Physical Foundations of Physiology II: Electrical Force, Potential, Capacitance, and Current 1.3

Learning Objectives

- Write Coulomb's law for electrostatic forces
- Define electrical potential at *x* as the work done moving a unit positive charge from infinity to *x*
- Write three equivalent but different descriptions of a conservative force
- Define electric field as the electric force per unit charge
- Describe the electric field as the negative gradient of the potential
- Recognize Gauss's law
- Write the formula for capacitance in terms of charge and voltage
- Write the formula for capacitance in terms of area, dielectric constant, and plate separation
- Describe how capacitance varies with area, dielectric, and plate separation
- Be able to calculate the capacitance of biological membranes given *k*, δ, and physical dimensions
- Be able to calculate electric field intensity and force on a charged particle given *V*(*x*, *y*, *z*)
- Write Kirchhoff's Current Law and Kirchhoff's Voltage Law
- Be able to calculate the time constant for a simple RC circuit.

COULOMB'S LAW DESCRIBES ELECTRICAL FORCES

Electric charge is a fundamental property of some subatomic particles. Electrons have negative charge and protons have positive charge. These designations of positive and negative are arbitrary but rigidly accepted by convention. Separated electrical charges in a vacuum (see Figure 1.3.1) experience a force that is described by Coulomb's law:

$$\mathbf{F} = \frac{q_1 q_2}{4\pi\varepsilon_0 r^2}$$

[1.3.1]

$$\mathbf{F}_{1\text{ on }2} = \frac{q_1 q_2 \mathbf{r}_{12}}{4\pi\varepsilon_0 r^3} = -\mathbf{F}_{2\text{ on }1}$$

The bold face symbols signify vector quantities. **F** is the force; q_1 and q_2 are electrical point charges, in coulombs, that are separated by the distance r, in meter; ε_0 is a constant, the electrical permittivity of space, which has the value of $8.85 \times 10^{-12}\ \mathrm{C^2\ N^{-1}\ m^{-2}}$. The lower equation signifies that the direction of the force is along the line between the two charges. The magnitude of the force is proportional to the product of the charges and inversely proportional to the square of their separation. Its sign depends on the signs of the point charges. Two positive charges, or two negative charges, result in a positive force which is repulsive and directed away from their center as indicated in Figure 1.3.1. Two charges of opposite sign experience a negative force which is attractive along a line connecting them.

If the intervening space is not vacuum, but some medium, the equation is altered slightly by the inclusion of a **dielectric constant**, κ, whose value depends on the medium:

[1.3.2]
$$\mathbf{F}_{1\text{ on }2} = \frac{q_1 q_2 \mathbf{r}_{12}}{\kappa 4\pi\varepsilon_0 r^3}$$

The dielectric constant for the vacuum is 1.0. For all other materials, $\kappa > 1.0$. The reduced force in the presence of a dielectric material is due to charges present in the material that reorient themselves in the presence of the external point charges and thereby screen the charges from each other. Materials with asymmetric charge distributions within their materials typically have large dielectric constants.

THE *ELECTRIC POTENTIAL* IS THE WORK PER UNIT CHARGE

Suppose there is a positive charge of magnitude q_{fixed} fixed in space at some location. We have another charge, a unit positive charge, located infinitely far away so that the force between the charges initially is effectively zero. If we bring the unit positive charge q_{test} toward the fixed charge at a constant velocity, then its kinetic energy does not change. As we approach the fixed charge, the repulsive force becomes larger and larger and we must apply an external force to keep the q_{test} at constant velocity. Because our applied external force, $\mathbf{F}_{\text{ext}}$, has moved through a distance, we have performed work on the body, given as

[1.3.3]
$$\text{Work}_{i \Rightarrow f} = \int_i^f \mathbf{F}_{\text{ext}} \cdot d\mathbf{s}$$

This work is the amount of energy we have expended in moving the positive q_{test} toward the positive q_{fixed}. Where did that energy go? If we release q_{test}, we find that it moves away from q_{fixed} and gains kinetic energy which is exactly equal to the energy we used to move

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q_{test} toward q_{fixed}. We say that the energy we used to move q_{test} was stored as **potential energy**, U. We define the potential at any place A in space as being the work done to bring a positive unit charge from infinite separation to point A:

$$U_A = \frac{\mathrm{Work}_{\infty \Rightarrow A}}{q_{test}} = \int_{\infty}^{A} \frac{\mathbf{F}_{ext} \cdot \mathbf{ds}}{q_{test}} \qquad [1.3.4]$$

The unit of potential here is joules coulomb^{-1} = volts. The usefulness of the potential is that the work can be determined easily by multiplying the potential times the charge. $\mathbf{F}_{ext}$ in this equation is the external force required to move the positive test charge with no change in velocity. It is exactly equal to and opposite in sign to $\mathbf{F}_{int}$, the interacting electrostatic force. This is, in turn, given by Coulomb's law (see Eqn [1.3.1]). Since it is directed along $\mathbf{ds}$, we can write

$$\begin{aligned} U_A &= -\int_{\infty}^{A} \frac{\mathbf{F}_{int} \cdot \mathbf{ds}}{q_{test}} = -\int_{\infty}^{A} \frac{q q_{test}}{4\pi\varepsilon_0 r^2 q_{test}} \mathrm{d}r \\ U_A &= \frac{1}{4\pi\varepsilon_0} \frac{q}{r_A} \end{aligned} \qquad [1.3.5]$$

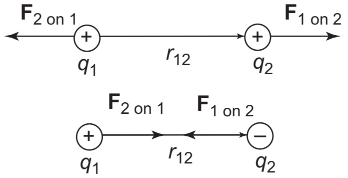

FIGURE 1.3.1 Electrical forces between separated point charges. q indicates charge. Like charges repel, so that the force of q_1 on q_2 is directed away from q_1 on a line connecting their centers. The force of q_1 on q_2 is exactly opposite to the force of q_2 on q_1. Unlike charges attract with forces opposite but in line with the vector connecting their centers.

From this definition of the potential, it should be clear that the potential surrounding a positive charge is positive: it takes work to bring a positive charge toward it. The potential surrounding a negative charge is negative, as we can get energy out of bringing a positive charge toward it. These lead us to an important conclusion: **a separation of charge produces an electric potential**. The potential defined in this way is a scalar quantity, having magnitude but not a direction, whereas the electrical force is a vector. This comes about from integrating the dot product of $\mathbf{F}_{int}$ with $\mathrm{d}\mathbf{s}$ where $\mathrm{d}\mathbf{s}$ is the distance increment that points along the pathway taken from infinite separation to point A. The dot product means that we add only those components of the force that are directed on the line connecting the centers of the charges. These conclusions are illustrated in Figure 1.3.2.

