3.3 Propagation of the Action Potential

Learning Objectives

- Define propagation of the action potential
- Define conduction velocity
- Describe how conduction velocity varies with axon diameter and with myelination
- Using the formula for a parallel plate capacitor, explain how myelin decreases membrane capacitance
- Using the formula for resistances in parallel, explain how internal resistance of the axoplasm varies with axon diameter
- Define the space constant and time constant
- Describe how the space constant and time constant vary with axon diameter and myelination
- Qualitatively account for how membrane capacitance and axoplasmic resistance explain the dependence of conduction velocity on myelination and axon diameter
- Describe saltatory conduction and explain what "jumps" from node to node

THE ACTION POTENTIAL MOVES ALONG THE AXON

Consider Figure 3.3.1, which shows an axon of a motor neuron that has been impaled at intervals by recording electrodes. If an action potential is begun at the far left by depolarization to threshold, each succeeding recording electrode records an action potential. Note that the successive action potentials have similar waveforms but they are observed at each electrode at successively later times. The action potential is **propagated** along the surface of the nerve. The action potential moves over the surface of the cell, appearing some distance away after some elapsed time.

THE VELOCITY OF NERVE CONDUCTION VARIES DIRECTLY WITH THE AXON DIAMETER

The action potentials shown in Figure 3.3.1 do not have identical waveforms due to the stimulation artifact that dies out with distance along the axon. After this initial stimulation artifact decays away, all subsequent action potentials are essentially identical. The identical waveform of the action potential as it travels over the axon is a variant of the "all-or-none" description of the action potential. As the action potential appears later at longer distances from the point of initiation, we can define a **conduction velocity** of action potential propagation equal to the distance between the recording electrodes divided by the delay in time between action potentials recorded at the two sites. The velocity of action potential conduction has been determined for myelinated and unmyelinated fibers of different sizes (see Table 3.3.1).

Within each category of nerve fiber, myelinated or unmyelinated, the conduction velocity varies with the diameter of the nerve. For myelinated fibers, the conduction velocity varies approximately in proportion to the diameter. In unmyelinated fibers, the conduction velocity varies approximately with the square root of the diameter.

THE ACTION POTENTIAL IS PROPAGATED BY CURRENT MOVING AXIALLY DOWN THE AXON

How is the action potential conducted down the length of the axon? Recall that the action potential is triggered by a depolarization of the membrane to threshold. In order for an action potential to move from one place to another along the axon, the depolarization that triggers the action potential must precede it. Depolarization of the membrane proceeds **electrotonically** or passively. As shown in Figure 3.3.2, the local depolarization of the neuron's axon membrane spreads out from the origin of the depolarization.

THE TIME COURSE AND DISTANCE OF ELECTROTONIC SPREAD DEPEND ON THE *CABLE PROPERTIES* OF THE NERVE

Recall from Figures 3.2.4 and 3.2.5 that a hyperpolarizing or depolarizing stimulus was not faithfully reproduced in the axon: the signal was distorted. This distortion is a consequence of the **cable properties** of the nerve. The cable properties of the nerve refer to the passive or electrotonic properties and not to the active properties that give rise to the action potential. Each length of axon is characterized by an Ohmic resistance to current across the membrane (R_m), a capacitance (C_m), a resistance through the external solution that bathes the membrane (R_o), and a resistance through the
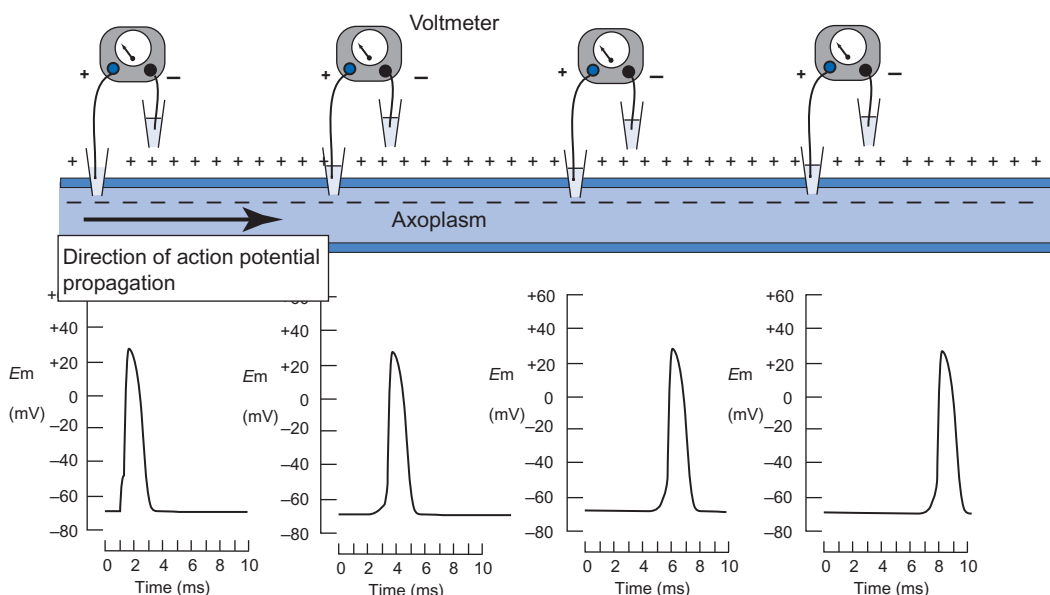
FIGURE 3.3.1 Appearance of action potentials at later times down the axon from the point of stimulation. The output of each voltmeter is shown below it.

