LETTERS TO THE EDITOR

On an Ion Displacement Membrane Model

Dear Sir:

Since the publication of the Ion Displacement Membrane Model—hereafter referred to as IDM (Hladky and Harris, 1967), I have determined that the equations given are only an approximation of the knock-on case with sites restricted to isolated channels. The following exact interpretation of the equations should replace the first paragraph under Formulation of the Model.

"Suppose that a cation must make $n + 1$ transverse jumps (relative to the membrane) in order to cross from one side to the other. Then the membrane can be thought of as having n layers such that an ion proceeds across by jumping from a site in one layer to a site in an adjacent layer. We assume that $X_{j,i}$ is the probability that the ion displaced by this process is of species j where $X_{j,i}$ is the solute fraction of that species in the ith layer. A cation of a particular species in the ith layer can be displaced from that layer by an ion striking it from either the $(i - 1)$th or the $(i + 1)$th layer. In the former case, i.e. when it is struck from the left, let the probability that it jumps to the right be d. The probability that it jumps to the left will then be $1 - d$. In the latter case, when it is struck from the right, let the probability that it jumps to the left be l and the probability that it jumps to the right be $1 - l$. For simplicity, and in the absence of any better information, we suppose that the jump probabilities, d and l, are the same for each layer."

In addition some minor changes of wording are necessary in the rest of the paper: "layer" for "site" wherever the word "site" is associated with the index i or the number n; "through a given region in the membrane" for "in a given type of channel" (following equation 33); and "using the same sites" for "moving in the same channel" (following equation 34).

There are three errors in the type which were not caught in the proofs. Equations 2 and 21 should read as

$$M'_{j,i} = X_{j,i}[(1 - d)M_{i-1} + lM'_{i+1}] \qquad (2)$$

and

$$M_i/M'_i = M_0 d/[M'_{n+1} d^{-i+1} + M_0(1 - d^{n-i+1})] \qquad (\Delta\varphi > 0), \quad (21)$$

respectively. The subscript on J in equation 14 should be j.

The assumption that $X_{j,i}$ gives the probability that an ion of species j is displaced from layer i assumes that the occupation probabilities for sites are independent of the direction from which an ion is now approaching the site. This condition will be satisfied if ion exchanges within layers are rapid and/or if a sequence of jumps is not restricted to a particular line of sites. The error involved in applying equations 2 and

$$M_{j,i} = X_{j,i}[M_{i-1} d + M'_{i+1}(1 - l)] \qquad (1)$$

to isolated chains of sites is seen most simply by considering several sequences of jumps within the membrane.

Let the electric potential increase towards the right. Then in knock-on displacements, whenever an ion is struck from the right, it will move to the left. In equations 1 and 2, $l = 1$. Let B, C, and D represent typical ions occupying the $(i-1)$th, ith, and $(i+1)$th sites at times when no jumps are occurring in the chain. The following sequences of jumps are then the only types which can lead to an ion entering the ith site (ignoring the possibility of more than one sequence occurring at any one time) (see Fig. 1):

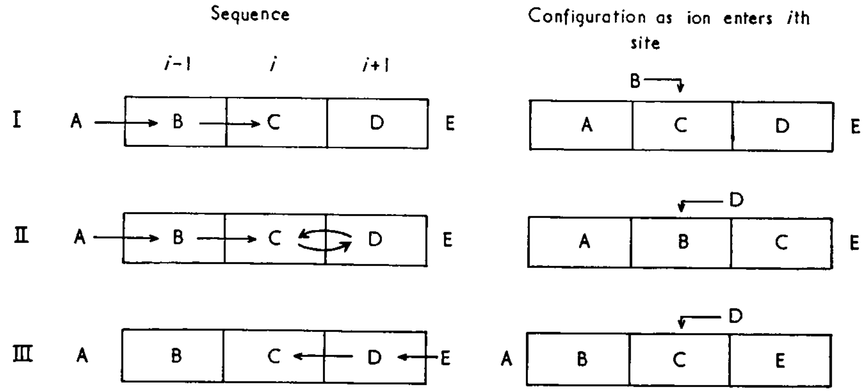

FIGURE 1 See text.

Thus whenever an ion is approaching site i from the left, the site is occupied by an ion typical of that site "at rest," i.e. when no jumps are occurring. By contrast, on some occasions when an ion approaches from the right, the chain will be in the configuration of case II and the ith site will be occupied by an ion typical of the $(i-1)$th site "at rest." The quantity $X_{j,i}$ is no longer well defined. The correct equations to replace 1 and 2 can be written down by noticing that the probabilities of the occurrence of cases II and III, given that an ion is entering site i from the right, are

$$(M_i - M_n)/(M'_{n+1} + M_i - M_n) \tag{3}$$

and

$$M'_{n+1}/(M'_{n+1} + M_i - M_n), \tag{4}$$

respectively. Equations 2 are then replaced by

$$M'_{j,i} = X_{j,i}[(1-d)M_{i-1} + M'_{i+1}M'_{n+1}/(M'_{n+1} + M_i - M_n)] \\ + X_{j,i-1}M'_{i+1}(M_i - M_n)/(M'_{n+1} + M_i - M_n) \tag{5}$$

where the $X_{j,i}$ now refer to sites "at rest." Equations 1 are valid as written for $\Delta\varphi > 0$. In the knock-on case, $l = 1$, equations 9 of IDM immediately yield

$$M_i = M_0 d^i. \tag{6}$$

Hence equations 5 may be rewritten as

$$M'_{j,i} = X_{j,i}[(1-d)M_{i-1} + M'_{i+1}] - (X_{j,i} - X_{j,i-1})M_0(d^i - d^n). \tag{7}$$

Equations 1 and 2 are in error for linear chain knock-on displacement kinetics to the extent that the second term on the right of equations 7 is appreciable. For two special cases, $d = 0$ and $d = 1$, equations 7 reduce to equations 2. Single file diffusion applied to neutral molecules corresponds to $d = 1$.

For knock-loose displacements the situation is somewhat different. Here there is no correlation between the directions of two successive jumps. If we take a time average of the occupancy of a site, this quantity then gives us both $M_{j,i}/M_i$ and $M'_{j,i}/M'_i$. To say the same thing in different words, ions of species j are a fraction, $X_{j,i}$, of the ions displaced in some direction. We know that of these d go towards the right and l towards the left. Thus in this case equations 1 and 2 are correct.

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REFERENCE

HLADKY, S. B., and J. D. HARRIS. 1967. *Biophys. J.* 7:535.

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