THE IDEA OF POTENTIAL IS LIMITED TO *CONSERVATIVE FORCES*

THE CONSERVATION OF ENERGY THEOREM STATES THAT ENERGY MAY BE CONVERTED BUT NOT DESTROYED

The First Law of Thermodynamics is the conservation of energy theorem. It states that in ordinary mechanical events, the total energy is constant. It is written in differential form as

$$\mathrm{d}\mathbf{E} = \mathrm{d}q - \mathrm{d}w \qquad [1.3.6]$$

where $\mathbf{E}$ is the total energy, q in this case is the heat energy, and w is the work. This is another unfortunate case where variables are used to denote completely different quantities. In thermodynamics, q symbolizes

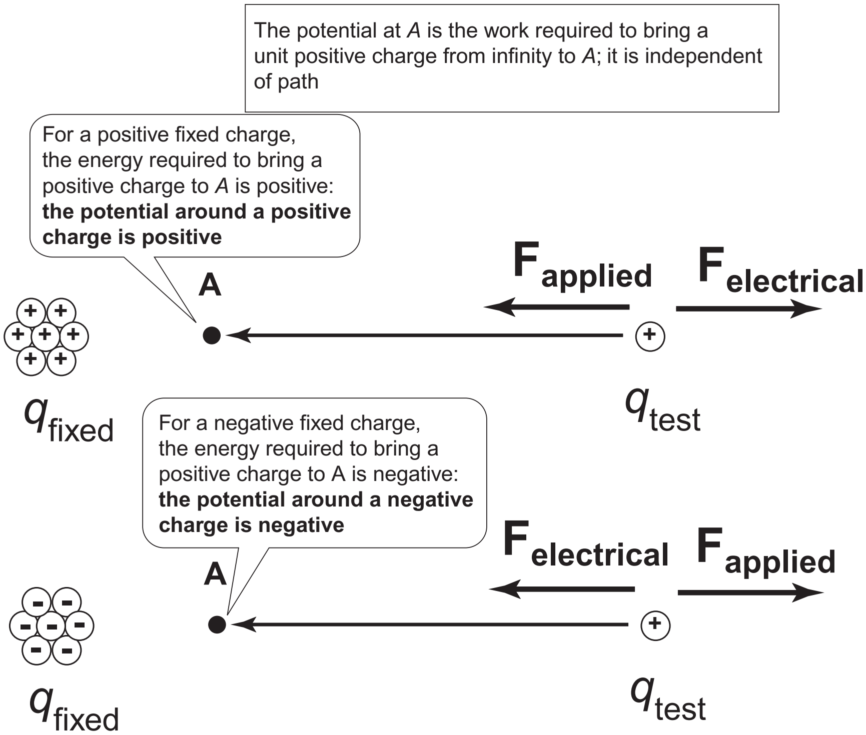

FIGURE 1.3.2 Definition of the electrical potential. The potential at a point A is defined as the work required to bring a unit positive charge (q_{test}) from infinite separation to point A. If there is a fixed positive charge near A, it takes work to bring q_{test} to A (we must apply a force to overcome the repulsive force and we move that force through a distance) and the potential is positive. If there is a fixed negative charge near A, then q_{test} is attracted to it and it takes energy (work) to slow q_{test}—the work is negative because the applied force is opposite to the direction of movement.

heat, and in electrostatics it symbolizes charge. The appearance of heat in this equation is extremely important, because it turns out that there are theoretical limits in the conversion of heat energy to useful work, and this gives rise to the concepts of entropy and free energy.

This equation assumes that heat and work are alternate forms of energy. We take the equivalence of mechanical, thermal, chemical, and electrical energies for granted but historically this idea took some time to develop. In writing that any energy change in the system is the balance between work output and heat input, it is assumed that work is equivalent to heat. The equality of mechanical work and heat was established in 1845 by Joule.

The signs of dq and dw in this equation are important, and are consequences of the definitions of heat and work. The quantity dq is *defined* as the heat absorbed *by* the system from its surroundings, and dw is *defined* as the work done *by* the system on its surroundings (see Figure 1.3.3). The "system" here is anything we have drawn a conceptual line around, usually in agreement with some physical boundary, that sets part of the universe off from the rest of it. In the case of electrostatics, the system is the set of charges distributed in space.

THE WORK DONE BY A CONSERVATIVE FORCE IS PATH INDEPENDENT

The work done by moving q_{test} toward q_{fixed} is the work done by the surroundings (us) on the system of interacting charged particles. It is equal but opposite in sign to the work done by the interacting force. There may be heat generated by the necessity to apply more force than the interacting force in order to overcome friction, if the charges move through some medium, but this is separate from the interacting force (the coulombic or electrostatic force) itself. The coulombic force itself generates no heat at all. It belongs to a class of forces called **conservative forces** that do not dissipate energy as heat. Conservative forces are characterized by three equivalent statements:

1. The work done by a conservative force depends only on the initial and final positions, and not on the path (see Figure 1.3.4).
2. The potential difference between two points depends only on the end points and not the path.
3. The total work done by a conservative force acting around a closed loop is zero.

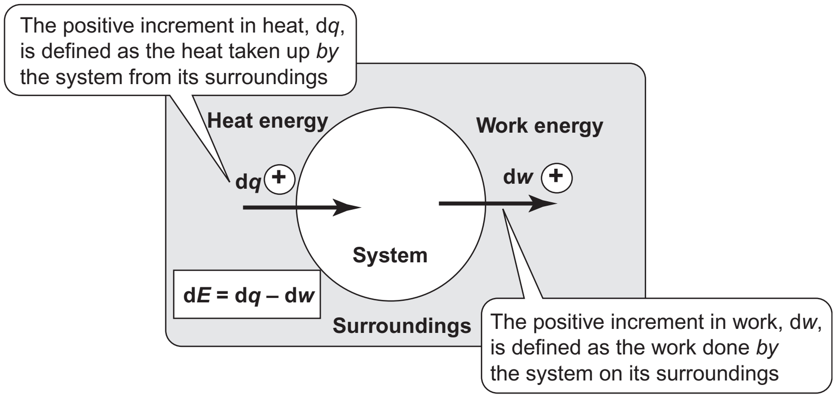

FIGURE 1.3.3 Theorem of the Conservation of Energy. The system is any part of the universe that we have enclosed by some boundary, real or imagined. Positive heat flow is defined as heat energy that is absorbed by the system from its surroundings. Similarly, positive work is defined as work that is done by the system on its surroundings. By these definitions, conservation of energy means that dE = dq − dw. In order to write this equation, it is assumed that heat and work have the same units, that of energy. Here work can be electrical, mechanical, or chemical.

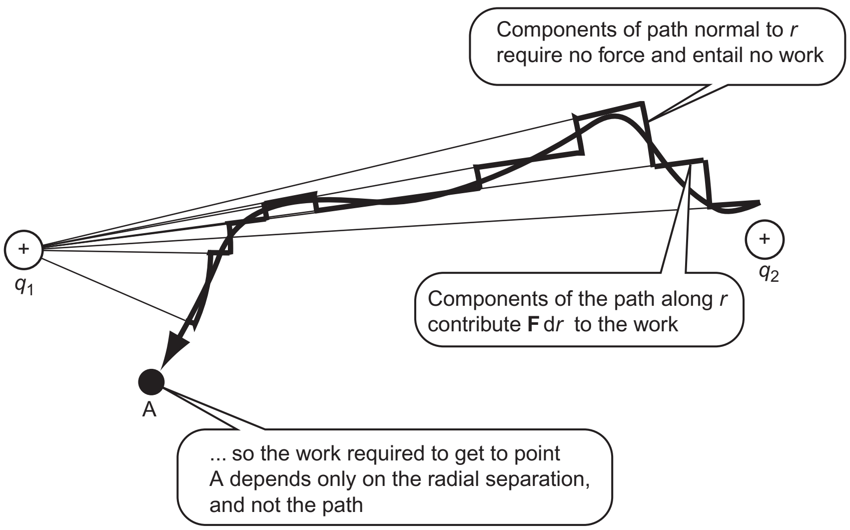

FIGURE 1.3.4 Potential is independent of the path. Any path from start to finish can be successively approximated by a series of paths oriented either parallel to the vector connecting the charges or perpendicular to it. Those components of the path perpendicular to the vector require no force and therefore contribute nothing to the potential at point A, which is defined as the work necessary to bring a unit positive charge (here shown as q_2) from infinite separation to point A. Components of the path oriented parallel to the vector connecting the point charges contribute **F** dr to the force. Therefore, the total work (potential) moving the charge depends only on the radial separation and not the path taken.