TABLE 3.3.1 Velocity of Nerve Impulse Conduction as a Function of Axon Size

| Nerve Fiber Type	Diameter (μm)	Conduction Velocity (m s^{-1})	Physiological Function
Aα	12−22	70−120	Somatic motor
Aδ	1−5	12−30	Pain, sharp
C	0.5−1.2	0.2−2	Pain, ache

axoplasm that fills the axon (R_i). A schematic diagram of this electrical model is shown in Figure 3.3.3.

If we pass a constant current across the membrane between nodes A and B, for example, so that some new membrane potential E is established, we should expect that the membrane potential Ex at some point x away from the current source will depend on the distance from the current source and, because of the capacitances, it will also depend on the time since the current was turned on. The cable properties determine this dependence on position x and time t.

CAPACITANCE DEPENDS ON THE AREA, THICKNESS, AND DIELECTRIC CONSTANT

The membrane acts much like a parallel plate capacitor. The expression for the capacitance of a parallel plate capacitor is given as

[3.3.1]
$$C = \frac{\kappa \varepsilon_o A}{\delta}$$
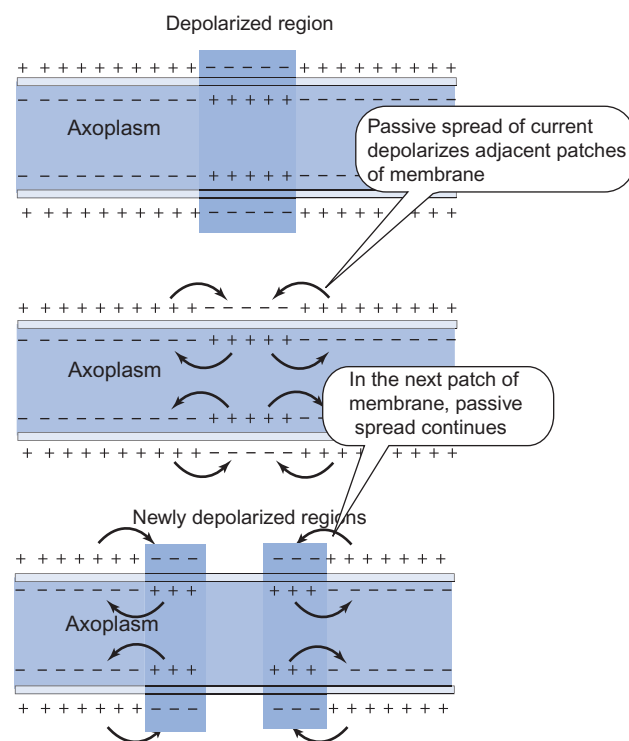
FIGURE 3.3.2 Passive spread of a depolarization to adjacent areas of membrane. Depolarization of a patch of membrane spreads to adjacent areas. If the depolarization reaches threshold in the nearby patch, an action potential will be initiated. If there is no action potential, the spread of depolarization will decay away with time and distance from the original depolarized area.

where C is the capacitance (in F = C V^{-1}), κ is the dielectric constant characteristic of the material between the plates (a dimensionless ratio), ε_0 is the electrical permittivity of the vacuum = 8.85×10^{-12} C^2 J^{-1} m^{-1},
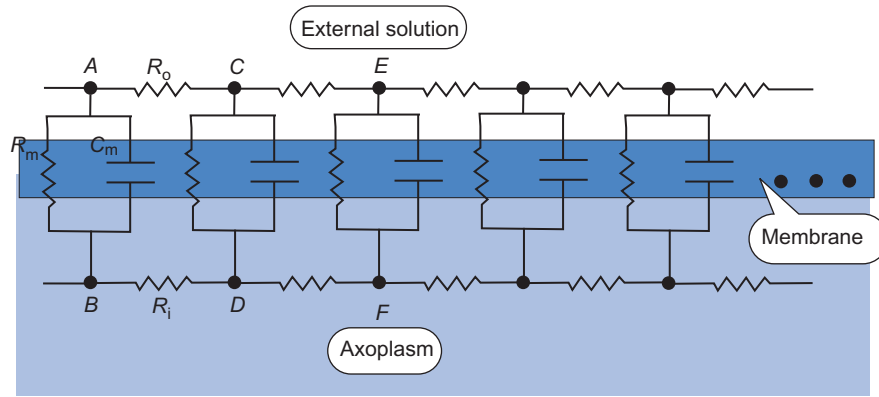
FIGURE 3.3.3 Schematic diagram of the electrical model of an axon.

A is the area (m^2), and δ is the distance between the plates (m). Since $1 \text{ J} = 1 \text{ V C}$, the units of C come out in C V^{-1}. From this equation, it should be clear that the capacitance depends directly on the area of the membrane. It is common to normalize the capacitance by dividing by the area. The **specific capacitance $C_m = C/A$** is this normalized capacitance.

The real membrane is *not* a parallel plate capacitor, but a concentric, coaxial capacitor. This does not materially affect the analysis presented here, as detailed in Appendix 3.3.A1.

