A THERMODYNAMIC ANALYSIS OF FLUXES AND FLUX-RATIOS IN BIOLOGICAL MEMBRANES

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ABSTRACT Flux and flux-ratio equations are derived on the basis of the phenomenological equations of irreversible thermodynamics. Deviations of flux-ratios from that given by the often quoted Ussing (1949) relation are predicted, even in the absence of active transport, by considering the dependence of coupled fluxes on the membrane potential. The treatment is extended to include the interpretation of fluxes measured with tracers. Estimation of the numerical values of the resistance coefficients show that the voltage dependence of the entrainment terms can adequately account for the departures from the Ussing relation and the discrepancies between isotopically and electrically measured membrane conductances.

INTRODUCTION

The flux-ratio equation of Ussing (1949) has been used extensively to determine the presence of active transport across cell membranes.

Deviations from the "normal" flux-ratios have been reported by Keynes (1955) and Hope and Walker (1965) amongst others. Meares and Ussing (1959) re-examined the flux-ratio equation to take into account frictional drag due to the movement of other materials through the membrane.

More recently Hoshiko and Lindley (1964) and Kedem and Essig (1965) have provided a derivation of the flux-ratio equation on the basis of the phenomenological equations of irreversible thermodynamics. These authors have provided an expression which shows that even for the case when no active transport occurs the usual flux-ratio equation may not be applicable.

The present treatment extends the work of these authors to obtain a general flux-ratio equation in a particularly simple form. Deviations from normal flux-ratios are obtained by considering the dependence of the coupled fluxes on membrane potential. In this way the experimental results can be interpreted directly in terms of the theory.

The treatment is also extended to obtain expressions for the ratio of fluxes estimated with tracers. It is shown that this introduces an additional correction term in the flux-ratio equation as has already been pointed out by Kedem and Essig (1965).

THE FLUX EQUATION

The system to be considered consists of two compartments separated by a membrane which extends from $x = 0$ (the internal boundary) to $x = \delta$ (the external boundary).

It will be assumed that there are no temperature gradients. All fluxes are taken to be in the x direction only (i.e. normal to the membrane).

In the membrane, in the steady state, the net force on any species is zero. That is, the driving force on a substance is balanced by frictional forces.

Thus
$$F_j = \sum_i^n F_{ij} = 0 \tag{1}$$

or
$$F_{jj} = -\sum_{i \neq j} F_{ij} \tag{2}$$

where F_{jj} is the conservative or driving force per mole. F_{ij} is the frictional or dissipative force per mole of j, due to the relative velocity, V_{ji}, between species j and i. The summation in equation 2 includes the membrane component, i.e. the frictional force exerted by the membrane.

The usual assumption concerning the linear relationship between F_{ij}, C_i, and V_{ji} is now applied to give

$$F_{jj} = -\sum_{i \neq j} F_{ij} = \sum_{i \neq j} C_i R_{ij} V_{ji} \tag{3}$$

where R_{ij} is a resistance coefficient. Taking velocities relative to the membrane (subscript m) yields

$$V_{ji} = V_{jm} - V_{im}\,.$$

Substitution of the gradient of the electrochemical potential for $(-F_{jj})$ then yields

$$-\text{grad}\ \mu_j = \sum_{i \neq j} C_i R_{ij} (V_{jm} - V_{im}) \tag{4}$$

and since $\phi_j = C_j V_{jm}$, then

$$-\text{grad}\ \mu_j = +\frac{\phi_j}{C_j} \sum_{i \neq j} C_i R_{ij} - \sum_{i \neq j} R_{ij} \phi_i \tag{5}$$

$$= -\sum_i^n R_{ij} \phi_i \tag{6}$$

where R_{jj} has been defined by

$$R_{jj} = -\sum_{i \neq j} \frac{C_i}{C_j} R_{ij}. \tag{7}$$

The Onsager reciprocal relation applies to R_{ij} in equation 6 i.e.

$$R_{ij} = R_{ji}.$$

The derivation of equation 5 follows closely that of Nims (1961). Equation 5 can be rearranged to give

$$\phi_j = C_j \frac{[-\text{grad}\, \mu_j + \sum_{i \neq j} R_{ij}\phi_i]}{\sum_{i \neq j} C_i R_{ij}}. \tag{8}$$

The electrochemical potential μ_j, is given by

$$\mu_j = \mu_{oj} + \text{R}T \ln C_j + \text{R}T \ln \gamma_j + \bar{v}_j P + z_j F \psi. \tag{9}$$

The symbols have their usual meaning (see Glossary). For simplicity it will now be assumed that the activity coefficient γ_j, the coefficients R_{ij}, and the pressure P, are independent of x. The treatment could be performed without these assumptions, but the expressions would take on additional complexity.