POTENTIAL DIFFERENCE DEPENDS ONLY ON THE INITIAL AND FINAL STATES

If the potential depends only on the position, then it is a state function, one that is independent of path and dependent only on the **state** of the system. Thus we can associate a potential with any position, A and B:

$$
\begin{aligned}
U_A &= -\int_{\infty}^{A} \frac{\mathbf{F}_{int} \cdot \mathbf{ds}}{q_{test}} \\
U_B &= -\int_{\infty}^{B} \frac{\mathbf{F}_{int} \cdot \mathbf{ds}}{q_{test}} \qquad [1.3.7] \\
U_{A \Rightarrow B} &= -\int_{A}^{B} \frac{\mathbf{F}_{int} \cdot \mathbf{ds}}{q_{test}} = U_B - U_A
\end{aligned}
$$

If A = B, where A is the initial state and B is the final state, we can write

$$U_{initial \Rightarrow final} = 0 = -\oint_{initial}^{final} \mathbf{F}_{int} \cdot \mathbf{ds} \qquad [1.3.8]$$

This is the mathematical statement that the work performed by the system around any closed loop is zero. This turns out to be equivalent to the statement that the potential is a function of position (state) only and not of the path used to get to that position.

THE *ELECTRIC FIELD* IS THE NEGATIVE GRADIENT OF THE POTENTIAL

The **electric field intensity** is *defined* as the electric force per unit charge:

$$\mathbf{E} = \frac{\mathbf{F}_{int}}{q_{test}} \qquad [1.3.9]$$

Insertion of this into Eqn [1.3.7] and differentiating, we get

$$\mathbf{E} = -\frac{dU}{dS} \qquad [1.3.10]$$

This equation is not correct as written yet, because we have a vector (the electric field intensity) on one side and a scalar on the other! We need to take a particular kind of derivative, the **gradient**, to convert the scalar potential into a vector force. Equation [1.3.10] is correct as written as long as the axis of $\mathbf{ds}$ corresponds with the direction of $\mathbf{F}$. The full three-dimensional vector equation is

$$
\begin{aligned}
\mathbf{E} &= -\mathbf{i}\frac{\partial U}{\partial x} - \mathbf{j}\frac{\partial U}{\partial y} - \mathbf{k}\frac{\partial U}{\partial z} \qquad [1.3.11] \\
\mathbf{E} &= -\nabla U
\end{aligned}
$$

where $\mathbf{i}$, $\mathbf{j}$, and $\mathbf{k}$ are unit vectors in the x, y, and z directions. The expression on the right-hand side of Eqn [1.3.11] is called the **gradient** of the function U. It is a vector whose components on each axis are the slope of the potential projected onto that axis. Generally, the gradient is a vector that does not align with any axis. Instead, it points in the direction of the steepest slope of the potential surface in three dimensions. The force points down this slope. It is the negative of the gradient of the potential. The last equation shows the gradient written in operator notation. The operator ∇ is called **del** and is defined as

$$\nabla = \mathbf{i}\frac{\partial}{\partial x} + \mathbf{j}\frac{\partial}{\partial y} + \mathbf{k}\frac{\partial}{\partial z} \qquad [1.3.12]$$

FORCE AND ENERGY ARE SIMPLE CONSEQUENCES OF POTENTIAL

The usefulness of potential is that it simplifies the idea of force and energy. The force on a charge q is given easily by multiplying it times the electric field, which is $-$grad U. The energy cost in moving a charge from one potential to another is just $q\Delta U$:

$$
\begin{aligned}
\mathbf{F} &= -q\nabla U \qquad [1.3.13] \\
\Delta \text{ Energy} &= q\Delta U
\end{aligned}
$$

where ∇ is the del operator and Δ signifies the difference between final and initial states. The electric potential, U, here is in units of volts. If charge is in coulombs, the force is in units of coulomb-volt per meter; a volt-coulomb is a joule = 1 N m = 1 kg m^2 s^{-2}; therefore, the force is in units of 1 N m/m = N. The energy is in units of joules. From now on we will abandon use of U as a symbol for the potential; physiologists typically use V, E, or ψ as symbols of potential.

GAUSS'S LAW IS A CONSEQUENCE OF COULOMB'S LAW

Gauss's law is written as

$$\oint \mathbf{E} \cdot \mathbf{ds} = \frac{q}{\varepsilon_0} \qquad [1.3.14]$$

where the integral is taken over *any* closed surface of the dot product of the electric field and the area vector, equal to the area increment $\mathbf{ds}$ and oriented perpendicular to the surface. What this says is that this dot product, summed over any closed surface, is equal to the charge enclosed by the surface divided by ε_0, the electrical permittivity of space. If there is no enclosed charge, the surface integral is zero. This equation is a variant of Coulomb's law (see Eqn [1.3.1]). To see how this equation works, we consider a spherically symmetrical distribution of positive charges as shown in Figure 1.3.5.

The evaluation of the surface integral is simplified by choosing an appropriate surface. In this case, we choose a sphere centered on the symmetrical charge. By symmetry, the electric field is directed radially outward, pointing along the vector $\mathbf{ds}$. Similarly, the electric field is everywhere constant in magnitude at a

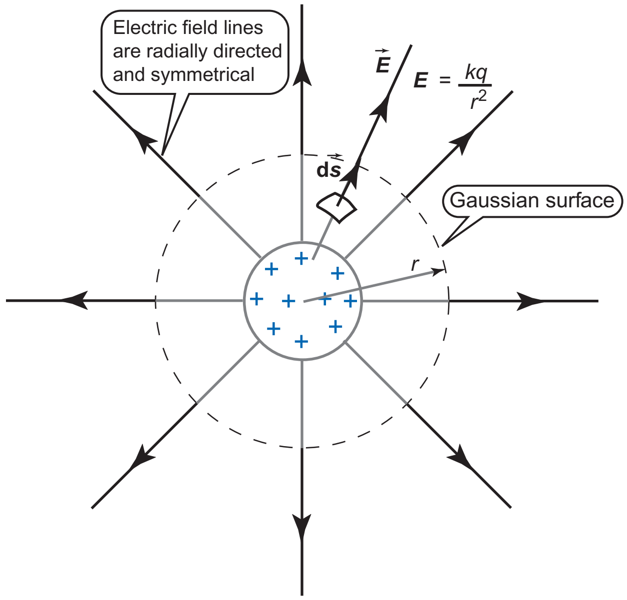

FIGURE 1.3.5 Electric field surrounding a spherically symmetrical distribution of positive charge. d**s** is a vector having a magnitude of the area increment and directed normal to the closed surface. In this case, we take the Gaussian surface, indicated here by a *dashed line*, to be a sphere centered on the symmetrically distributed charge. The electric field vector and the surface normal vector are pointing in the same direction, so that the angle between them, θ, is zero and the dot product of **E** and d**s** is **E** d**s**, because cos $\theta = 1$.

prescribed distance, r, from the center of the charged body. Thus we can write

$$\oint E \cdot ds = E 4\pi r^2 = \frac{q}{\varepsilon_0}$$

[1.3.15]

$$E = \frac{q}{4\pi r^2 \varepsilon_0}$$

which is the magnitude of the electric field ($\mathbf{E} = \mathbf{F}/q$, the electric force per charge) from Coulomb's law (see Eqn [1.3.1]).

