GENERAL CONTINUUM ANALYSIS
OF TRANSPORT THROUGH PORES

II. NONUNIFORM PORES

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ABSTRACT   A general continuum derivation of the nonelectrolyte (J_s) and volume (J_v) flux through a pore whose cross section is a function of axial position (nonuniform) is given. In general, the flux equations cannot be reduced to the same form as for a uniform pore and it is not possible to characterize the pore kinetics by three constants as in the uniform pore case. However, it is shown that under certain conditions, the nonuniform pore equations can be approximated by the uniform pore form and can be characterized by three constants ($\bar{\omega}, \bar{\sigma}, L_p$). The only condition needed to reduce the J_v equation to the uniform form is that the solution be dilute. The deviation of the J_s equation from the uniform form is characterized by an asymmetrical function of J_v whose maximum value is estimated. It is shown that the maximum possible fractional deviation of the J_s equation from the uniform form is given by the parameter: $0.5\bar{\sigma}J_v/\bar{\omega}RT$. Since this parameter is less then 0.15 for most membrane studies, the nonuniform J_s equation can usually be approximated by the uniform pore form. The general results are illustrated by explicit calculations on several models of nonuniform pores. It is shown, for example, that the "equivalent pore radius" defined in the usual way is a function of the experimental parameter that is measured and is not unique.

INTRODUCTION

It was shown in the first paper (I) of this series (Levitt, 1975) that, if the assumptions of continuum hydrodynamics are used, then the solute (J_s^0) and volume (J_v^0) flux through a pore with a uniform cross section (indicated by superscript "0") can be described by the following equations:

$$J_s^0 = (1 - \sigma)J_v(c_2 e^\kappa - c_1)/(e^\kappa - 1); \quad \kappa = -(1 - \sigma)J_v/\omega RT \qquad (1)$$

$$J_v^0 = L_p(\Delta p - \sigma RT \Delta c), \qquad (2)$$

where ω and L_p are the diffusive and hydraulic permeability. (The notation is defined in paper I.) It was also shown that the reflection coefficient (σ) that appears in Eq. 1 is identical to the σ in Eq. 2. Eqs. 1 and 2 provide a theoretically rigorous description of the pore kinetics in terms of three parameters (ω, σ, L_p) which are characteristic

of the pore and do not depend on the volume flux or the bulk concentrations (if the solution is dilute).

However, since most biological or artificial membranes which have pores large enough for the continuum description to be applicable do not have pores with a uniform cross section, it is important to determine whether nonuniform pores can also be described by Eqs. 1 and 2. For the case of two membranes in series (a special case of a nonuniform pore) it has been shown that, in general, the kinetic equations are very complicated and that the membrane parameters become functions of J_v and the bulk concentrations (Patlak et al., 1963). For example, the membrane parameters depend on the direction of J_v (rectification). The complexity is, of course, greater for the general case where the pore has a continuously varying cross section than it is for the special case of two uniform pores in series. However, it will be shown in this paper that these complex equations reduce to the simple and useful form of Eqs. 1 and 2 under either of the following conditions: (*1*) the volume flux is small enough, or (*2*) the pore is large enough. In fact, it will be shown that if the pore is large enough for the continuum description to be valid, then the membrane kinetics can usually be well approximated by Eqs. 1 and 2 with the three parameters functions only of the pore structure.

In the first section of the paper the general results will be derived and the reduction of the general equations to the form of Eqs. 1 and 2 will be described. This derivation requires only a small extension of the methods that were previously used for the uniform pore. In the second section, these results will be discussed and illustrated by the use of three examples. Although the derivation in section I is somewhat involved, the final results can be simply expressed and will be summarized in section II.

I. DERIVATION OF GENERAL RESULTS

The presence of the varying pore cross section introduces a small modification of the form of the drag equation that was derived for the uniform pore (I). While the uniform pore could be characterized by the parameter $\lambda = a/R_p$, (where a and R_p are the solute and pore radius, respectively) it is necessary to use a function of $x(f(x) = R_p(x)/a)$ to characterize the nonuniform pore. Also, the average velocity of the water ($\overline{V}$) becomes a function of x and is described by:

$$\overline{V}(x) = \overline{V}_w J_w/\pi R_p^2(x), \tag{3}$$

where $\overline{V}_w J_w$ is the average volume flux of water and does not depend on x. With these modifications, the form of the drag equation becomes:

$$D = \eta a H_f(\beta,x)[U - G_f(\beta,x)\overline{V}(x)], \tag{4}$$

where the subscript f indicates that H and G depend on the total function $f(x)$ and the rest of the notation is the same as in the preceding paper (Levitt, 1975).