With the assumptions above, equation 8 becomes

$$\phi_j = \frac{1}{\sum_{i \neq j} R_{ij} C_i} \left[-\text{R}T \frac{dC_j}{dx} - z_j C_j F \frac{d\psi}{dx} + C_j \sum_{i \neq j} R_{ij} \phi_i \right]. \tag{10}$$

Multiplying both sides of equation 10 by the integrating factor

$$\exp\left\{\frac{z_j F}{\text{R}T}\left(\psi - \sum_{i \neq j} \frac{R_{ij}\phi_i}{z_j F} x\right)\right\}$$

and integrating from $x = 0$ where $\psi = \psi_m$ and $C_j = C_j'$ to $x = \delta$ where $\psi = 0$ and $C_j = C_j''$.

All concentrations refer to values in the membrane; these are related to the external concentrations via the partition coefficient ξ. Hence it follows that,

$$\phi_j = \frac{\text{R}T\left\{C_j' \exp\left[\frac{z_j F \psi_m}{\text{R}T}\right] - C_j'' \exp - \left[\sum_{i \neq j} \frac{R_{ij}\phi_i \delta}{\text{R}T}\right]\right\}}{X_j} \tag{11}$$

where

$$X_j = \int_0^\delta \sum_{i \neq j} R_{ij} C_i \exp \left[\frac{z_j F}{RT} \left(\psi - \sum_{i \neq j} \frac{R_{ij}}{z_j F} \phi_i x \right) \right] dx. \tag{12}$$

THE FLUX-RATIO

Since the net flux of a species is given by

$$\text{Net flux} = \text{efflux} - \text{influx},$$

it has been traditional to regard the two terms in equation 11 as the efflux and influx respectively (Teorell 1949) and in the remainder of this paper this definition of the fluxes will be adopted. The assignment is not unique as some arbitrary expression could be added and subtracted from each term respectively, leading to different expressions for influx and efflux. Indeed Simons[1] obtains a more determinate expression for influx and efflux which allows for the interaction between the unidirectional efflux and influx.

Assuming for the present the validity of the identification of influx and efflux via equation 11 it follows that

$$\ln \left(\frac{\text{influx}}{\text{efflux}} \right) = \ln \frac{C_j''}{C_j'} - \frac{z_j F}{RT} \left[\psi_m + \frac{\sum_{i \neq j} R_{ij} \phi_i \delta}{z_j F} \right]. \tag{13}$$

It is of some interest to note that many of the fluxes ϕ_i in the last term in equation 13 will depend on the membrane potential ψ_m, while at the same time being independent of x. Write

$$\phi_i = f_i(\psi_m). \tag{14}$$

At some particular value of ψ_m, say E_m, influx will equal efflux. From equations 13 with 14,

$$\begin{aligned} E_m &= \frac{RT}{z_j F} \ln \left(\frac{C_j''}{C_j'} \right) - \sum_{i \neq j} \left[\frac{R_{ij}}{z_j F} f_i(E_m) \delta \right] \\ &= E_j - \sum_{i \neq j} \left[\frac{R_{ij}}{z_j F} f_i(E_m) \delta \right] \end{aligned} \tag{15}$$

where E_j is the Nernst equilibrium potential for species j, from which it follows that the membrane potential for flux equality must differ from the Nernst potential by an amount which depends on the entrainment term. Substitution of equation 15

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[1] Simons, R. G. 1967. Manuscript in preparation.

into 13 gives

$$\ln\left[\frac{\text{influx}}{\text{efflux}}\right] = \frac{z_jF}{RT}\left\{(E_m - \psi_m) + \frac{\delta}{z_jF}\sum_{i\neq j} R_{ij}[f_i(E_m) - f_i(\psi_m)]\right\}. \tag{16}$$

The second term on the right vanishes for $\psi_m = E_m$ and for values of ψ_m near E_m may be expanded as a Taylor's series

$$\frac{\delta}{z_jF}\sum_{i\neq j} R_{ij}[f_i(E_m) - f_i(\psi_m)] = a(E_m - \psi_m) + \cdots, \tag{17}$$

where a is a constant given by

$$a = \frac{\delta}{z_jF}\sum_{i\neq j} R_{ij}\frac{\partial f_i(E_m)}{\partial \psi_m}. \tag{17 a}$$