THE *CAPACITANCE* OF A PARALLEL PLATE CAPACITOR DEPENDS ON ITS AREA AND PLATE SEPARATION

As described in Chapter 1.2, the ability to store electric charge is characterized by the capacitance, *defined* as

[1.3.16]

$$C = \frac{Q}{V}$$

where C is the capacitance, Q is the charge, and V is the potential, in volts. We now consider a particular type of device to store charge, a parallel plate capacitor, as described in Figure 1.3.6.

The two charged plates will be attracted to each other and so must be held apart by some dielectric material that insulates the plates and keeps the charges separated. There will be some fringing of the electric field around the edges of the plate, which we shall ignore. The resulting electric field within the capacitor is uniform, which can be proved by integrating the Coulomb force over the uniformly distributed charge on a plane, which we will not do here. We draw a rectangular closed surface, one side of which is in the middle of the dielectric and the other in the middle of the plate. Since the plate is a good conductor, the electric field within the plate is zero—the voltage difference in the plate is zero. The closed surface integral is just the constant electric field times the area of the surface in the dielectric. The situation is illustrated in Figure 1.3.7.

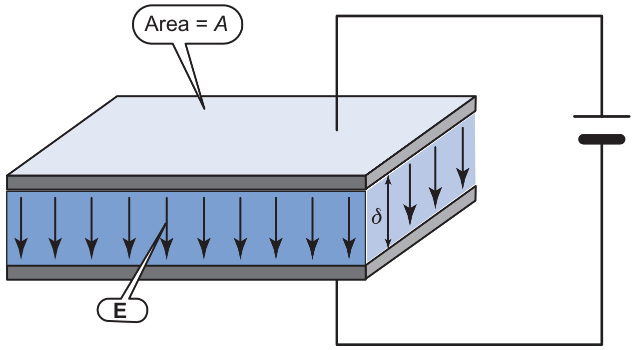

FIGURE 1.3.6 A parallel plate capacitor. Two plates, each of area A, are separated by a distance δ. They are charged by connecting them to a battery that produces a capacitance current until the potential difference between the two plates is equal to that across the two poles of the battery, so that the net potential difference across the entire circuit loop is zero. At this point, there is no more current flow. The separation of charges produces a uniform electric field between the two plates.

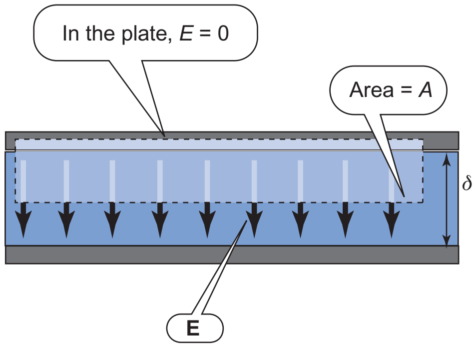

FIGURE 1.3.7 Parallel plate capacitor with a Gaussian surface. The Gaussian surface is the box indicated by the *dashed lines*. The electric field is constant within the capacitor and oriented as shown. The integral of **E** d**s** in the plate is zero because **E** is zero there. The integral of **E** d**s** in the dielectric between the plates is **E***A*. The integral of **E** d**s** on the sides of the enclosed surface is zero because **E** and d**s** are orthogonal in this region.

Application of Gauss's law according to the description in the legend of Figure 1.3.5 gives

$$\oint \mathbf{E} \cdot d\mathbf{s} = \mathbf{E}A = \frac{q}{\varepsilon_0}$$

[1.3.17]

$$\mathbf{E} = \frac{q}{\varepsilon_0 A}$$

Since the electric field is uniform, its relation to V from Eqn [1.3.10] is given as

$$\mathbf{E} = -\frac{dV}{dx} = \frac{V_1 - V_2}{\delta} \quad [1.3.18]$$

The capacitance is calculated as

$$C = \frac{q}{V_1 - V_2} \quad [1.3.19]$$

Substituting in for q from Eqn [1.3.17] and for $V_1 - V_2$ from Eqn [1.3.18], we have

$$C = \frac{\varepsilon_0 A}{\delta} \quad [1.3.20]$$

The presence of a dielectric between the plates reduces **E** for a given charge, and therefore increases the capacitance. The formula for parallel plates with a dielectric is

$$C = \frac{\kappa \varepsilon_0 A}{\delta} \quad [1.3.21]$$

where κ is the dielectric constant, a dimensionless ratio.

According to Eqn [1.3.21], the capacitance increases linearly with the area and inversely with the separation between the plates, and is increased by materials with high dielectric constants.

BIOLOGICAL MEMBRANES ARE ELECTRICAL CAPACITORS

Biological membranes share some of the features of parallel plate capacitors and act as electrical capacitors. Their structure is detailed in Chapter 2.4. Briefly, biological membranes consist of an asymmetric bilayer of lipid molecules that assemble to form an interior insulating core. This effectively separates two plates—the surfaces of each bilayer—from each other. The separation distance is typically quite small, on the order of 7 nm. This bilayer structure is shown in Figure 1.3.8. From it, you can see the resemblance of the bilayer to a parallel plate capacitor.

The dielectric constant of some materials is shown in Table 1.3.1. This constant varies with temperature and the chemical make-up of the dielectric. Materials that are polar and mobile, such as water, can orient their partial charges with the electric field, and reduce the field within the dielectric. In this way, more charge can be added to the surfaces of the plates and therefore these dielectrics have a high dielectric constant.

TABLE 1.3.1 Dielectric Constant of Some Materials

Material	Dielectric Constant, κ
Air	1.00059
Water	80
Glycerol	43
Acetic acid	6.2
Benzene	2.3
CCl_4	2.2
Oleic acid	2.46
Hexanol	13.3
Hexane	1.89
Stearic acid	2.29
Monopalmitin	5.34

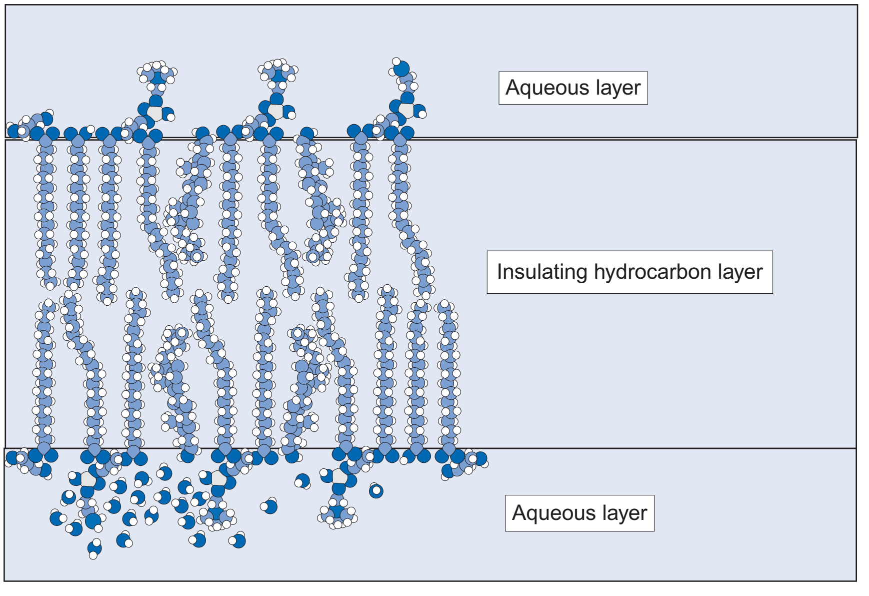

FIGURE 1.3.8 Lipid bilayer membrane consisting of various lipid molecules arranged with their hydrocarbon tails toward the interior of the bilayer and their water-soluble parts facing the water phase.