CHARGE BUILDUP OR DEPLETION FROM A CAPACITOR CONSTITUTES A CAPACITATIVE CURRENT

The relationship among charge, volts, and capacitance is

$$[3.3.2] \qquad C = \frac{Q}{V}$$

where C is the capacitance, Q is the charge (in coulombs) on the capacitor, and V is the voltage difference across the capacitor. When the capacitor is charging or discharging, there is a capacitative current given as

$$[3.3.3] \qquad i = \frac{dQ}{dt} = C\frac{dV}{dt}$$

The capacitive current is given this special name because current does not pass through the dielectric, but charge builds up on one side and is taken away from the other, so effectively there is a charge movement across the capacitor without a charge flow through the dielectric.

THE TRANSMEMBRANE RESISTANCE DEPENDS ON THE AREA OF THE MEMBRANE

Adding membrane area is like adding resistances in parallel—the overall resistance actually decreases. The conductances add, whereas the inverse of the resistances add. The total conductance of a patch of membrane is the conductance per unit area times the area. Let G be the total conductance of a membrane of area A,

and G_M be the specific conductance per unit area. Similarly, let R be the total resistance, which is the inverse of the conductance, and R_M be the specific resistance. Then the resistance of a patch of membrane is given as

$$G = G_m A$$

$$[3.3.4] \qquad \frac{1}{G} = \frac{1}{G_m A} = \frac{1}{G_m}\frac{1}{A}$$

$$R = \frac{R_m}{A}$$

Here the specific resistance, R_m, is given in units of $\Omega \text{ cm}^2$, and R is in Ω. These units may seem peculiar, that the resistance per unit area is given as $\Omega \text{ cm}^2$, but this is a consequence of Ohm's Law that gives the current as being inversely proportional to the resistance.

THE AXOPLASMIC RESISTANCE DEPENDS ON THE DISTANCE, AREA, AND SPECIFIC RESISTANCE

The resistance of an electrolyte solution such as that in the axon is typically given as its **specific resistance**, ρ. This is the resistance between two faces of a cube 1 cm on a side. Since resistances in series add, the resistance of a length of solution is just the length times the specific resistance. The resistance of an area of electrolyte solution is the specific resistance divided by the area, as in Eqn [3.3.4]. So the equivalent resistance of the axoplasm is given as

$$[3.3.5] \qquad R_i = \frac{\rho_i d}{A}$$

where d is the distance and A is the cross-sectional area. Since R_i has the units Ω, ρ_i has the units $\Omega \text{ cm}$.

THE EXTRACELLULAR RESISTANCE ALSO DEPENDS ON THE DISTANCE, AREA, AND SPECIFIC RESISTANCE

The resistance provided by the extracellular electrolyte solution is entirely analogous to the axoplasmic

resistance. However, the area involved here is not precisely known and it is large. Because the area appears in the denominator of Eqn [3.3.5], typically the outside resistance is small compared to the axoplasmic resistance. We will treat R_o as being zero, so that the voltage everywhere along the axon on the outside is zero.

CABLE PROPERTIES DEFINE A *SPACE CONSTANT* AND A *TIME CONSTANT*

Consider part of the schematic diagram of Figure 3.3.3 shown in Figure 3.3.4. Analysis of the currents as a function of distance will allow us to characterize the axon in terms of its **cable properties**. These include a **space constant** and a **time constant**.

One of Kirchoff's circuit laws states that **the sum of all currents out of any node must be zero**. This is just another way of saying that there is a conservation of total charge. Applying this principle to node (x) in Figure 3.3.4, we have

[3.3.6] $$i(x) = i(x + dx) + i_m$$

where $i(x)$ is the current passing down the axon into the node at (x), i_m is the current that passes through the membrane at this node, and $i(x + dx)$ is the current that passes down to the next node at $(x + dx)$. The current across the membrane, i_m, has two parts: one part that passes through the resistance and a second part that either charges or discharges the capacitor.
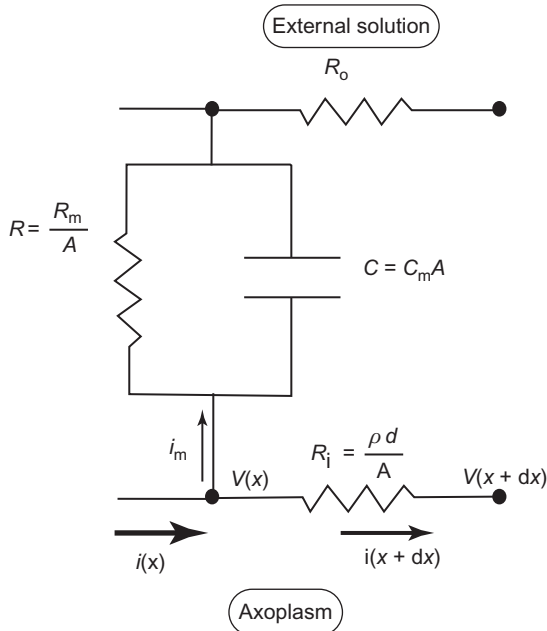
FIGURE 3.3.4 Currents at a patch of membrane area of the axon. C is the capacitance of the membrane; C_m is the specific capacitance; R is the resistance across the axon membrane; and R_m is the resistance per unit area; i_m is the current across the membrane; $i(x)$ is the current down the axon at node x. R_i is the internal resistance of the axoplasm and ρ_i is its specific resistance.