Substitution of equation 17 into 16 gives, for small values of $(E_m - \psi_m)$:

$$\ln\left[\frac{\text{influx}}{\text{efflux}}\right] = \frac{z_jF}{RT}(1 + a)(E_m - \psi_m). \tag{18}$$

We see that a expresses the effect of entrainment. In the absence of entrainment a is zero and

$$\ln\left[\frac{\text{influx}}{\text{efflux}}\right] = \frac{z_jF}{RT}(E_m - \psi_m), \tag{19}$$

the expression used by Ussing (1949) as the criterion to distinguish between active and passive membrane transport. Departures from the Ussing relation (equation 19) have been reported by Hodgkin and Keynes (1955) and Hope and Walker (1965) both of whom find experimentally that

$$\ln\left[\frac{\text{influx}}{\text{efflux}}\right] = n\frac{z_jF}{RT}(E_m - \psi_m) \tag{20}$$

where n is a constant of order 2.5. Observed departures from the Ussing relation have in the past been interpreted in terms of active transport, in-file pore transmission, etc. It is seen from equation 18 that a simple explanation could be advanced in terms of the voltage dependence of the entrainment term in equation 13. Whether or not this is a reasonable hypothesis depends on the numerical values of the R_{ij} in the membrane, and this will be examined in a later section.

THE MEASUREMENT OF FLUXES AND FLUX-RATIOS BY TRACERS

The only practical way of estimating the efflux or influx of a species is the use of isotopic tracers. It is usually assumed that the labelled and unlabelled species (j^*

and j) are kinetically identical and that

$$\phi_j = \frac{C_j}{C_{j*}}\phi_{j*} \tag{21}$$

where ϕ_{j*} is the isotopic flux estimated by adding tracer to one side of the membrane only. It is therefore of interest to compare the practically estimated influxes or effluxes (equation 21) with the two terms in equation 11. Equation 11 written for the tracer species becomes:

$$\phi_{j*} = \frac{RT\left\{C'_{j*}\exp\left(\frac{z_jF\psi_m}{RT}\right) - C_{j*}''\exp\left(-\sum_{i\neq j*}\frac{R_{ij*}\phi_i\delta}{RT}\right)\right\}}{X_{j*}}. \tag{22}$$

Tracer Estimation of Efflux

For this situation, $C''_{j*} = 0$ and

$$\phi_{j*}\ (\text{efflux}) = \frac{RT\left\{C'_{j*}\exp\left(\frac{z_jF\psi_m}{RT}\right)\right\}}{X_{j*}}. \tag{23}$$

In general $X_{j*} \neq X_j$ since the summation in expression 12 in the one case excludes C_{j*} and ϕ_{j*} which are small, and in the other C_j and ϕ_j which are much larger. Comparison of equation 23 with the first term in equation 11 gives

$$\phi_j\ (\text{efflux}) = \frac{X_{j*}}{X_j}\left[\frac{C_j'}{C'_{j*}}\phi_{j*}^{(\text{efflux})}\right]. \tag{24}$$

Thus the use of equation 21 to determine the efflux as defined, is in error by the factor X_{j*}/X_j.

Tracer Estimation of Influx

For this case, $C_{j*}' = 0$, and from equation 22

$$\phi_{j*}(\text{influx}) = RT\,\frac{C_{j*}''\exp\left[-\sum_{i\neq j*}\frac{R_{ij*}\,\phi_i\,\delta}{RT}\right]}{X_{j*}}. \tag{25}$$

From equations 11 and 25 we obtain

$$\phi_j(\text{influx}) = \frac{X_{j*}\exp\left[-\sum_{i\neq j}\frac{R_{ij}\,\phi_i\,\delta}{RT}\right]}{X_j\exp\left[-\sum_{i\neq j*}\frac{R_{ij*}\,\phi_i\,\delta}{RT}\right]}\,\frac{C_j''}{C_{j*}''}\,\phi_{j*}^{(\text{influx})} \tag{26}$$

