## THE NERNST EQUATION AND ION FLOW

The flow of any ion through a membrane channel protein is driven by the electrochemical gradient for that ion. This gradient represents the combination of two influences: the voltage gradient and the concentration gradient of the ion across the membrane. When these two influences just balance each other the electrochemical gradient for the ion is zero and there is no *net* flow of the ion through the channel. The voltage gradient (membrane potential) at which this equilibrium is reached is called the equilibrium potential for the ion. It can be calculated from an equation that will be derived below, called the Nernst equation.

The Nernst equation is

$$V = \frac{RT}{zF} \ln \frac{C_o}{C_i}$$

where

$V$ = the equilibrium potential in volts (internal potential minus external potential)
$C_o$ and $C_i$ = outside and inside concentrations of the ion, respectively
$R$ = the gas constant (2 cal mol$^{-1}$ K$^{-1}$)
$T$ = the absolute temperature (K)
$F$ = Faraday's constant ($2.3 \times 10^4$ cal V$^{-1}$ mol$^{-1}$)
$z$ = the valence (charge) of the ion
ln = logarithm to the base e

The Nernst equation is derived as follows:

A molecule in solution (a solute) tends to move from a region of high concentration to a region of low concentration simply due to the random movement of molecules, which results in their equilibrium. Consequently, movement down a concentration gradient is accompanied by a favorable free-energy change ($\Delta G < 0$), whereas movement up a concentration gradient is accompanied by an unfavorable free-energy change ($\Delta G > 0$). (Free energy is introduced in Chapter 2, and discussed in the context of redox reactions in Panel 14–1, p. 830.)

The free-energy change per mole of solute moved across the plasma membrane ($\Delta G_{conc}$) is equal to $-RT \ln C_o / C_i$.

If the solute is an ion, moving it into a cell across a membrane whose inside is at a voltage $V$ relative to the outside will cause an additional free-energy change (per mole of solute moved) of $\Delta G_{volt} = zFV$.

At the point where the concentration and voltage gradients just balance,

$$\Delta G_{conc} + \Delta G_{volt} = 0$$

and the ion distribution is at equlibrium across the membrane.

Thus,

$$zFV - RT \ln \frac{C_o}{C_i} = 0$$

and, therefore,

$$V = \frac{RT}{zF} \ln \frac{C_o}{C_i}$$

or, using the constant that converts natural logarithms to base 10,

$$V = 2.3 \frac{RT}{zF} \log_{10} \frac{C_o}{C_i}$$

For a univalent ion,

$$2.3 \frac{RT}{F} = 58 \text{ mV at } 20^\circ\text{C} \quad \text{and} \quad 61.5 \text{ mV at } 37^\circ\text{C}$$

Thus, for such an ion at 37°C,

$$V = +61.5 \text{ mV for } C_o / C_i = 10,$$

whereas

$$V = 0 \text{ for } C_o / C_i = 1.$$

The $K^+$ equilibrium potential ($V_K$), for example, is
$61.5 \log_{10}([K^+]_o / [K^+]_i)$ millivolts
($-89$ mV for a typical cell where $[K^+]_o = 5$ mM and $[K^+]_i = 140$ mM).

At $V_K$, there is no net flow of $K^+$ across the membrane.

Similarly, when the membrane potential has a value of
$61.5 \log_{10}([Na^+]_o / [Na^+]_i)$,
the $Na^+$ equilibrium potential ($V_{Na}$),
there is no net flow of $Na^+$.

For any particular membrane potential, $V_M$, the net force tending to drive a particular type of ion out of the cell, is proportional to the difference between $V_M$ and the equilibrium potential for the ion: hence,
for $K^+$ it is $V_M - V_K$
and for $Na^+$ it is $V_M - V_{Na}$.

The number of ions that go to form the layer of charge adjacent to the membrane is minute compared with the total number inside the cell. For example, the movement of 6000 $Na^+$ ions across 1 μm$^2$ of membrane will carry sufficient charge to shift the membrane potential by about 100 mV.

Because there are about $3 \times 10^7$ $Na^+$ ions in a typical cell (1 μm$^3$ of bulk cytoplasm), such a movement of charge will generally have a negligible effect on the ion concentration gradients across the membrane.