EXAMPLE 1.3.1 Capacitance of Planar Lipid Bilayers

Dr. Alexandre Fabiato at VCU drilled a narrow and clean hole with a diameter of 250 μm = 0.25 mm into a Lexan partition that separated two electrolyte solutions. He "painted" some phospholipids over the hole using a Teflon stick cut at an angle and dipped into a solution of lipids dissolved in hexane. After "thinning" (passive removal of the hexane through the aqueous phase), the membranes form a planar lipid bilayer (see Figure 1.3.9). Dr. Fabiato measured the capacitance of the membrane using an AC signal connected to electrodes immersed in the solutions. He derived a capacitance of 350 pF (350×10^{-12} F). Calculate the specific capacitance of the membrane Dr. Fabiato made, in F cm^{-2}.

The specific capacitance is just the capacitance per unit area of membrane: $C_m = C/A$. The measured capacitance is 350×10^{-12} F and the area A is πr^2, where $r = 0.0125$ cm; therefore,

$$C_m = 340 \times 10^{-12}\ \text{F}/4.9 \times 10^{-4}\ \text{cm}^2 = \mathbf{0.71\ \mu F\ cm^{-2}}$$

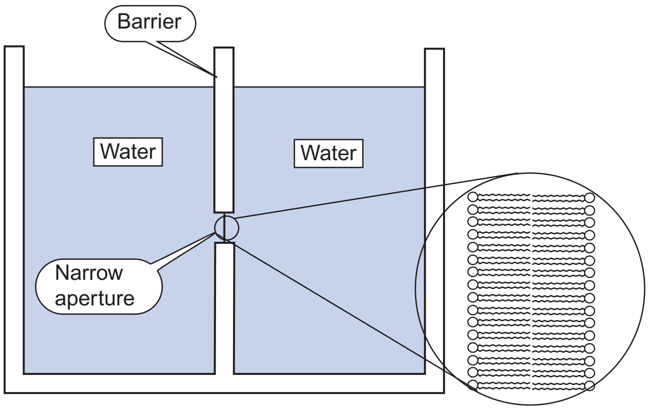

FIGURE 1.3.9 Planar lipid bilayer formed in a narrow hole between two aqueous compartments.

What Is the Approximate Thickness of the Bilayer?

Equation [1.3.19] allows us to calculate the thickness as $\delta = \kappa\varepsilon_0/C_m$, where C_m is the specific capacitance. We do not know κ, but the dielectric constant for lipid-like substances has been determined, as examples shown in Table 1.3.1. Here we use $\varepsilon_0 = 8.85 \times 10^{-12}\ C^2\ J^{-1}\ m^{-1}$ and $C_m = 0.71 \times 10^{-6}\ C\ V^{-1}\ cm^{-2}$ that we calculated earlier. Using the dielectric constant for *n*-hexane as an example, we calculate

$$\delta = 1.89 \times 8.85 \times 10^{-12}\ C^2\ J^{-1}\ m^{-1}/0.71 \times 10^{-6}\ CV^{-1}\ cm^{-2} \times (100\ cm\ m^{-1})^2 = \mathbf{2.36 \times 10^{-9}\ m}$$

The calculated values of δ (Table 1.3.2) are of the same order as expected from electron micrographs of membranes.

If the potential across a membrane is 80 mV, and its thickness is 7 nm, What is the electric field intensity?

The field is uniform inside a capacitor, and so is given by $\mathbf{E} = -\Delta V/\Delta x$, where ΔV is the potential difference and Δx is the separation of the plates. Thus the electric field is

$$\mathbf{E} = -80 \times 10^{-3}\ V/7 \times 10^{-9}\ m = -\mathbf{11.4 \times 10^6\ V\ m^{-1}}$$

TABLE 1.3.2 Calculated δ for Various κ

κ	δ (nm)
1.89	2.36
2.29	2.85
2.46	3.07
5.34	6.67

ELECTRIC CHARGES MOVE IN RESPONSE TO ELECTRIC FORCES

As mentioned in the section "Force and Energy Are Simple Consequences of Potential," the usefulness of the concept of potential lies in the ease of calculating the force on a charged particle or the energy needed to move from one region to another. The electrical force on a charged particle is given as

$$\mathbf{F} = -q\nabla U = q\mathbf{E} = ze\mathbf{E} \qquad [1.3.22]$$

where U is the potential, often written as V, q is the charge, **E** is the electric field, z is the valence (+/− integral number of charges per particle), and e is the unit charge of the electron. Thus, a charged particle, of either sign, in an electric field is subjected to an accelerating force. Ions in solution are subjected to these forces and accelerate on account of them. These ions accelerate until they reach a terminal velocity, v, at which point the electrical force is matched by a drag force on the particle by the surrounding solution. Figure 1.3.10 illustrates this situation.

MOVEMENT OF IONS IN RESPONSE TO ELECTRICAL FORCES MAKES A CURRENT AND A SOLUTE FLUX

The drag force on a particle moving through a solution is proportional to its velocity and directed opposite to it. Further, the electrical force given in Eqn [1.3.22] at

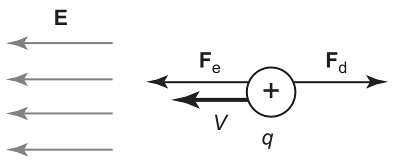

FIGURE 1.3.10 Forces on a charged particle in solution subjected to a constant electric field. The electrical force, $\mathbf{F}_e$, is the product of the charge, q, on the particle and the electric field, $\mathbf{E}$. This electrical force accelerates the charged particle and it moves through the solution. This movement produces a drag force, $\mathbf{F}_d$, which is proportional to the velocity, $\mathbf{v}$. The particle reaches a terminal velocity when the net force on the particle is zero: $\mathbf{F}_e + \mathbf{F}_d = 0$.

the terminal velocity is equal but opposite to $\mathbf{F}_d$. Therefore, we can write

$$\mathbf{F}_d = -\beta v \qquad [1.3.23]$$
$$\mathbf{F}_e = -\mathbf{F}_d$$
$$\mathbf{F}_e = \beta v$$

where β is a drag coefficient or **frictional coefficient**. Thus ions subjected to a constant electrical field will move at a constant terminal velocity, v, and that velocity will be proportional to the electric field. This movement of charged particles constitutes a movement of charge from place to place, and so it is an electrical current. Further, because solute particles carry the charge, the movement also forms a solute flow. The solute flux is related to the velocity by

$$\mathbf{J}_s = vC \qquad [1.3.24]$$

where J and v are written as vectors and C is the concentration of the solute (see Figure 1.3.11). Because each solute particle carries the charge ze, the **current density** is

$$\mathbf{i} = ze\mathbf{J}_s \qquad [1.3.25]$$

This expression can be converted into Ohm's law by using Eqns [1.3.22]–[1.3.24]:

$$\mathbf{i} = ze\mathbf{J}_s = zevC$$
$$\mathbf{i} = zeC\frac{\mathbf{F}_e}{\beta} \qquad [1.3.26]$$
$$\mathbf{i} = \frac{z^2e^2C}{\beta}(-\nabla V)$$

The last equation is an analogue of Eqn [1.2.3] for the one-dimensional form of Ohm's law:

$$J_e = -\sigma\frac{d\psi}{dx} \qquad [1.2.3]$$

EXAMPLE 1.3.2 Forces on Charged Particles

Consider the planar lipid bilayer in Example 1.3.1, which has a potential difference of 80 mV across it. What would the electric force be on a Na^+ ion in the middle of the bilayer?