Equation 26 may be simplified using the facts that $R_{ij*} = R_{ij}$ and $R_{ij} = R_{ji}$. Hence,

$$\phi_j(\text{influx}) = \frac{X_{j*}}{X_j} \exp\left[\frac{\delta R_{jj*}\, \phi_j^{(\text{net})}}{RT}\right] \frac{C_j''}{C_{j*}''}\, \phi_{j*}^{(\text{influx})}. \tag{27}$$

At the resting potential $\psi_m = E_m$ and $\phi_j^{(\text{net})} = 0$ and

$$\phi_j(\text{influx}) = \frac{X_{j*}}{X_j} \frac{C_j''}{C_{j*}''}\, \phi_{j*}^{(\text{influx})}. \tag{28}$$

At the resting potential the tracer estimation for influx differs from the Ussing/Teorell value by a factor X_{j*}/X_j similar to that for the effluxes. At other membrane potentials particularly for large depolarizations, $\phi_j^{(\text{net})}$ may become large and must be taken into account.

Estimation of Flux-Ratio by Tracers

From equations 24 and 27 we have

$$\ln\left[\frac{\text{influx}}{\text{efflux}}\right] = \ln\left[\frac{\text{influx}}{\text{efflux}}\right]_{\substack{\text{tracer}\\ \text{estimated}}} + \frac{\delta R_{jj*}\, \phi_j}{RT} \tag{29}$$

and substituting for the flux-ratio proper from equation 13 yields

$$\ln\left[\frac{\text{influx}}{\text{efflux}}\right]_{\substack{\text{tracer}\\ \text{estimated}}} = \ln\frac{C_j''}{C_j'} - \frac{z_jF}{RT}\left[\psi_m + \frac{R_{jj*}\, \phi_j\, \delta}{z_jF} + \sum_{i\neq j} \frac{R_{ij}\, \phi_i\, \delta}{z_jF}\right]. \tag{30}$$

Equation 30 for the flux-ratio estimated with tracers and calculated using the usual equation (21) is therefore formally different from that given by equation 13. If as before we make the substitution (14), we find that instead of equation 18 we obtain

$$\ln\left[\frac{\text{influx}}{\text{efflux}}\right]_{\substack{\text{tracer}\\ \text{estimated}}} = \frac{z_j F}{RT}\,(1 + a')\,(E_m - \psi_m) \tag{31}$$

where instead of equation 17 *a*

$$a' = + \frac{\delta}{z_jF}\left[\sum_{i\neq j} R_{ij} \frac{\partial}{\partial\psi}\,[f_i(E_m)] + R_{jj*} \frac{\partial}{\partial\psi}\,[f_j(E_m)]\right]. \tag{32}$$

NUMERICAL VALUES OF R_{ij}

Ion-Membrane Resistance Coefficient, R_{mj}

An estimate of the order of magnitude of the R_{mj} values can be obtained from observed values of the electrical resistance of the membrane. An average value for this is 1000 ohm cm^2 corresponding to a conductance, G, given by

$$G = 10 \text{ mho m}^{-2}. \tag{33}$$

The conductance of a species j may also be expressed in terms of the mobilty, u_j, of that species. Thus

$$G_j = z_j u_j C_j F/\delta. \tag{34}$$

The mobility in turn satisfies the Einstein relation

$$u_j = \frac{FD_j}{\mathrm{R}T}$$

where D_j is the diffusion constant for the species j. Inspection of equation 10 reveals that u_j must satisfy the relation

$$u_j = \frac{F}{\sum_{i \neq j} C_i R_{ij}}$$

For dilute solutions, or when the membrane makes a dominating contribution in the summation in the denominator above, u_j will be essentially constant, as is usually assumed. In this case,

$$u_j = \frac{F}{C_m R_{mj}} \text{ approx.} \tag{35}$$

Comparison of equations 35 and 34 gives

$$R_{mj} = \frac{Z_j F^2 C_j}{C_m G_j \delta}. \tag{36}$$

C_j refers to the concentration in the membrane; i.e. with above-assumed external concentration of 100 mole m^{-3}

$$C_j = 100\, \xi \text{ mole m}^{-3} \tag{37}$$

where ξ is the partition coefficient. From equations 33, 36, and 37 we find

$$R_{mj} \sim 10^{16}\, \xi \text{ MKS}. \tag{38}$$

since C_m, the concentration of membrane molecules is 10^3 mole m^{-3} from the known density and average molecular weight of membrane lipoid. Values of $\xi \sim 10^{-4}$ are usually quoted for the bulk-phase partition coefficient in oil. Because of the finite distance over which the oil-water partition coefficient is established at an interface, and the very small thickness of the membrane, it is likely that the effective value of ξ will be closer to unity. The actual value is not known. However, for later comparison of R_{mj} with other resistance estimates, the uncertainty associated with the unknown value of the partition coefficient may be avoided by estimating the total resistance *per mole* of solute j. From equation 35 this is given by F/u_j or

$$\text{Membrane resistance/mole} = C_m R_{mj} = 10^{19}\,\xi \text{ MKS.} \tag{39}$$

