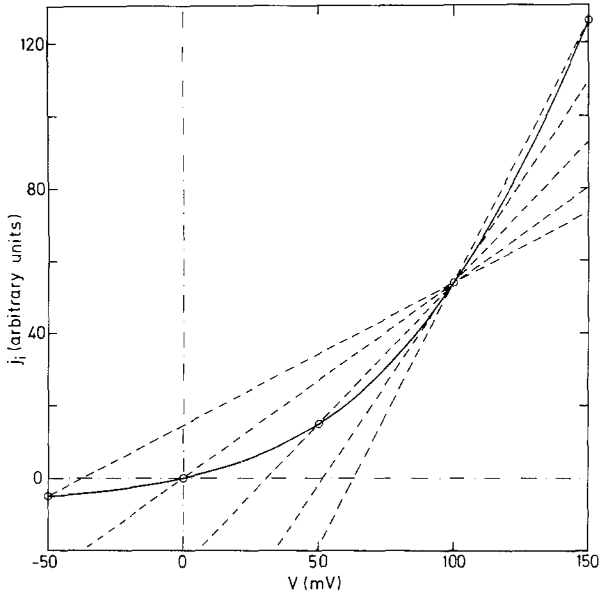

Fig. 1. Current-voltage relations for simple electrodiffusion model with $V_0 = 100$ mV, $V_i = 0$. The continuous curve is the steady-state current. The broken lines represent the externally measured instantaneous currents for holding potentials −50, 0, 50, 100, and 150 mV

Here V^- and V^+ are the potential steps at $x = -d$ and $x = +d$, respectively. In Figure 1 the steady-state current (continuous curve) and the externally measured instantaneous current (broken lines) are plotted for $V_0 \equiv V^- - V^+ = 100$ mV, $V_i = 0$ and several holding potentials. The fact that all curves intersect at $V = V_0$ is a special feature of this simple model. No time-independent reversal potential exists except for the particular case $V_i = V_0$. Then $j_i^{\text{stat}}(V)$ is linear and $n_i(x)$ is constant and independent of voltage so that no ion storage and depletion occurs.

5. Discussion

The investigation carried through in this paper suggests the following conclusions:

If a change in voltage V across a membrane (or any conducting system for that matter) leads to a change in the density of current carriers, then the current displays an initial transient behavior. The transient components do not reverse sign at the Nernst potential. The density changes occuring outside the membrane lead to an ordinary capacitive current contribution.

The existence of time-independent reversal potentials implies that steady-state conditions have to be established rapidly on a time-scale of the kinetics of the gating processes or that no appreciable density changes occur inside the membrane when the voltage is changed. In this last case the intrinsic J–V relations are identical with the instantaneous ones. Both cases exclude the possibility of the fluxes being carried by ions stored within the membrane.

In models where the local current is related linearly to the gradient of the electrochemical potential [as in Eq. (13)] non-linear steady-state current-voltage relations arize from the voltage dependence of the density of current carriers. Since the intrinsic current-voltage relations in squid giant axons bathed in seawater are linear (Hodgkin, Huxley and Katz, 1952) one expects density changes to be neglegible for these preparations. In *Xenopus* nodes, however, the intrinsic current-voltage relations are nonlinear (Hille, 1971) so one expects rapid density changes inside the membrane.

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Appendix I

If the potential ψ is not independent of y and z, a spatial average has to be performed before applying the analysis of Sec. 3. We use Gauss' theorem in the following form

$$\int_F dy\,dz\,\vec{\nabla}^2 \psi = \int_F dy\,dz\,\frac{\partial^2 \psi}{\partial x^2} + \oint dl\,\nabla_n \psi\,. \tag{30}$$

Here the double integrals extend over an area F of the y–z plane (at fixed x), the line integral extends over the boundary curve and ∇_n is the component of $\vec{\nabla}$ in the y–z plane normal to the boundary curve. In the limit of large areas F the line integral can be neglected. Introducing spatial averages

$$\bar{f} = F^{-1} \int_F dy\,dz\,f \tag{31}$$

one has for Poisson's equation

$$\frac{\partial^2 \bar{\psi}}{\partial x^2} = -\frac{4\pi}{\varepsilon}\bar{\varrho}\,. \tag{32}$$

The analysis of Sec. 3 can now be carried through for the spatially averaged quantities.

One usually does not have to average over large area. To see this consider the situation of localized and separated conduction channels in an otherwise homogeneous membrane. One then has to average only over the channel under consideration and some of its neighborhood. The reason is that ψ becomes independent of y and z away from the channel so that again the last term in (30) can be neglected.