The electric force on a charged particle is given as $\mathbf{F}_e = q\mathbf{E}$. We calculated the electric field intensity, $\mathbf{E}$, in this case to be -11.4×10^6 V m^{-1}. The charge on any ion is ze, where z is the valence or integral number of charges on the particle and e is the charge on the electron. In this case, $z = +1$ and the charge on the electron is given in various units.

The most useful unit here is the coulomb: $1e = 1.6 \times 10^{-19}$ C.

The force is thus given as

$$\begin{aligned}\mathbf{F}_e &= 1.6 \times 10^{-19}\ \text{C} \times -11.4 \times 10^6\ \text{V m}^{-1}\\ &= -1.82 \times 10^{-12}\ \text{V C m}^{-1}\\ &= -1.82 \times 10^{-12}\ \text{J m}^{-1}\\ &= -1.82 \times 10^{-12}\ \text{N m m}^{-1}\\ &= \mathbf{-1.82 \times 10^{-12}\ N}\end{aligned}$$

THE RELATIONSHIP BETWEEN *J* AND *C* DEFINES AN AVERAGE VELOCITY

Consider the right cylindrical tube shown in Figure 1.3.11 that contains solute particles moving to the right at average velocity v. In time Δt, the particles travel a horizontal distance $\Delta x = v\Delta t$. All of the solute particles in the volume $A\Delta x$ will have crossed a cross-sectional plane in the cylinder. Thus the flux will be the total number of solute particles in that volume, per unit area per unit time. The number of solute

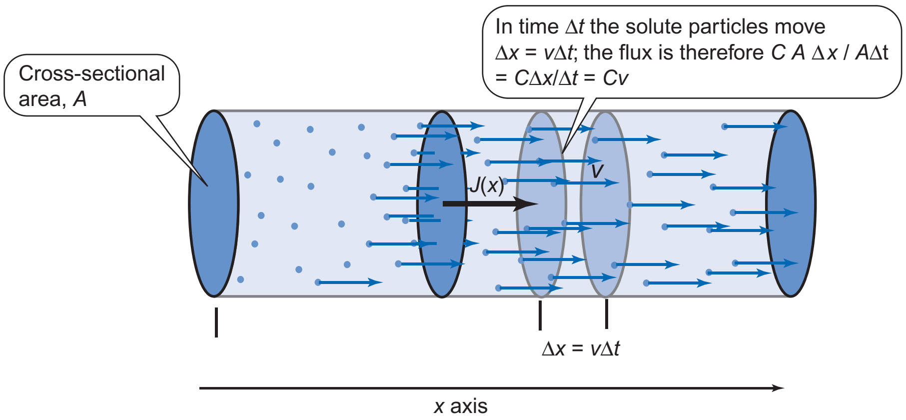

FIGURE 1.3.11 Relationship among J, C, and v. If solutes have an average velocity v, they sweep out a distance $v\Delta t$ in time Δt, and this corresponds to an entire volume of solute, equal to $Av\Delta t$, moving to the right. The number of solute particles in this volume is $CAv\Delta t$. The flux is this number per unit area, per unit time: $J = CAv\Delta t/A\Delta t = Cv$.

particles in the volume $A\Delta x$ is $CA\Delta x$. Thus the flux is given as

$$J = \frac{CA\Delta x}{A\Delta t} \qquad [1.3.27]$$
$$J = Cv$$

From this equation, it is clear that the ratio of J/C defines an average velocity for solute particles.

OHM'S LAW RELATES CURRENT TO POTENTIAL

According to the discussion earlier, a difference in potential produces a force on charged particles, and the force is proportional to the negative gradient of the potential. The movement of charges in response to a potential makes a current, a flow of charges. It is given as

$$I = \frac{\Delta q}{\Delta t} \qquad [1.3.28]$$

The current I is given in amperes = coulomb s^{-1}. **Current is defined as the movement of positive charge**, so that the movement of cations (positive ions) constitutes a current in the direction of the flow; the movement of anions (negative ions) makes a current in the opposite direction to the flow. The current due to an ion is related to its flow by

$$I_x = z\mathfrak{F}Q_x \qquad [1.3.29]$$

where I_x is the current of ion x, in coulombs s^{-1}, Q_x is the flow of ion x in mol s^{-1}, z is the integral charge per ion (+/−1, 2, ...) and $\mathfrak{F}$ is the Faraday (9.649×10^4 coulombs $mol^{-1} = 6.02 \times 10^{23}$ electrons - $mol^{-1} \times 1.6 \times 10^{-19}$ coulombs $electron^{-1}$); $z\mathfrak{F}$ converts mol to coulombs. Note that current is an extensive variable, while current density is an intensive variable.

The movement of charge through matter-filled space encounters resistance from the matter. Those materials that offer little resistance are called **conductors**. Other materials, such as membrane lipids and the myelin sheath that surrounds nerve axons, offer high resistance and are called **insulators**. The current is greater if the potential driving it is greater and is less according to the resistance of the material through which the current flows. This is Ohm's Law:

$$I = \frac{\Delta\psi}{R} = \frac{E}{R} \qquad [1.3.30]$$

where I is the current, $\Delta\psi$ is the potential difference, often symbolized as E or V, and R is the **resistance**. Resistance has the units of ohms = volts/amps, symbolized as Ω. Ohm's law can also be written as

$$I = g\,\Delta\psi \qquad [1.3.31]$$

where $g = 1/R$ is the **conductance**. The SI unit for conductance is the siemen = amp/volt.

A battery is a device for using chemical reactions to create a voltage difference. In effect, chemicals trap electrons, with their negative charges, at fixed distances from their positively charged nuclei. Different chemicals will then have different potentials for their electrons. In chemistry these are called **oxidation potentials**. These refer to the energy required to remove the electron from the chemical. The movement of electrons from one chemical to another can then release energy equal to the difference in the oxidation potentials times the number of charges that move. If we hook up a battery in series with a resistance, we can produce a current which is given by Ohm's Law (see Eqn [1.3.30]). This situation is shown schematically in Figure 1.3.12.

KIRCHHOFF'S CURRENT LAW AND KIRCHHOFF'S VOLTAGE LAW

The circuit shown in Figure 1.3.12 is a simple circuit in which a resistor is placed over the terminals of a battery. When the circuit is completed, current flows and this can be measured with an ammeter. **Kirchhoff's Voltage Law states that the total voltage differences around any loop must be zero**. This is a restatement of the conservative nature of the electric force: the work done in any loop is zero. Since the only resistance is between nodes 2 and 4, the voltage differences around the loop are ΔV_{23} and ΔV_{71}, where ΔV_{71} is the voltage across the battery from the negative electrode to the positive electrode. Thus, $\Delta V_{71} = -\Delta V_{17} = -E$, the voltage provided by the battery. The total voltage drop around the loop is given as $0 = \Delta V_{23} + \Delta V_{71} = \Delta V_{23} - E$. Solving this for ΔV_{23}, we find $\Delta V_{23} = E$ and therefore the current through the resistor is $I = E/R$.

Kirchhoff's Current Law states that the sum of current into any node must be zero. Thus if there is a current $I_{23} = E/R$ that enters node 3, there must be a current $I_{34} = I_{23}$ that leaves node 3. The total current into node 3 is $I_{23} - I_{34} = 0$. I_{34} is negative in this last equation because it leaves node 3—it is the opposite direction (with respect to node 3) of the current I_{23}, but it is equal in magnitude.