J_s Equation

The derivation follows the same general procedure that was used in the first paper of this series for the uniform pore (Levitt, 1975). That paper should be consulted for details and the definition of symbols. Equating the drag to the gradient of the chemical potential and solving for J_s:

$$J_s = \int_0^{R_p-a} cU(x,\beta)\,d\beta = A(x)\frac{dc}{dx} + B(x)J_vc,$$

$$A(x) = -2\pi akT\eta^{-1}\int_0^{f-1} H_f^{-1}\beta d\beta,$$

$$B(x) = 2f^{-1}\int_0^{f-1} G_f\beta d\beta, \tag{5}$$

where $\bar{V}_wJ_w$ has been approximated by the total volume flux J_v.[1] Eq. 5 is of the same form as was found for the uniform pores except that A and B are now functions of x. It is a linear first order differential equation which has the exact solution:

$$c(x) = J_s e^{-g(x)}\int_0^x e^{g(\alpha)}A^{-1}d\alpha + c_1 e^{-g(x)}$$

$$g(x) = J_v\int_0^x BA^{-1}d\alpha, \tag{6}$$

where c_1 is the bulk concentration on side 1. Setting $c(L)$ equal to c_2 and solving for J_s:

$$J_s = (c_2 e^{g(L)} - c_1)/\int_0^L e^{g(x)}A^{-1}dx. \tag{7}$$

This is the general solution and cannot be simplified. However, by the use of one additional restriction, Eq. 7 can be reduced to a simpler form as follows: Write $B(x)$ as:

$$B(x) = \tilde{B}[1 - b(x)] \tag{8}$$

$$\tilde{B} = s(L)^{-1}\int_0^L BA^{-1}dx; \quad s(x) = \int_0^x A^{-1}(\alpha)\,d\alpha.$$

It follows from this definition that:

$$\int_0^L bA^{-1}dx = 0. \tag{9}$$

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[1] One must be careful about making this approximation in the derivation of the J_v equation (Eq. 2) since it can introduce a large error for the case where J_v approaches zero and $J_s \neq 0$. However, since J_v enters the J_s equation as an additive convective term which is unimportant for the case where J_v approaches zero and $J_s \neq 0$, no significant error is introduced by the use of this approximation in the derivation of the J_s equation.

Also, if B is a constant, than $\tilde{B} = B$ and $b(x) = 0$.

Substituting Eq. 8 into the definition of $g(L)$ (Eq. 6):

$$g(L) = J_v \tilde{B} s(L). \tag{10}$$

The denominator in Eq. 7 can be simplified if it is assumed that:

$$\tilde{B} J_v \int_0^x b A^{-1} d\alpha < \approx 0.3 \tag{11}$$

so that the exponential can be expanded as follows:

$$\int_0^L e^g A^{-1} dx = \int_0^L e^{J_v \tilde{B} s} e^{-J_v \tilde{B} \int_0^x b A^{-1} d\alpha} A^{-1} dx$$

$$\approx \int_0^L e^{J_v \tilde{B} s} A^{-1} dx - J_v \tilde{B} \int_0^L e^{J_v \tilde{B} s} \left[\int_0^x b A^{-1} d\alpha \right] A^{-1} dx. \tag{12}$$