The current i_m can be written as

[3.3.7] $$i_m = \frac{V(x) - V_r}{R_m} A + C_m A \frac{dV}{dt}$$

where $V(x)$ is the membrane potential at position x and V_r is the membrane potential at rest at which the net membrane current is zero. The first part of the right-hand side of this equation is just Ohm's law for the current through the resistance across the membrane. The second part is from Eqn [3.3.3] and describes that part of the current that either charges or discharges the capacitor. Substituting Eqn [3.3.7] into Eqn [3.3.6], we have

[3.3.8] $$i(x) = i(x + dx) + \frac{V(x) - V_r}{R_m} A + C_m A \frac{dV}{dt}$$

This equation can be rearranged, using $A = 2\pi a\, dx$ as the surface area of the membrane element, where a is the radius of the axon. Insertion of the area in Eqn [3.3.8] and rearranging, we obtain

[3.3.9] $$\frac{i(x + dx) - i(x)}{dx} = -2\pi a \frac{V(x) - V_r}{R_m} A - 2\pi a C_m A \frac{dV}{dt}$$

In the limit as $dx \to 0$, the left-hand side of this equation is the definition of the derivative. Taking this limit, we derive

[3.3.10] $$\frac{di}{dx} = -2\pi a \frac{V(x) - V_r}{R_m} - 2\pi a C_m \frac{dV}{dt}$$

There is another relationship between i and $V(x)$ that we can use here, and that is Ohm's law through R_i. There would be no longitudinal current unless there is a voltage gradient in x. Ohm's law gives the longitudinal current, i, in Eqn [3.3.10] as

[3.3.11]
$$i = \frac{V(x) - V(x + dx)}{R_i}$$
$$i = -\frac{V(x + dx) - V(x)}{(\rho_i dx / \pi a^2)}$$
$$i = -\frac{\pi a^2}{\rho_i} \lim_{dx \to 0} \left[\frac{V(x + dx) - V(x)}{dx} \right]$$
$$i = -\frac{\pi a^2}{\rho_i} \frac{dV}{dx}$$

Substituting this result for i into Eqn [3.3.10], we derive

[3.3.12] $$-\frac{\pi a^2}{\rho_i} \frac{d^2 V}{dx^2} = -2\pi a \frac{V - V_r}{R_m} - 2\pi a C_m \frac{dV}{dt}$$

which can be rearranged to

[3.3.13] $$V - V_r = \frac{R_m \pi a^2}{2\pi a \rho_i} \frac{d^2 V}{dx^2} - \frac{R_m}{2\pi a} 2\pi a C_m \frac{dV}{dt}$$

If we let $V' = V - V_r$, this equation has the form

[3.3.14] $$V' = \lambda^2 \frac{d^2 V'}{dx^2} - \tau \frac{dV'}{dt}$$

Here λ is identified as a **space constant** and τ is a **time constant**, so named because they govern the spatial and time derivatives of the voltage when a constant current is injected across the membrane. By comparison with Eqn [3.3.13], their values are given as

[3.3.15]
$$\lambda = \sqrt{\frac{R_m \pi a^2}{\rho_i 2\pi a}} = \sqrt{\frac{R_m}{\rho_i} \frac{a}{2}}$$
$$\tau = R_m C_m$$

Note that at steady state, when $dV/dt = 0$, the space constant defines the way in which the voltage varies with distance. This would be the case when a constant current has been passed across the membrane for a sufficiently long time to charge all the capacitors to their steady-state level. In this case, Eqn [3.3.14] becomes

[3.3.16]
$$V' = \lambda^2 \frac{d^2 V'}{dx^2}$$

The relevant solution to this differential equation is

[3.3.17]
$$V = (V_0 - V_r)e^{(-x/\lambda)} + V_r$$

This equation means that the voltage falls off exponentially from the point of current application to the nerve to its value some large distance away. Here the resting **variable V_0 refers to the voltage at $x = 0$ and V_r is the resting voltage some large distance away**. The equation looks this way because of the boundary conditions that $V = V_0$ when $x = 0$, and $V = V_r$ when $x = \infty$. These boundary conditions arise because of the way that we set up the situation: the current at a specified point on the axon is constant and it is applied for sufficiently long times that the capacitors are all charged and the capacitative currents go to zero. Under these conditions, at steady state, the voltage at the point of current application will be V_0 and the voltage far away (actually, infinitely far away) will be the resting membrane potential. This condition is called **electrotonus**.

Note that the space constant described in Eqn [3.3.15] consists of two resistances: the resistance to current flow across the membrane and the resistance to current flow down the interior of the axon. If the resistance across the membrane becomes larger, as occurs in myelinated fibers, then the space constant will be larger. If the resistance of the axoplasm is smaller, as occurs when the axon is larger (and therefore has a larger cross-sectional area, which participates in the determination of R_i), then the space constant will be larger. Figure 3.3.5 shows the voltage as a function of distance from the point of application of an inward current sufficient to depolarize the cell to -40 mV without the engagement of the active behavior of the axon, say in a TTX-poisoned nerve. In myelinated fibers, the voltage decreases slowly away from the point of current injection because λ, the space constant, is large. In contrast, the steady-state voltage in unmyelinated fibers decays rapidly away from the point of injection of the current.