THE TIME CONSTANT CHARACTERIZES THE CHARGING OF A CAPACITOR IN A SIMPLE RC CIRCUIT

Suppose now that we include a capacitor in the circuit shown in Figure 1.3.12. This expanded circuit is shown in Figure 1.3.13. Initially, with the switch open, there will be no potential across the capacitor, and no current in the circuit. If we flip the switch, current will begin to flow because there will be potential differences in the circuit. But the capacitor is filled with a dielectric that disallows current flow! How can current flow across the

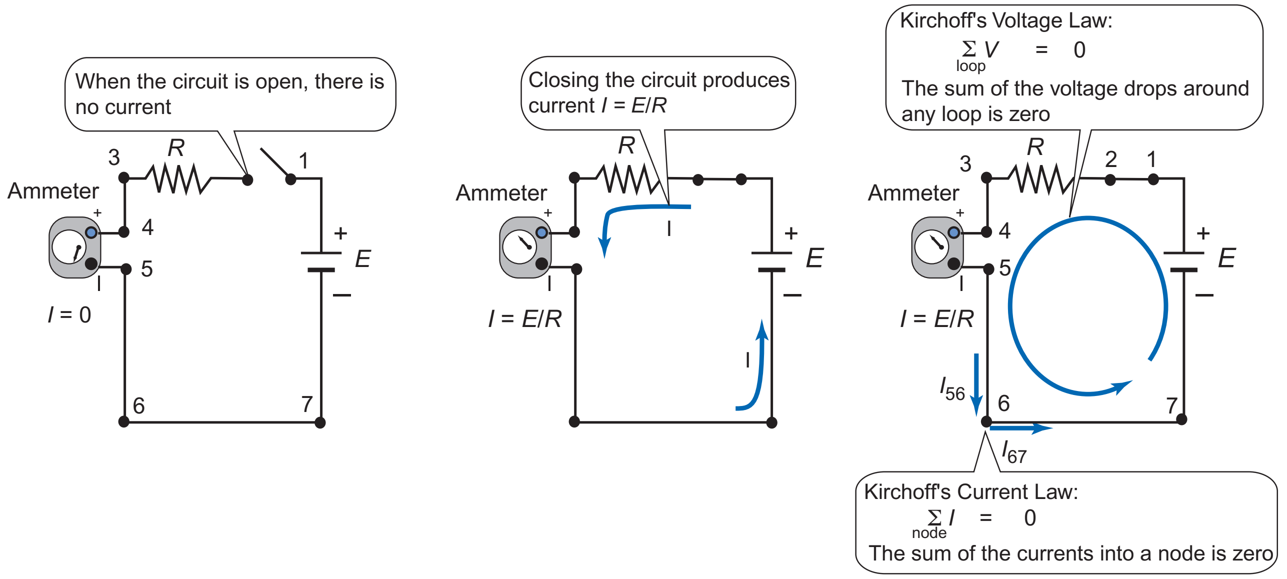

FIGURE 1.3.12 Ohm's Law, Kirchhoff's Current Law, and Kirchhoff's Voltage Law. When the circuit is completed by closing the switch between nodes 1 and 2, current flows as described by Ohm's Law: $I = \Delta V_{23}/R$, where ΔV_{23} is the voltage difference across the resistor (between nodes 2 and 3) and R is the resistance. In this circuit, the only resistance is between nodes 2 and 3 and all other resistances are negligible. Kirchhoff's Current Law (KCL) states that the sum of currents into a node is zero. At node 6, for example, the sum of the currents is $I_{56} - I_{67}$, the negative sign indicating that the current is out of the node. Thus, $I_{56} - I_{67} = 0$ or $I_{56} = I_{67}$. Kirchhoff's Voltage Law (KVL) states that the sum of voltage drops around any closed loop is zero. For the circuit shown, the voltage drops are from nodes 2 to 3, where $\Delta V_{23} = I\,R = E$; and from nodes 7 to 1 where $\Delta V_{71} = -\Delta V_{17} = -E$. Thus the voltage drop around the loop is $\Delta V_{23} + \Delta V_{71} = E - E = 0$. All of the other voltage drops between nodes (ΔV_{45}, ΔV_{56}, ΔV_{67}, and ΔV_{12}) are zero because the resistances in this part of the circuit are negligible.

capacitor? The current in this case is a **capacitive current**, not a **resistive current**, like the kind shown in Figure 1.3.12. The flow of positive ions onto the top plate of the capacitor produces an electric field (a force per unit charge) that repels positive charges from the bottom plate. This movement of charges away from the bottom plate is the capacitive current. As the charges move away, there is a separation of charges on the capacitor and it now has a potential difference given by $V = q/C$. Charges continue to move until the potential across the capacitor is equal but opposite to the potential across the battery, E.

To analyze the time course of current and voltage in the circuit, we make use of Kirchhoff's Voltage Law that says the sum of the voltage drops in the circuit must be zero. We write

[1.3.32]
$$\begin{aligned} \Delta V_{61} + \Delta V_{23} + \Delta V_{45} &= 0 \\ -E + \frac{dq}{dt}R + \frac{q}{C} &= 0 \end{aligned}$$

where q is the charge on the capacitor and dq/dt is the current through the resistor, which is also the current across the capacitor. We can separate variables in Eqn [1.3.32] and integrate to solve this equation for q as a function of t. The rate of charging of the capacitor is given as

[1.3.33]
$$q = EC\left(1 - e^{-\frac{t}{RC}}\right)$$

where t is the time and the combined terms RC is called the **time constant** because it describes the time taken to charge the capacitor. The current can be obtained from differentiation of q to give

[1.3.34]
$$I = \frac{E}{R} e^{-\frac{t}{RC}}$$

The time course of charge and current is shown in Figure 1.3.14. In Eqn [1.3.33], if $t = RC$, then $q = EC(1 - 1/e)$, so the time constant is the time required for the charge to be $1/e = 0.37$ of its final value.

SUMMARY

Some particles in nature either repel or attract other particles, and the force developed between them varies inversely with the square of their separation. These particles are said to be "charged," and there is no more basic description or explanation of their interaction than Coulomb's law that quantifies it. Charges have two types: positive and negative. Like charges repel, unlike charges attract.

This electrostatic force is a conservative force, meaning that the work performed in moving a charge around any closed loop is zero. Conservative forces also mean that the work done in moving a particle around depends only on the initial and final states, and not the path. Equivalently, the potential energy associated with a distributed set of charges depends only on the position and not on the path it takes to get there.