It will be shown below that the inequality expressed by Eq. 11 is satisfied in most membrane studies. Since the derivative of $s(x)$ is equal to $A(x)^{-1}$, the first integral in Eq. 12 is exact and the second can be integrated by parts:

$$\int_0^L e^g A^{-1} dx \approx J_v^{-1} \tilde{B}^{-1} [e^{J_v \tilde{B} s(L)} - 1] - e^{J_v \tilde{B} s(L)} \int_0^L b A^{-1} dx + \int_0^L e^{J_v \tilde{B} s} b A^{-1} dx, \tag{13}$$

where the second term on the right is zero (Eq. 9). Substituting Eqs. 10 and 13 into Eq. 7 and rearranging the J_s equation can be written in the form:

$$J_s = J_s^0(c_1, c_2, J_v)/(1 + Q(J_v))$$

$$Q(J_v) = J_v \int_0^L e^{J_v \tilde{B} s} b A^{-1} dx/(e^{J_v \tilde{B} s(L)} - 1) \tag{14}$$

and where J_s^0 is given by Eq. 1 and has the same functional form as for the uniform pore with an average $\bar{\omega}$ and $\bar{\sigma}$ defined by:

$$1/\bar{\omega} = -RT s(L), \quad \bar{\sigma} = 1 - \tilde{B}. \tag{15}$$

By analogy with the case for the uniform pore, the local permeability ($\omega(x)$) and local reflection coefficient ($\sigma(x)$) can be defined as follows:

$$\omega(x) = -A(x)/RT, \quad \sigma(x) = 1 - B(x). \tag{16}$$

Substituting these definitions into the expressions for ω, σ, and b (Eqs. 8, 15):

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$$1/\bar{\omega} = \int_0^L \omega(x)^{-1}\,dx; \quad \bar{\sigma} = \bar{\omega} \int_0^L \omega(x)^{-1}\sigma(x)\,dx; \quad b = (\sigma(x) - \bar{\sigma})/(1 - \bar{\sigma}).$$

$$(17)$$

It is easy to show that if c_1 and c_2 are interchanged and the sign of J_v is reversed, then the sign of J_s^0 is also reversed. Thus J_s^0 is symmetrical and all the assymmetry that leads to rectification of J_s is in $Q(J_v)$. Since Q is a complicated function which cannot be easily evaluated, the main advantage of the decomposition of J_s in Eq. 14 is that it provides a simple estimate of the deviation of J_s from J_s^0 and a criterion for when J_s can be approximated by J_s^0. Q can be written in the form:

$$Q(J_v) = J_v \int_0^L e^{\kappa s(x)/s(L)} bA^{-1}\,dx/(e^\kappa - 1)$$

$$\kappa = -(1 - \bar{\sigma})J_v/\bar{\omega}RT.$$

$$(18)$$

The parameter κ is a measure of the importance of the convective transport $((1 - \bar{\sigma})J_v)$ relative to the diffusive $(\bar{\omega}RT)$. For most membrane studies κ is less than one and it can be made as small as one wishes by controlling J_v. In the appendix, the value of κ is estimated for a uniform pore for the case where there is just one solute present and J_v is obtained from Eq. 2 ($\Delta p = 0$). It is shown, for example, that for a glucose concentration difference across the membrane as large as 0.2 molar, κ will be less than 0.3 for any pore that is large enough to allow the use of continuum theory. If κ is small (less than about 0.3) then the exponential in Q can be expanded and a maximum estimate of Q obtained $(s(x) < s(L))$:

$$Q(J_v) \approx \frac{J_v}{e^\kappa - 1} \int_0^L bA^{-1}\,dx + \frac{J_v}{s(L)} \int_0^L s(x)b\,ds < 0.5\,J_v s(L)\,|\,b\,|_{max}$$

$$= 0.5\,\kappa \tilde{B}^{-1}\,|\,b\,|_{max} \approx 0.5\,\bar{\sigma}\kappa/(1 - \bar{\sigma}), \quad (19)$$

where Eq. 9 and the relation $dx = A\,ds$ has been used and it has been assumed in the last equality that the maximum value of b ($|\,b\,|_{max}$) is approximately equal to $\bar{\sigma}$ (see Eq. 17). This inequality (Eq. 19) shows that, for example, if $\kappa = 0.3$ and $\bar{\sigma} < 0.5$ then Q is less than 0.15 so that J_s deviates from J_s^0 by at most 15%. Furthermore, since κ can be controlled (by varying J_v) the deviation of J_s from J_s^0 can be made insignificant. An upper bound can be placed on Q even if κ is not small:

$$Q(J_v) < \frac{J_v\,|\,b\,|_{max}}{e^\kappa - 1} \int_0^L e^{\kappa s(x)/s(L)}\,dx = \frac{|\,b\,|_{max}}{\tilde{B}} = \frac{|\,\sigma(x) - \bar{\sigma}\,|_{max}}{(1 - \bar{\sigma})^2}. \quad (20)$$

Thus even if κ is large Q will be small if $\sigma(x)$ is small (the pore is large) for all values of x.