From Eqn [3.3.17], the space constant is the distance for the voltage difference, $(V - V_r)$, to fall from $V_0 - V_r$ to within $1/e$ of $V_0 - V_r$, which is $0.367 \times [V_0 - V_r]$. This can be readily seen by letting $x = \lambda$, at which point $V - V_r = [V_0 - V_r] \times 1/e$. The larger space constant in myelinated fibers means that a depolarization maintains a higher voltage at longer distances, because more of the current travel down the axon to change the membrane potential as opposed to going through the membrane. Equation [3.3.15] predicts that the space constant will vary with the square root of the axon diameter. This is the case with unmyelinated fibers. In myelinated fibers, the value of R_m increases proportionate to the radius. So the overall length constant would be proportional to the square root of the square of the radius or approximately proportionate to the radius.

Substituting in for R_m and ρ_i from Eqns [3.3.4] and [3.3.5] into Eqn [3.3.15], and using the area terms $2\pi ad$ for the surface area (relevant to R_m) or πa^2 for the cross-sectional area (relevant to R_i), we obtain

[3.3.18]
$$\lambda = \sqrt{\frac{R_m}{\rho_i} \frac{a}{2}}$$
$$= \sqrt{\frac{2\pi a dR}{(\pi a^2/d)R_i} \frac{a}{2}}$$
$$= \sqrt{\frac{dR}{(R_i/d)}}$$
$$= \sqrt{\frac{R}{R_i} d^2}$$

It is important to note that the units of these resistances are different because of the way in which they have been normalized. R_m is the resistance per unit area, and so its units are Ω cm^2. The specific resistivity, ρ_i, is in units of resistance per unit area per unit length, so its units are Ω cm. Insertion of these units in Eqn [3.3.18] gives the proper units of distance in the calculation of λ. R and R_i are resistances, in Ω. Since these resistances depend on the distance down the axon, the distance used is included in the calculation of R and R_i. Sometimes it is convenient to express the resistances as resistances per unit length. These variables are commonly noted as r_m and r_i, with units of Ω cm and Ω cm^{-1}, respectively. This is equivalent to identifying

[3.3.19]
$$r_m = dR$$
$$r_i = \frac{R_i}{d}$$

in Eqn [3.3.18]. The utility of this nomenclature is that the space constant is then given simply as

[3.3.20]
$$\lambda = \sqrt{\frac{r_m}{r_i}}$$

The **temporal** properties of cables can be made readily apparent by using a **space clamp**. This is accomplished

Extracellular space
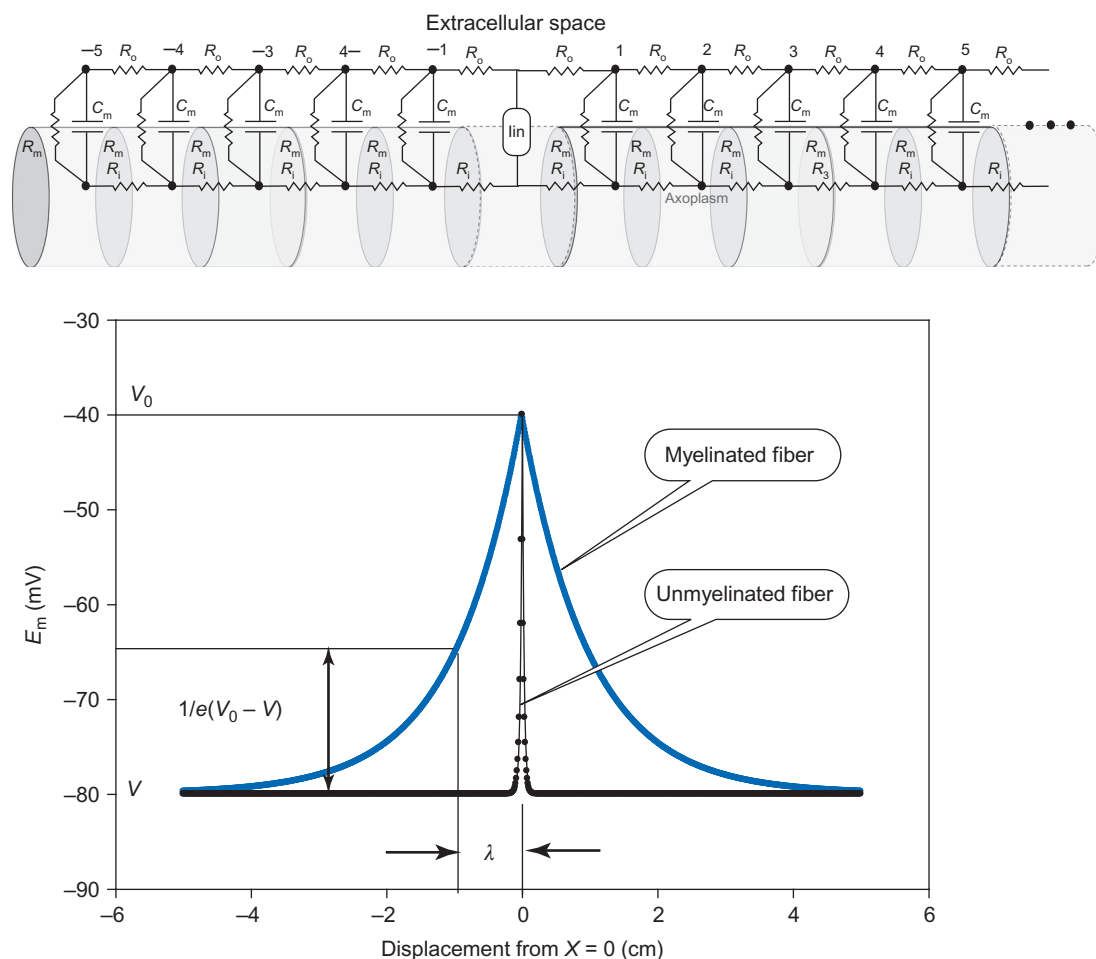
FIGURE 3.3.5 Steady-state voltage as a function of distance from the point of injection of current in myelinated and unmyelinated nerve fibers. In unmyelinated nerves, the voltage drops off quickly with distance, implying a small space constant because R_m is small and R_i is large. In myelinated fibers, the voltage drops off much less with distance, indicating a large space constant.