Ion-Ion Resistance Coefficient, R_{ij}

The order of magnitude of R_{ij} required to give the necessary value to the entrainment term may be estimated from equation 17 a. In making this estimate, we assume for simplicity that all R_{ij} have a similar magnitude $\overline{R_{ij}}$. Comparison of equation 20 with 18 shows that,

$$(1 + a) \sim 2.5$$

or

$$a \sim 1.5. \tag{40}$$

Thus from equation 17 a

$$a = \frac{\delta}{z_j F} \overline{R_{ij}} \sum_{i \neq j} \frac{\partial f_i}{\partial \psi_m} = 1.5. \tag{41}$$

Note that in equation 41 R_{mj} must not be included because $f_m = 0$. Now G (the total conductance) is given by

$$G = G_{\mathrm{K}} + G_{\mathrm{Na}} + G_{\mathrm{Cl}} \text{ etc.}$$

Thus

$$\sum_{i \neq j} \frac{\partial f_i}{\partial \psi_m} = \sum_{i \neq j} \frac{G_i}{|z_i| F}. \tag{42}$$

For the flux-ratio, of say potassium ions, the summation in the expression for a (equation 17 a) excludes the term $\partial f_{\mathrm{K}}/\partial \psi_m$ (i.e. G_{K}/F) which could in some cases be the dominant term.

However when tracer interaction is taken into account the flux ratio is given by equation 31 and a' now includes the contribution from the conductances of all ions except the tracer ions.

For this case

$$\sum_{i \neq j^*} \frac{\partial f_i}{\partial \psi_m} \sim \frac{G}{F} = 10^{-4}. \tag{43}$$

Substituting equation 43 in 41 with $\delta = 10^{-8}$ m we get

$$\overline{R_{ij}} = \frac{1.5F}{\delta G/F} \sim 10^{17} \text{ MKS.} \tag{44}$$

As with R_{mj}, a more meaningful numerical comparison can be made in terms of the resistance per mole of j, i.e. the force/mole at unit relative velocity. From equation 3 this is $C_i R_{ij}$ and using equation 37,

$$\text{Ion-ion resistance/mole} = 100\,\xi\,\overline{R_{ij}} = 10^{19}\,\xi\ \text{MKS} \tag{45}$$

By comparison of equations 39 and 45, the ion/membrane and the ion/ion resistances are seen to be of similar order of magnitude, independent of the value of the partition coefficient. Thus the voltage dependence of the entrainment term in equation 13 provides a possible explanation of the observed departures from the expression for the flux-ratio equation (19).

DISCUSSION

The experimental results of Hodgkin and Keynes (1955) and Hope and Walker (1965) show that the flux-ratio, as measured with tracers, is given by

$$\ln\left[\frac{\text{influx}}{\text{efflux}}\right] = n\,\frac{z_j F}{RT}\,(E_m - \psi_m) \tag{46}$$

where n is a constant of order 2.5. Indirect evidence that this is the form of the flux-ratio comes from the measurement of the electrical conductivity of the membrane. From the flux-ratio equation (46) it follows that,

$$G_j = n\,\frac{F^2 z_j^2}{RT}\,\phi_j \tag{47}$$

where ϕ_j is the influx or efflux at the cross-over potential. The total conductance due to the fluxes of all charged species is then given by

$$G = \sum G_j. \tag{48}$$

Measurements of conductivity reported by Keynes (1954), and Williams, Johnston, and Dainty (1964) again show that $n > 1$.