The reduction of the general equation for J_s (Eq. 7) to the form of Eq. 1 was based on the assumption of the inequality in Eq. 11 which can now be rewritten as:

$$\tilde{B} J_v \int_0^x bA^{-1}\,dx < \kappa |b|_{max} \approx \kappa\bar{\sigma} < 0.3. \tag{21}$$

From the above discussion of the relative size of κ and $\bar{\sigma}$, it is clear that this inequality should be satisfied in most membrane studies.

As in the case of a uniform pore, J_s^0 for a nonuniform pore can be written in the form:

$$J_s^0 = \bar{\omega}RT\Delta c + (1 - \bar{\sigma})\tilde{c} J_v. \tag{22}$$

However, as will be shown below, $\tilde{c}$ is no longer equal to $\bar{c}$ (the mean integrated concentration) as is true for a uniform pore. Rather, $\tilde{c}$ is simply defined by setting Eq. 22 equal to Eq. 1 and solving for $\tilde{c}$:

$$\tilde{c} = (c_2 e^\kappa - c_1)/(e^\kappa - 1) + \Delta c/\kappa. \tag{23}$$

Expanding the exponentials in Eq. 23 the following approximation to $\tilde{c}$ is obtained:

$$\tilde{c} \approx (c_1 + c_2)/2 + \kappa(c_2 - c_1)/12. \tag{24}$$

Eqs. 23 and 24 for $\tilde{c}$ are identical to the uniform pore expression for $\bar{c}$ (Levitt, 1975). Eq. 24 differs from the exact result (Eq. 23) by less than 5% for absolute values of κ as large as ± 2.5. It is easy to show that for a nonuniform pore $\tilde{c}$ does not equal $\bar{c}$. Consider the case where $J_v = 0$ ($\kappa = 0$) so that $\tilde{c} = (c_1 + c_2)/2$ exactly. However, for $J_v = 0$, $\bar{c}$ equals (see Eq. 5):

$$\bar{c} = L^{-1} \int_0^L c(x)\,dx = c_1 + L^{-1}\bar{\omega}RT\Delta c \int_0^L dx \int_0^x A^{-1}(\alpha)\,d\alpha, \tag{25}$$

and $\bar{c}$ may differ greatly from $\tilde{c}$ if A is not a constant.

J_v Equation

The derivation follows exactly the same procedure as for the uniform pore case up to the point of the evaluation of the sum (see paper I, Eq. 43 [Levitt, 1975]):

$$\sum_i \int_{S_i} V^0 \cdot \Pi \cdot ds = -\sum_i G_f \nabla D_i + \eta R_p \nabla^2 J_f,$$

where the sum is over all the solute molecules in the pore and D_i is the drag on the ith molecule. As in the case of a uniform pore, the second term on the right contributes a small concentration dependent term to L_p which can be neglected if the solution is dilute. Substituting the gradient of the chemical potential (neglecting the Δp term) for D and converting the sum to an integral over the pore volume weighted by the concentration:

$$\sum_i \int_{S_i} V^0 \cdot \Pi \cdot ds = -RT \int_0^L \bar{V}(x) \frac{dc}{dx} \int_0^{R_p - a} 2\pi b \, G_f db$$

$$= -RT\bar{V}_w J_w \int_0^L B(x) \frac{dc}{dx} dx. \tag{25}$$

Writing B in the form of Eq. 8:

$$\sum_i \int_{S_i} V^0 \cdot \Pi \cdot ds = RT\bar{V}_w J_w \tilde{B} \Delta c + RT\bar{V}_w J_w \tilde{B} \int_0^L b \frac{dc}{dx} dx. \tag{26}$$