experimentally by passing a thin wire down the axon, effectively making $R_i = 0$. This removes the spatial dependence of $V(x,t)$ caused by passing a current. Here $dV/dx = 0$ and Eqn [3.3.14] becomes

[3.3.21] $$V' = -\tau \frac{dV'}{dt}$$

This is a familiar equation for exponential decay. The applicable solution is

[3.3.22] $$V = (V_0 - V_r)e^{-(t/\tau)} + V_r$$

where the time constant, $\tau = R_m C_m$ does not vary very much from myelinated to unmyelinated fibers because myelination increases R_m according to the thickness of the myelin layer, but it decreases C_m inversely with the thickness of the myelin layer. The time constant describes the characteristic time for the capacitor to charge or discharge from the initial value to the final value. Here $V_0 - V_r$ refers to the difference between the membrane potential initially and the membrane potential at steady state after injection of current. Note that, as with the space constant, the time constant is defined as the time necessary for the voltage difference to decay

to $1/e = 0.367$ of the difference to its new value. Each patch of membrane is identical in this way, but the distributed nature of the capacitors and resistances makes the response of each membrane dependent on its distance from the current source. In this way, the patches of membrane nearer the current source charge faster than exponentially, and those further away charge slower than exponentially. This phenomenon is easily modeled using electronic networks.

THE CABLE PROPERTIES EXPLAIN THE VELOCITY OF ACTION POTENTIAL CONDUCTION

As we discussed in the section "The Action Potential Is Propagated by Current Moving Axially Down the Axon," the action potential occurs at a specified location x because the membrane is depolarized to threshold at that location. If the depolarization occurs earlier at location x, then the action potential also occurs earlier at that location and the velocity of nerve impulse conduction is faster. Myelinated nerves have a longer space constant. Thus the depolarization occurring some distance x away
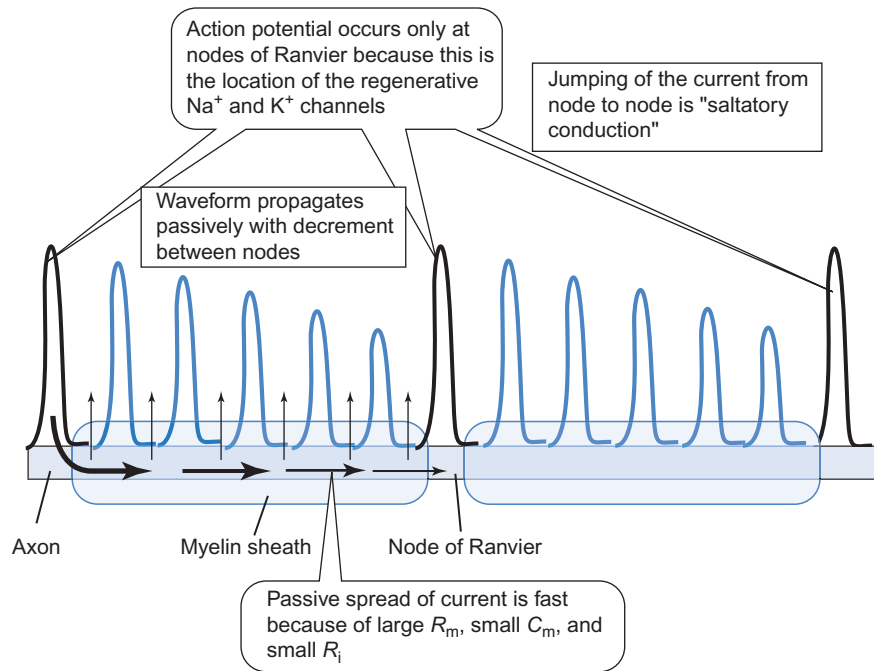
FIGURE 3.3.6 Saltatory conduction. The inward current accompanying an action potential travels down the axon to depolarize adjacent parts of the cell. In myelinated fibers, little of the current is lost across the membrane because the transmembrane resistance is high (myelin insulates the axon) and little is lost to discharging the capacitor of the axon because the capacitance is low. Enough current remains to depolarize the axon at the next node of Ranvier where voltage-gated Na^+ channels reside. In this way, myelin increases conduction velocity. In between nodes, the "action potential" does not involve active currents across the membrane: it is a passive spread of the waveform of the action potential. Its decrement shown here is exaggerated for illustrative purposes.