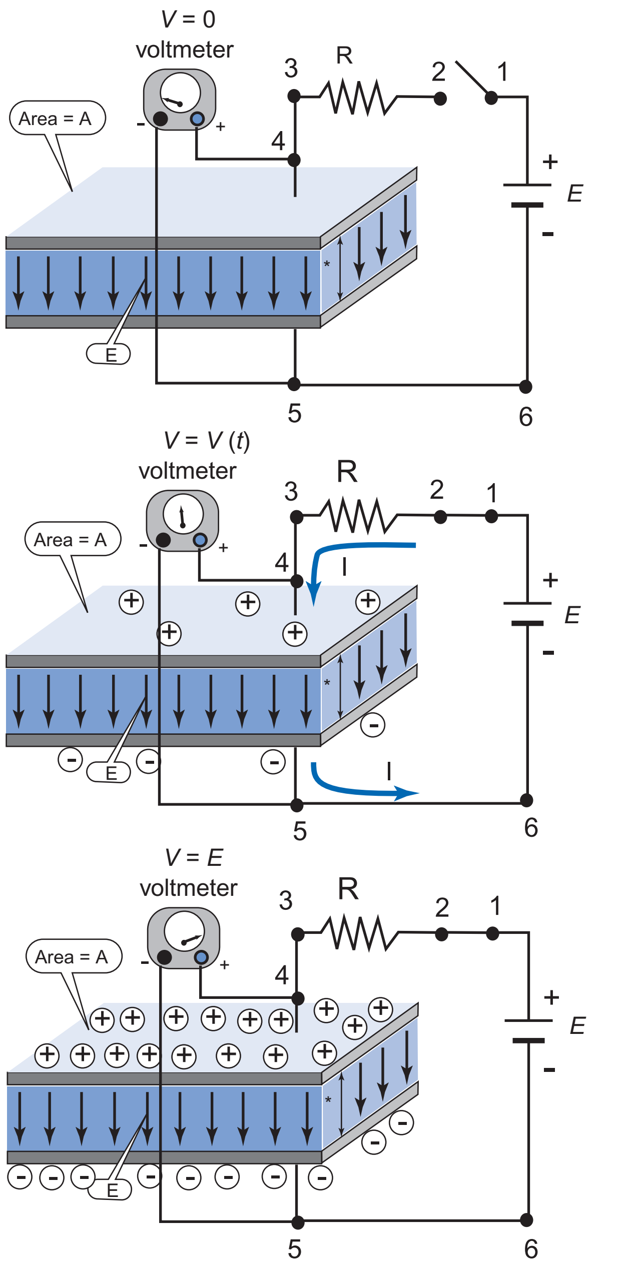

FIGURE 1.3.13 Charging of a capacitor. The capacitor consists of two parallel conducting plates separated by a dielectric, or insulating, material. At the start, top, the circuit is broken by a switch and there is no potential difference across the capacitor. When the switch is closed, middle panel, charge begins to move, making a current. The positive charges on the top plate repel positive charges on the bottom plate, which move back to the battery, completing the circuit for the current. This is a capacitive current, because there is no flow across the dielectric but there is a flow in the circuit. The separation of charges across the capacitor creates a potential difference related to the capacitance of the capacitor: $V = qC$. This builds up as current continues to flow until V is exactly opposite to E. At this point, current flow stops and the capacitor is fully charged.

The electrical potential at a point, A, is defined as the work necessary to bring a unit positive charge from infinite separation to that point. Therefore, positive fixed charges are associated with positive potential and negative fixed charges are associated with negative potential. Separation of charge produces a potential. The potential is measured in volts. The charge is measured in coulombs. Energy is measured in joules or volt-coulombs. Because the potential is defined as the integral of the work to move a unit positive charge from infinity to A, the electric force per unit positive charge is the negative derivative of the potential. The potential is a scalar whereas the force is a vector. The derivative here is the **gradient**, which converts the scalar potential into a force vector. The electric force per unit positive charge is the electric field.

The capacitance is defined as: $C = Q/V$, where Q is the charge and V is the potential difference across the capacitor. The capacitance of a parallel plate capacitor depends on several physical characteristics of the capacitor and is given as

$$C = \frac{k\varepsilon_0 A}{\delta}$$

where κ is the dielectric constant that depends on material between the plates, ε_0 is a physical constant, A is the area of the plates, and δ is the spatial separation of the plates. Biological membranes form capacitors with very small δ.

Ions move in response to electrical forces. This movement forms both a solute flux and an electrical current. Movement in response to electrical forces accelerates ions in solution until a terminal velocity is reached. At this point, the net force on the ion is zero and is the balance between the electrical force and the drag or frictional force on the solute particle by the solution. The average terminal velocity is the flux divided by the concentration. Ohm's Law is given as $I = E/R$.

Conservation of charge and the conservative nature of the electric force give rise to Kirchhoff's Current Law and Kirchhoff's Voltage Law. Kirchhoff's Current Law states that the sum of all currents into any node of a circuit must be zero. Kirchhoff's Voltage Law states that the potential differences around any closed loop must sum to zero. When a capacitor is connected in series with a resistor and a voltage source (a battery), the capacitor gradually becomes charged until the potential across it exactly opposes the potential of the battery. The time course of charging depends on RC, the product of the resistance and the capacitance. When the capacitor is fully charged, current in the circuit goes to zero. The value of RC is the time constant for the circuit, which is the time that the charge takes to get to within $1/e$ of its final value.

REVIEW QUESTIONS

1. What do we mean by "electric potential"?
2. What makes an electrical potential difference between two points?
3. How much energy is gained by charge q over a potential difference V?
4. What is meant by "electric field intensity"?
5. What is the relationship between charge and voltage for a parallel plate capacitor?

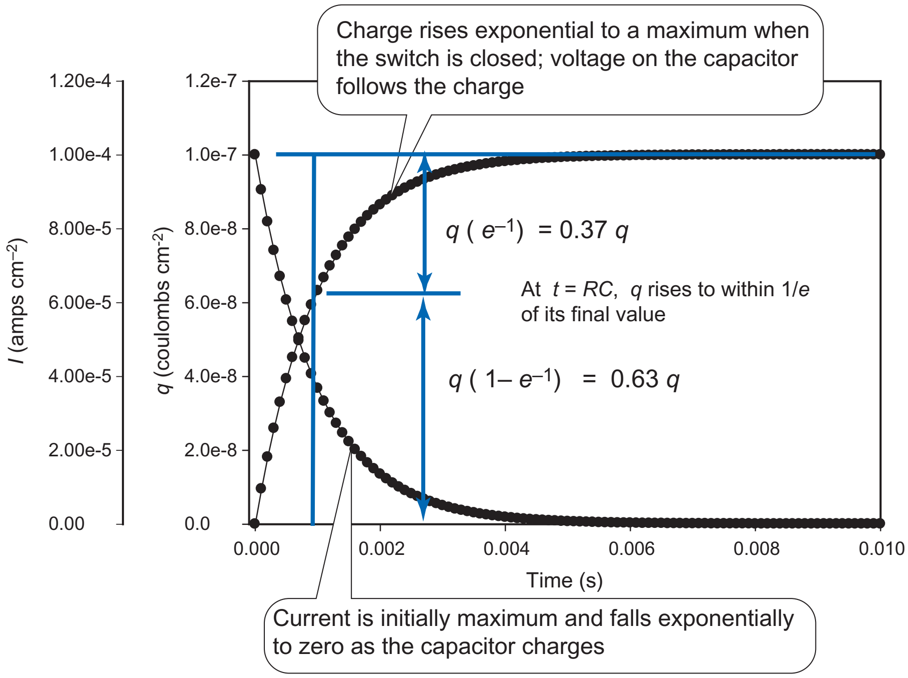

FIGURE 1.3.14 Charging of a capacitor in series with a resistor. Here the specific capacitance was taken as 1 μf cm^{-2} and the specific resistance was taken as 1000 Ω cm^2 and the time constant $RC = 1$ ms. The charge rises exponentially to reach a maximum and the current simultaneously decreases exponentially from an initial value to zero. The time constant is the time required for q to rise to with $1/e$ of its final value, which is the same as the time required for I to decrease to within $1/e$ of its final value or for I to decrease to $1/e\ I_0$.

6. Why do biological membranes act as tiny capacitors?
7. How does capacitance depend on membrane thickness and surface area? What is the dielectric constant?
8. What is the relationship between average solute velocity and solute flux?
9. What is the frictional coefficient and how does it relate to velocity and flux?
10. What is Kirchhoff's Current Law? What is Kirchhoff's Voltage Law?
11. What is meant by "resistive current"? "Capacitive current"?
12. Why does current stop in an RC circuit?
13. What is meant by the term "time constant"? What is the time constant in a simple RC circuit?