Solving Eq. 5 for dc/dx and substituting into Eq. 26 (using Eq. 9):

$$\sum_i \int_{S_i} V^0 \cdot \Pi \cdot ds = RT\bar{V}_w J_w \tilde{B} \Delta c - RT(\bar{V}_w J_w)^2 \tilde{B}^2 \int_0^L b(1-b) A^{-1} c \, dx. \tag{27}$$

Manipulating Eq. 27 in exactly the same manner as for the uniform pore (see paper I, Eq. 55 [Levitt, 1975]), the J_v equation is obtained:

$$J_v = \bar{L}_p(\Delta p - \bar{\sigma} RT \Delta c); \quad \bar{\sigma} = 1 - \tilde{B}$$

$$\bar{L}_p = \bar{L}_p^0/(1 + M(c)); \quad M(c) = RT \tilde{B}^2 \bar{L}_p^0 \int_0^L b(1-b) A^{-1} c \, dx. \tag{28}$$

Thus the $\bar{\sigma}$ in the J_v equation is identical to the $\bar{\sigma}$ in the J_s^0 part of the J_s equation. $\bar{L}_p^0$ is the hydraulic permeability of the nonuniform pore when no solutes are present. M is a concentration-dependent term which arises from the second term in Eq. 27. An upper bound for M can be obtained as follows:

$$M < RT \tilde{B}^2 \bar{L}_p^0 |b|_{max} c_{max} \int_0^L A^{-1} dx = \tilde{B}^2 |b|_{max} c_{max} \bar{L}_p^0/\bar{\omega}$$

$$\approx c_{max}(1 - \bar{\sigma})^2 \bar{\sigma} L_p^0/\bar{\omega}. \tag{29}$$

It is shown in the Appendix (Eq. 42) that for a uniform pore:

$$(1 - \bar{\sigma})^2 \bar{\sigma} \bar{L}_p^0/\bar{\omega} < 4\bar{V}_s \quad \text{or} \quad M < 4\bar{V}_s c_{max}. \tag{30}$$

If the solution is dilute, M can be neglected and $L_p = L_p^0$.

II. DISCUSSION AND ILLUSTRATION OF RESULTS

The main results obtained in section I can be briefly summarized: The equations describing the solute and volume flux through a pore with a varying cross section usually can be well approximated by:

$$J_s = J_s^0/(1 + Q(J_v)); \quad J_v = \bar{L}_p(\Delta P - \bar{\sigma} RT \Delta c)$$

$$1/\bar{\omega} = \int_0^L \frac{dx}{\omega(x)}; \qquad \bar{\sigma} = \bar{\omega} \int_0^L \omega(x)^{-1} \sigma(x) \, dx$$

$$\bar{L}_p = \bar{L}_p^0/(1 + M(c)). \tag{31}$$

The functions $\omega(x)$ and $\sigma(x)$ are the "local" permeability and reflection coefficient and are defined by Eqs. 5 and 16. J_s^0 has the same form as for a uniform pore and can be well approximated by:

$$J_s^0 = \bar{\omega} RT \Delta c + (1 - \bar{\sigma}) \tilde{c} J_v,$$

$$\tilde{c} = (c_1 + c_2)/2 + \kappa(c_2 - c_1)/12. \tag{22}$$

Q (Eq. 18) is an asymmetrical function that provides a measure of the deviation of J_s from J_s^0. It is small in most membrane studies. $\bar{L}_p^0$ is the hydraulic permeability of the pore when no solute is present and M is a function of c that can be neglected if the solution is dilute. Thus, the J_s and J_v equations for a nonuniform pore can usually be well approximated by the uniform pore equations with $\bar{\omega}$ and $\bar{\sigma}$ defined by Eq. 31.

In general, $\omega(x)$ and $\sigma(x)$ are functions of $f (= R_p(x)/a)$ and, therefore, they depend on the pore radius ($R_p(x)$) at all values of x, not just the local value. However, in the following examples it will be assumed that, to a first approximation, $\omega(x)$ and $\sigma(x)$ are equal to the corresponding functions for a uniform pore that has the same radius as the local value. That is, the local value of G_f and H_f will be approximated by the uniform pore functions G_λ and H_λ.