from the point of stimulation is greater in the myelinated nerve. This is due to the fact that:

- more of the current can travel down the axon, because its resistance is less due to its larger size;
- less of the current crosses the membrane, because its resistance is larger in the myelinated fibers;
- less current is required to depolarize the membrane, because the membrane capacitance is smaller due to the greater thickness of the myelin (see Eqn 3.3.1).

All of this conspires for depolarization to be reached sooner at distances remote from the source of stimulation. When depolarization is reached sooner, the action potential occurs sooner and action potential velocity increases.

SALTATORY CONDUCTION REFERS TO THE "JUMPING" OF THE CURRENT FROM NODE TO NODE

As mentioned earlier in Chapter 3.2, myelinated fibers consist of axons that are surrounded by multiple coverings of the plasma membranes of Schwann cells in the peripheral nervous system and oligodendroglia cells in the central nervous system. These wrappings provide the increased resistance and decreased capacitance that produce a long space constant and allow for rapid nerve impulse conduction. These wrappings are not continuous, however. There are gaps between the Schwann cells, and each gap is called a **node of Ranvier**. The nodes themselves are only a $2-3 \, \mu m$ long, whereas

the internodal distance is typically $1-3 \, mm$. These nodes contain abundant voltage-gated Na^+ and K^+ channels. At each node, these channels respond to the depolarization of the membrane by undergoing the conductance changes that we discussed in Chapter 3.2. In between the nodes, the myelin insulates the nerve plasma membrane from the extracellular solution so that the resistance is large and few channels are present. Huxley and Stampfli experimentally established that the current occurs mainly at the nodes. Thus the current appears to "jump" from node to node. This is called **saltatory conduction** (from the Latin "saltatio" meaning "to leap" or "to dance"). In between the nodes, the membrane potential is conducted electrotonically, or passively, without the necessity of regenerating the action potential. The great advantage in speed is provided by the rapid electrotonic spread of depolarization from node to node. In addition, the electrotonic spread does not require the active generation of currents at every patch of membrane, so less inward current is required for action potential propagation and so less energy is used to pump out the Na^+ that enters the nerve with each action potential. Figure 3.3.6 illustrates saltatory conduction.

THE ACTION POTENTIAL IS SPREAD OUT OVER MORE THAN ONE NODE

Each action potential lasts about 2 ms. The conduction velocity in a large myelinated fiber is on the order of $100 \, m \, s^{-1}$. Thus the action potential is spread out over

a distance of $100 \text{ m s}^{-1} \times 0.002 \text{ s} = 0.2 \text{ m}$ or 20 cm. Since each node is separated by about 2 mm, the entire action potential at any one time is spread out over 100 nodes. This calculation should make it clear that the nerve impulse does not "jump" from node to node, as it occupies many nodes. The current that produces the action potential occurs only at the nodes, because that is where the channels are concentrated and where the axon membrane has contact with the extracellular fluid.

SUMMARY

The brief, pulse-like change in membrane potential, the action potential, moves along axons with definite velocity. The action potential propagates with essentially the same waveform all along the axon. The velocity of action potential propagation varies with myelination and axon size. In unmyelinated axons, the velocity varies approximately with the square root of axon diameter. In myelinated fibers, the velocity varies approximately in proportion to the diameter. The velocity of action potential propagation arises from the cable properties of nerves.

Depolarization starts the action potential. The action potential itself is a depolarization that passively spreads to nearby patches of membrane. When nearby patches of membrane reach threshold, they begin an action potential at that point. The rate of passive spread of current depends on the resistance of the membrane, the capacitance of the membrane, and the resistance of the axoplasm. These are quantitatively represented in the time constant and the length constant. The length constant describes the drop-off of membrane potential from a point of current injection at the steady state when we apply a constant inward current. It is an exponential decrease with distance, and the length constant is a factor in the exponential. It is the distance it takes $V_0 - V_r$ to fall to $1/e(V_0 - V_r)$. The time constant describes the time for the membrane capacitor to charge or discharge under conditions of space clamp.

If the resistance of the membrane is increased, more of the depolarizing current passes down the axon and discharges the capacitor on the membrane. Thus insulating the membrane with myelin increases the passive spread of current and increases conduction velocity. Decreasing the membrane capacitance also increases conduction velocity. Adding myelin increases the thickness of the membrane capacitor, which decreases its capacitance. Increasing the diameter of the axoplasm decreases the internal resistance, which facilitates passive spread of current and increases conduction velocity.

Myelinated nerves generate a true action potential only at the nodes of Ranvier. The nodes are breaks in the myelin sheath that occur between neighboring Schwann cells that form the sheath. The nodes are $2-3 \mu m$ long and occur about $1-3 \text{ mm}$ apart. The spread of the action potential between nodes is electrotonic, meaning that it spreads passively with some decrement between nodes. Current passes only at the nodes. This jumping of current from node to node is called saltatory conduction.