The analysis of Sec. 4 can be carried through without this averaging procedure. The important assumption is that currents in the y and z direction are negligible inside the membrane (Kramer, 1975).

Appendix II

We show that $V^{\gtrless}$ can be neglected in Equation (10). Consider the region $-\infty < x \leq -d$. Since the mobilities in the electrolyte solution are large (compared to those in the membrane) the ions may be considered Boltzmann distributed even in the presence of current flow. Taking into account only univalent ions ($q_i = q$) one then has

$$\frac{\partial^2 \psi}{\partial x^2} = -\frac{4\pi}{\varepsilon_0}\varrho^{<} = \frac{4\pi q n^{<}}{\varepsilon_0}\sinh\frac{q(\psi - \psi(-\infty))}{kT} \tag{33}$$

where $n^<$ is the ionic strength of the electrolyte. Integrating (33) with boundary condition $\psi'(-\infty) = 0$ yields

$$\psi'(-d) = -\frac{4\pi}{\varepsilon_0} Q^< = -\left[\frac{8\pi kT n^<}{\varepsilon_0}\left(\cosh \frac{q V^<}{kT} - 1\right)\right]^{1/2} \text{sign } V \tag{34}$$

$(V^< = \psi(-\infty) - \psi(-d))$ and therefore

$$\frac{Q^<}{V^<} = \left[\frac{\varepsilon_0 q^2 n^<}{4\pi kT}\right]^{1/2} \left[2\left(\frac{kT}{qV^<}\right)^2 \left(\cosh \frac{qV^<}{kT} - 1\right)\right]^{1/2}. \tag{35}$$

A similar relation holds for $Q^>/V^>$. The expression in the second bracket on the RHS of (35) is always larger than one and tends to one for $V^< \to 0$. For a millimolar ionic solution we then find

$$\frac{Q^<}{V^<} \geqslant \left[\frac{\varepsilon_0 q^2 n^<}{4\pi kT}\right]^{1/2} \sim 1.46 \cdot 10^8 \text{ cm}^{-1} \tag{36}$$

Since $V^>$ is of the same order of magnitude as $V^<$ and since

$$\frac{\varepsilon_m}{8\pi d} \sim 0.3 \cdot 10^6 \text{ cm}^{-1} \tag{37}$$

one can neglect the second expression on the LHS of Equation (10).

Glossary of Symbols

$A_m[V]$	functional cf. Equation (3)
C	membrane capacitance
d	one half the thickness of the membrane
$F[V]$	functional cf. Equation (1)
g_i	electrochemical potential inside membrane
$g_i^{\gtrless}$	electrochemical potentials outside membrane at $x \gtrless \pm d$, respectively
i	(index) refers to i-th ionic species
J	electric current across membrane
$j = j^> = j^<$	current density measured by external electrodes
$j_i(x)$	current density inside membrane in x-direction
$j_i^{\text{inst}}(x)$	instantaneous current density
j_i^{stat}	steady-state current density
k	Boltzmann constant
m	(index) is used in Sec. 2 to denote the independent diffusion currents
$n^<$	ionic strength of electrolyte at $x = -\infty$
n_i	density of ions inside membrane
$n_i^{\gtrless}$	density of ions outside membrane at $x = \pm\infty$, respectively
$Q^{\gtrless}$	charge per unit area of boundary layers at $x \gtrless \pm d$, respectively
Q_0	fixed charge per unit area of membrane
q	elementary charge
q_i	ionic charges
T	temperature
t	time
V	membrane potential ($= \psi(-\infty) - \psi(\infty)$)
V_i	Nernst potential
$V^{\gtrless}$	potential drops inside boundary layers (can be neglected, see Appendix II)
$V^{\pm}$	potential steps at $x = \pm d$, cf. Equation (29)
V_0	$= V^- - V^+$
w_i	activation energy inside membrane
x	spatial coordinate perpendicular to membrane

y, z	spatial coordinates parallel to membrane
ε	dielecric constant
ε_0	dielectric constant of electrolyte solution ($\sim$ 80)
ε_m	dielectric constant of membrane ($\sim$ 5)
$\psi(x)$	electrostatic potential
$\varrho^{\gtrless}$	charge density of boundary layers
ϱ_0	fixed charge density inside membrane
$\langle\,\rangle$	spatial average, cf. Equation (12)

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Note added in proof: We remind that the experimentally observed reversal potentials do not in general correspond to Nernst potentials of single ionic species but rather to some average weighted according to the specificity of the different types of conduction channels.