LETTER TO THE EDITOR

The Role of pH in the Punch-Through Effect in Frog Skin

Dear Sir:

The electrical characteristic of frog skin displays the property of rectification, and at large hyperpolarizations a nondestructive electrical breakdown occurs (Candia, 1970).

The electrical properties display many of the characteristics of those of a membrane consisting of two fixed-charge lattices, of opposite sign, in contact (Coster, 1965, 1969).

The experimental evidence presented by Candia, when interpreted in terms of the fixed-charge membrane theory, suggests that the double fixed-charge lattice is located at the outer diffusion barrier of the skin.

From the direction of rectification and the punch-through effect the negative fixed-charge lattice must be located on the outer side, and the positive fixed-charge lattice on the inner side, of the outer diffusion barrier of the skin.

Among other effects Candia also reported a dramatic change in the electrical characteristics on bubbling CO_2 through the bathing solution.

In particular, the slope resistances and the membrane potential at breakdown in the extreme hyperpolarizing region (punch-through) increased in the presence of CO_2 (Fig. 9 of Candia, 1970). As suggested by Candia this may be because of a pH effect (the pH changed from 8.6 to 6.2 on bubbling CO_2).

Similar dramatic effects with changes in external pH are observed in the electrical characteristics of the membranes of *Chara australis* (Coster, 1969).

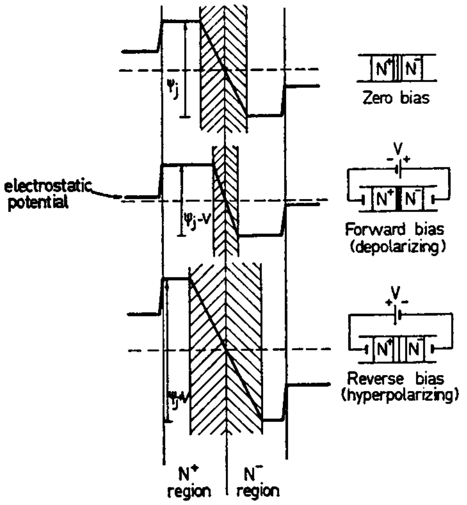
These effects are easily interpreted in terms of the double-lattice fixed-charge model of the membrane. With these membranes punch-through occurs when the central depletion layer, the width of which increases as the membrane is hyperpolarized (see Fig. 1), approaches one or both of the membrane boundaries.

In general, for nonsymmetrical membranes in which the lattices have different widths or have different concentrations of fixed charges, punch-through occurs when the depletion layer in only one of the fixed-charge regions reaches the membrane boundary. In this case punch-through is associated with a large increase in the minority ion conductance of that region. That is, a large increase in either anion conductance if $[N^+] > [N^-]$, or cation conductance if $[N^-] > [N^+]$.

The effect of pH on the electrical properties of such a membrane can be easily envisaged if the fixed-charge sites arise from ionized groups such as COO^- and NH_3^+ on membrane proteins.

Thus a decrease in pH should increase the concentration of positive fixed charge, $[N^+]$, and decrease the concentration of negative fixed charge, $[N^-]$.

The results obtained for *Chara* suggest that $[N^-] < [N^+]$ and that punch-through occurs in the N^- region. As the pH is increased $[N^-]$ increases and punch-through then occurs at a greater hyperpolarizing potential (Fig. 2). The large increase in chloride conductance which should be associated with punch-through in this case has been experimentally confirmed (Figs. 2 and 3 of Coster and Hope, 1968). The results presented by Candia for frog skin



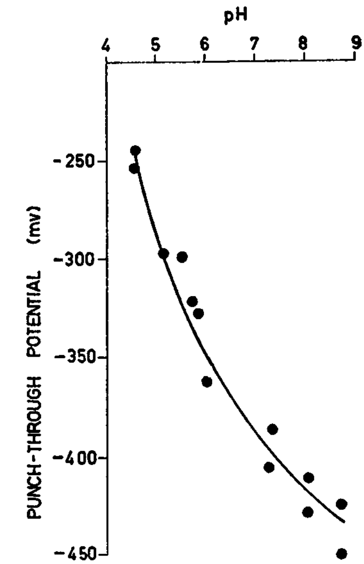


FIGURE 1

FIGURE 2

FIGURE 1 A schematic diagram showing the effect of applied bias on the width of the depletion layer (shown cross-hatched). The idealized profiles of electrostatic potential are also shown.

FIGURE 2 The effect of the pH of the external bathing solution on the punch-through potential of the membranes of cells of *Chara australis*.

show that a decrease in pH shifts the punch-through further into the hyperpolarizing region. In terms of the fixed-charge model this suggests that for frog skin $[N^-] > [N^+]$ and/or the width of the N^- lattice is greater than that of the N^+ lattice and that punch-through occurs in the N^+ lattice.

A decrease in pH and thus an increase in $[N^+]$ then leads to a contraction of the depletion layer in the N^+ region. A larger hyperpolarizing potential is then required to obtain the punch-through effect.

On this scheme punch-through in frog skin should be associated with a large relative increase in cation conductance.

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