Using the value of $a = 1.5$ (equation 40) in equation 17 yields

$$\sum_{i \neq j} R_{ij}\,[f_i(E_m) - f_i(\psi_m)] = \frac{1.5\,z_j F}{\delta}\,(E_m - \psi_m). \tag{49}$$

Substitution of equation 49 into 10 gives,

$$\phi_j = \frac{1}{\sum_{i \neq j} C_i R_{ij}} \left\{ -RT\,\frac{dC_j}{dx} - z_j C_j F \left[\frac{d\psi}{dx} - \frac{1.5}{\delta}\,(\psi_m - E_m) - \sum_{i \neq j} \frac{R_{ij} f_i(E_m)}{F z_j} \right] \right\}. \tag{50}$$

In equation 50 the last term, as well as 1.5 E_m/δ, is constant. Put their sum equal to b. Then,

$$\phi_j = \frac{1}{\sum\limits_{i \neq j} C_i R_{ij}} \left[-RT \frac{dC_j}{dx} - C_i z_i F \left(\frac{d\psi}{dx} - \frac{1.5\psi_m}{\delta} + b \right) \right]. \tag{51}$$

In equation 51, ψ_m/δ is the mean field strength and the equation shows that, at least for values of ψ_m near E_m, the effect of coupled flows is to add to the local field $d\psi/dx$, an additional field which is $\sim$1.5 times the mean field plus a constant field which is independent of the applied field.

Physically the former would be the drag of other charged ions on the species j, while the latter would be due to the drag of neutral molecules.

This latter effect was discussed by Dainty, Croghan, and Fensom (1963). They pointed out that the flow of water due to electro-osmosis when a current is flowing would increase the conductance due to an increase in the ion mobility (i.e. a drag effect).

The above analysis is of course only valid for membrane potentials near the cross-over value, E_m. For larger values of $(E_m - \psi_m)$ higher order terms in the Taylor's expansion (equation 17) would need to be retained in which case ln [influx/efflux] would become a non-linear function of $(E_m - \psi_m)$.

When the flux-ratio is estimated from tracer data, the discussion above is equally applicable provided that equation 32 is used in place of 17.

Reference to equation 32 shows that if all the metabolic flows were absent (e.g. when metabolic inhibitors are used) the factor $(1 + a') \neq 1$ since the flows of other charged ions and the isotope interaction term $R_{jj^*}f_j(E_m)$, will be present as long as $\psi_m \neq E_m$.

At this stage it should be emphasized again that influx and efflux have been defined in terms of the generally accepted terminology of Teorell (1949). Recently Simons (1967) has questioned this concept and has formulated an alternative concept of unidirectional fluxes. The treatment as presented here however is applicable to experimentally measured data.

CONCLUSIONS

From the work described in this paper the following conclusions may be drawn:

(*a*) Due to the interactions between the molecules passing continually through cell membranes, equality of influx and efflux for a given species occurs at a value of membrane potential different from the Nernst potential, equation 15.

(*b*) The voltage dependence of the entrainment term gives a departure of the logarithm of the (influx/efflux) ratio from that given by Ussing and Teorell by a factor $(1 + a)$ where a can be of order unity. (Equations 18, 32.)

(*c*) "Active transport" in the traditional sense can therefore be explained by the entrainment of a particular species by the influx of metabolites and efflux of metabolic products necessary for the maintenance of the living state.

(*d*) Tracer fluxes of a species j differ from Teorell fluxes (equations 21, 24, 28), the difference in the flux ratio being a factor

$$\exp \frac{R_{jj^*}\phi_j(\text{net})}{\mathrm{R}T}.$$

(*e*) The tracer entrainment term is $(1 + a')$ where $a' \neq a$, and the difference for some ions, e.g. potassium, under certain conditions could be significant.

(*f*) The average ion-ion resistance in the membrane R_{ij}, and the average ion-membrane resistance R_{mj}, are both estimated to be $10^{19}\ \xi$ MKS approximately, where ξ is the membrane partition coefficient.

GLOSSARY

C_i', C_i''	Concentrations of species i at the inner and outer membrane boundaries.
C_i	Concentration of species i in moles/liter, in the membrane.
E_m	Membrane potential at flux equality.
E_i	Nernst equilibrium potential for species i.
F	Faraday's number.
P	Pressure.
R_{ij}	Resistance coefficient coupling the force on i with the flux of j.
R	Universal gas constant.
T	Absolute temperature.
V_{ij}	Relative velocity of j with respect to i.
z_i	Valency of ion species i.
γ	Activity coefficient.
μ_{oi}	Standard chemical potential of i.
μ_i	Electrochemical potential of i.
$\bar{v}$	Partial molar volume.
ψ	Electrical potential.
ϕ_i	Flux of species i.

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