Example 1. The pore has a radius of R_1 for $0 < x < L_1$ and R_2 for $L_1 < x < L$ and is equivalent to two uniform pores in series. For this pore:

$$1/\omega = \int_0^{L_1} \omega(x)^{-1} \, dx + \int_{L_1}^L \omega(x)^{-1} \, dx = \omega_1^{-1} + \omega_2^{-1} \quad \text{or}$$

$$\dot{\omega} = \omega_1 \omega_2/(\omega_1 + \omega_2)$$

$$\bar{\sigma} = \bar{\omega}[\sigma_1 \omega_1^{-1} + \sigma_2 \omega_2^{-1}] = (\sigma_1 \omega_2 + \sigma_2 \omega_1)/(\omega_1 + \omega_2), \tag{32}$$

where ω_1, σ_1 and ω_2, σ_2 are the values for the two uniform parts of the pore. This example is identical to the case of two membranes in series that Patlak et al. (1963) solved by the application of the uniform pore equations (1 and 2) to the two parts of the membrane. It is easy to show that for the case where κ is small their general solution reduces to the form of Eq. 31 with $\bar{\omega}$ and $\bar{\sigma}$ defined by Eq. 32.

Example 2. The pore radius varies linearly from a $\lambda(= a/R_p)$ of 0.03 ($\sigma = 0.005$) at $x = 0$ to a λ of 0.3 ($\sigma \approx 0.48$) at $x = L$:

$$a/R_p(x) = \lambda(x) = 0.03 + 0.27 \, x/L; \quad dx = Ld\lambda/0.27. \tag{33}$$

It will be assumed that $\omega(x)$ and $\sigma(x)$ are equal to the corresponding equations for the equivalent uniform pore (neglecting the small "off axis" correction, see I, Eqs. 69, 70)

$$\omega(x)/\omega_0(x) = (1 - \lambda)^2/K_1; \quad \sigma(x) = \frac{16}{3}\lambda^2$$

$$K_1 = (1 - 0.75857\,\lambda^5)/$$
$$(1 - 2.105\,\lambda + 2.0805\,\lambda^3 - 1.7068\,\lambda^5 + 0.72603\,\lambda^6). \quad (34)$$

Substituting $\pi R_p^2 D_0$ for ω_0 and using Eqs. 31 and 33:

$$\pi a^2 D_0/\bar{\omega} = \int_0^L (1 - \lambda)^{-2}\lambda^2 K_1\,dx = \frac{L}{0.27}\int_{0.03}^{0.3}(1 - \lambda)^2\lambda^2 K_1\,d\lambda$$

$$= 0.108\,L, \quad (35)$$

where the integration in Eq. 35 and in the rest of this section has been obtained numerically. Usually, one can only measure the value of $\bar{\omega}$ relative to some other value, for example $\bar{\omega}_0$:

$$a^2\pi D_0/\bar{\omega}_0 = \frac{L}{0.27}\int_{0.03}^{0.3}\lambda^2\,d\lambda = 0.0333\,L. \quad (35)$$

Thus, for the pore described by Eq. 33:

$$\bar{\omega}/\bar{\omega}_0 = 0.308. \quad (36)$$

Similarly, one can determine the value of $\bar{\sigma}$:

$$\bar{\sigma} = \bar{\omega}\int_0^L \omega(x)^{-1}\sigma(x)\,dx = \frac{L}{0.27}\bar{\omega}\frac{16}{3}\int_{0.03}^{0.3}\omega(\lambda)^{-1}\lambda^2\,d\lambda = 0.325. \quad (37)$$

One can also define a $\bar{\lambda}_\omega$ and $\bar{\lambda}_\sigma$ which correspond to the values of λ that would give a uniform pore the same value of $\bar{\omega}/\bar{\omega}_0$ and $\bar{\sigma}$, respectively, as the nonuniform pore. For the results of Eqs. 36, 37, $\bar{\lambda}_\omega = 0.236$ and $\bar{\lambda}_\sigma = 0.247$. These values are different because ω and σ do not have the same functional dependence on λ. One can also define a $\bar{\lambda}_{L_p}$ which corresponds to the similar average for $\bar{L}_p$:

$$\bar{\lambda}_{L_p}^4 = \frac{1}{0.27}\int_{0.03}^{0.3}\lambda^4\,d\lambda \quad \text{or} \quad \bar{\lambda}_{L_p} = 0.206. \quad (38)$$

These values of $\bar{\lambda}$ are the experimental values of λ that one would assign to this pore (Eq. 33) if it was assumed to be uniform. This calculation demonstrates that the experimental value of the "equivalent (uniform) pore radius" is a function of the parameter (ω, σ, L_p) that is measured experimentally.

