where $P_j = D_j/L$. This expression can be solved for V, to get

$$V = \frac{RT}{F} \ln \left(\frac{\sum_{z=-1} P_j c_e^j + \sum_{z=1} P_j c_i^j}{\sum_{z=-1} P_j c_i^j + \sum_{z=1} P_j c_e^j} \right). \tag{2.71}$$

For example, if the membrane separates sodium ($\mathrm{Na}^+, z = 1$), potassium ($\mathrm{K}^+, z = 1$), and chloride ($\mathrm{Cl}^-, z = -1$) ions, then the GHK potential is

$$V_r = \frac{RT}{F} \ln \left(\frac{P_{\mathrm{Na}}[\mathrm{Na}^+]_i + P_{\mathrm{K}}[\mathrm{K}^+]_i + P_{\mathrm{Cl}}[\mathrm{Cl}^-]_e}{P_{\mathrm{Na}}[\mathrm{Na}^+]_e + P_{\mathrm{K}}[\mathrm{K}^+]_e + P_{\mathrm{Cl}}[\mathrm{Cl}^-]_i} \right). \tag{2.72}$$

It is important to emphasize that neither the GHK potential nor the GHK current equation are universal expressions like the Nernst equation. Both depend on the assumption of a constant electric field, and other models give different expressions for the transmembrane current and reversal potential. In Chapter 3 we present a detailed discussion of other models of ionic current and compare them to the GHK equations. However, the importance of the GHK equations is so great, and their use so widespread, that their separate presentation here is justified.

2.6.3 Electrical Circuit Model of the Cell Membrane

Since the cell membrane separates charge, it can be viewed as a capacitor. The capacitance of any insulator is defined as the ratio of the charge across the capacitor to the voltage potential necessary to hold that charge, and is denoted by

$$C_m = \frac{Q}{V}. \tag{2.73}$$

From standard electrostatics (Coulomb's law), one can derive the fact that for two parallel conducting plates separated by an insulator of thickness d, the capacitance is

$$C_m = \frac{k\epsilon_0}{d}, \tag{2.74}$$

where k is the dielectric constant for the insulator and ϵ_0 is the permittivity of free space. The capacitance of cell membrane is typically found to be 1.0 μF/cm^2. Using that $\epsilon_0 = (10^{-9}/(36\pi))$F/m, we calculate that the dielectric constant for cell membrane is about 8.5, compared to $k = 3$ for oil.

A simple electrical circuit model of the cell membrane is shown in Fig. 2.11. It is assumed that the membrane acts like a capacitor in parallel with a resistor (although not necessarily ohmic). Since the current is defined by dQ/dt, it follows from (2.73) that the capacitive current is $C_m dV/dt$, provided that C_m is constant. Since there can be no net buildup of charge on either side of the membrane, the sum of the ionic and capacitive currents must be zero, and so

$$C_m \frac{dV}{dt} + I_{\mathrm{ion}} = 0, \tag{2.75}$$

where $V = V_i - V_e$.

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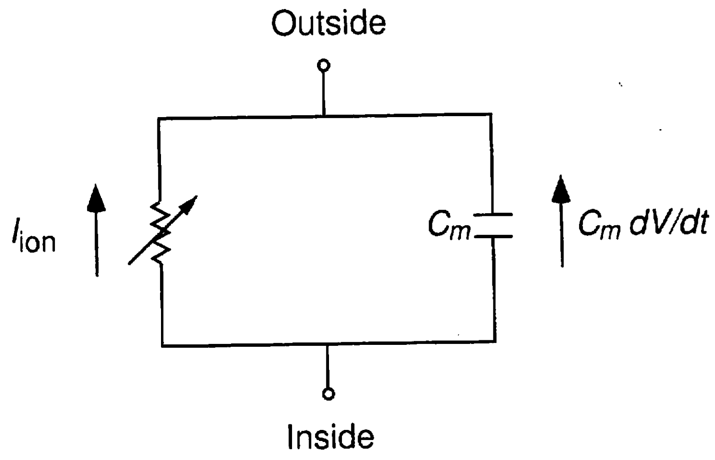

Figure 2.11 Electrical circuit model of the cell membrane.

We will meet this equation many times in this book, as it is the basis for much of theoretical electrophysiology. A significant challenge is to determine the form of I_{ion}. We have already derived one possible choice, the GHK current equation (2.68), and others will be discussed in Chapter 3.

Another common model describes I_{ion} as a linear function of the membrane potential. In Chapter 3 we will see how a linear I–V curve can be derived from more realistic models; however, because it is used so widely, we present a brief, heuristic, derivation here. Consider the movement of an ion S across a membrane. We assume that the potential drop across the membrane has two components. First, the potential drop due to concentration differences is given by the Nernst equation

$$V_{\mathrm{S}} = \frac{RT}{zF} \ln\left(\frac{[\mathrm{S}]_e}{[\mathrm{S}]_i}\right), \tag{2.76}$$

and, second, the potential drop due to an electrical current is rI_{S} (if the channel is ohmic), where r is the channel resistance and I_{S} is the transmembrane current (positive outward) of S. Summing these two contributions we find

$$V = rI_{\mathrm{S}} + V_{\mathrm{S}}, \tag{2.77}$$

and solving for the current, we get the current–voltage relationship

$$I_{\mathrm{S}} = g(V - V_{\mathrm{S}}), \tag{2.78}$$

where $g = 1/r$ is the *membrane conductance*. The current I_{S} and conductance g are usually specified per unit area of membrane, being the product of the single channel conductance times the number of channels per unit area of membrane.