Example 3. The asymmetry function ($Q(J_v)$; Eq. 18) will be determined for the pore of example 2 (Eq. 33). In order to simplify the calculation $\omega(x)$ will be approximated by $\omega_0(x)$. This approximation should not significantly effect the relative value of Q. Integrating Eq. 18 numerically, it can be shown that for κ of ± 1, Q is ± 0.074. That is, for this relatively large κ the assymetry in J_s is only about 7% for this pore. For κ of ± 4, the assymetry becomes ± 0.24. These errors are significantly less than the maximum estimate obtained in section I (Eq. 19).

CONCLUSION

It was shown in section I that, under rather general conditions, the solute and volume flux through a nonuniform pore can be described by the uniform pore equations 1 and 2 (and $\bar{\omega}, \bar{\sigma}, \bar{L}_p$). Although general relations between $\bar{\omega}, \bar{\sigma}$ and the pore structure were derived, they will not be of much practical use since the actual shape of the pore is not usually known. These results are important, however, because they show that the behavior of a nonuniform pore (i.e. J_s and J_v) can be completely characterized by three parameters that depend only on the pore shape and do not depend on the bulk concentrations or J_v. These parameters ($\bar{\omega}, \bar{\sigma}, \bar{L}_p$) can be determined experimentally from Eqs. 1 (or 22) and 2 by exactly the same procedure that is used for a uniform pore. Since a variety of pore shapes will have the same values of $\bar{\omega}, \bar{\sigma}$ or $\bar{L}_p$, these experimental parameters cannot be used to determine the shape of a nonuniform pore. In fact, as was illustrated in example 2, one cannot even define a unique "equivalent pore radius" for a nonuniform pore.

APPENDIX

Most of the results in the text are based on the assumption that κ (Eq. 18) is "small". In this section the magnitude of κ (and also the inequality appearing in Eq. 30) will be estimated for a uniform pore. The value of κ depends on J_v which, in general, will be affected by the membrane concentration differences of many different solutes (i.e., a sodium gradient established by active transport). However, if only one solute is present (and $\Delta P = 0$), then Eqs. 1 and 2 form a closed set that can be solved exactly:

$$\kappa = -(1 - \sigma)J_v/\bar{\omega}RT = (1 - \sigma)\sigma L_p^0 RT \Delta c/\bar{\omega}RT$$

$$= \sigma(1 - \sigma)L_p^0 \Delta c/\omega. \tag{39}$$

Using the uniform pore approximations for ω and σ (Eq. 34), Poiseuille's law for L_p^0, and $\bar{V}_s = 4/3\pi a^3 N_A$:

$$\kappa = \kappa' \Delta c \bar{V}_s; \quad \kappa' = 3(1 - 16\lambda^2/3) K_1/(1 - \lambda)^2. \tag{40}$$

It will be assumed that the maximum value of λ is 0.3 since this is roughly the upper limit of the validity of the continuum assumptions and the explicit expressions for ω and σ. Thus, κ'

ranges from a limiting value of 3 for $\lambda = 0$ to a maximum of 7.55 for $\lambda = 0.3$. For a glucose concentration difference of 0.2 molar:

$$\kappa < 7.55\,(0.2 \text{ mol/liter})\,(0.18 \text{ liter/mol}) = 0.27 \tag{41}$$

The inequality in Eq. 30 can be similarly evaluated:

$$(1 - \sigma)^2 \sigma L_p^0 / \bar{\omega} = 3(1 - 16\lambda^2/3)^2 K_1 / (1 - \lambda)^2 < 3.9\ \bar{V}_s. \tag{42}$$

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