REVIEW QUESTIONS

1. What effect does myelination have on conduction velocity? What does myelin do to transmembrane resistance? Membrane capacitance?
2. What effect does axon diameter have on conduction velocity?
3. What effects does axon size have on the internal resistance to current flow along the axon length?
4. What is the time constant of an axon? Why is it relatively unaffected by myelination? How would you measure the time constant?
5. What is the space constant of an axon? What determines its value? What effect does myelination have on the space constant? How would you measure the space constant?
6. What is meant by "saltatory conduction"? What jumps from node to node?

APPENDIX 3.3.A1 CAPACITANCE OF A COAXIAL CAPACITOR

USE OF GAUSS'S LAW TO DERIVE CAPACITANCE

In Chapter 1.3, we discussed Gauss's law and how it can be used to determine the electric field intensity between the plates of a capacitor, and how that could be used to determine the capacitance. Gauss's law is a direct consequence of Coulomb's law and is written as

[3.3.A1.1] $$\oint \mathbf{E} \cdot d\mathbf{s} = \frac{q}{\varepsilon_0}$$

where the integral is the integral over a closed surface of the dot product of the electric field and the area vector, equal to the area increment and oriented normal to the surface. What this says is that this dot product, evaluated over *any* close 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 allows us to determine the electric field intensity from a given charge.

The second necessary idea here connects the electric field intensity to the voltage. The electric field is the negative of the spatial derivative of the potential; specifically, the electric field is the negative gradient of the potential (see Chapter 1.3 for a discussion of the gradient). We can write this as

[3.3.A1.2] $$\mathbf{E} = -\nabla V$$

where $\mathbf{E}$ is the electric field and V is the voltage. Knowing $\mathbf{E}$ from Gauss's law, and the enclosed charge, q, we can obtain V. This enables us to determine the capacitance as

[3.3.A1.3] $$C = \frac{q}{V}$$
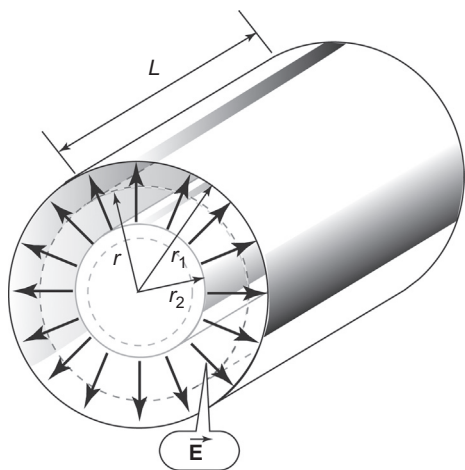
FIGURE 3.3.A1.1 Coaxial capacitor consists of concentric cylinders. The inner cylinder has an outer radius of r_1 (the charges are located on its surface) and the outer cylinder has an inner radius of r_2. Both cylinders are of length L. The electric field is oriented radially outward between the two concentric cylinders.

THE CAPACITANCE OF A COAXIAL CABLE

We now consider the capacitance of a coaxial, cylindrical capacitor as shown in Figure 3.3.A1.1. The inner radius is r_2 and the outer radius is r_1. We consider a length, L, of the capacitor and draw a Gaussian surface as shown so that one side of the closed surface is inside the inner cylinder and the other is in the middle of the capacitor at a radius of r. This is indicated in the figure by a dashed line. The Gaussian surface is of length L and encloses itself at the ends by two circles oriented parallel to the electric field. By symmetry, the electric field is directed radially outward and is normal to the Gaussian surface we have chosen, precisely for that reason. Thus, Gauss's law gives

[3.3.A1.4]
$$\oint \mathbf{E} \cdot \mathbf{ds} = \mathbf{E} 2\pi r L = \frac{q}{\varepsilon_0}$$

$$\mathbf{E} = \frac{q}{\varepsilon_0 2\pi r L}$$

From the definition of $\mathbf{E}$ and V, we have

[3.3.A1.5]
$$\mathbf{E} = -\nabla V = -\frac{dV}{dr}$$

because of the radial symmetry of this situation. Here $-dV/dr$ gives the magnitude of $\mathbf{E}$, not its direction. In the same way, Eqn [3.3.A1.4] gives the magnitude of $\mathbf{E}$ and not its direction. We equate these two to evaluate the potential difference across the capacitor:

$$-\frac{dV}{dr} = \frac{q}{\varepsilon_0 2\pi r L}$$

[3.3.A1.6]
$$\int_2^1 -dV = \int_2^1 \frac{q}{\varepsilon_0 2\pi L} \frac{dr}{r}$$

$$V_2 - V_1 = \frac{q}{\varepsilon_0 2\pi L} \ln \frac{r_1}{r_2}$$

The capacitance is then calculated as $q/\Delta V$:

[3.3.A1.7]
$$C = \frac{q}{V_2 - V_1} = \frac{\varepsilon_0 2\pi L}{\ln(r_1/r_2)}$$

This is the final equation for the capacitance for a coaxial capacitor. This reverts to the formula for a parallel plate capacitor if the separation of the plates is small compared to their radii. To see this, we write

[3.3.A1.8]
$$r_1 = r_2 + \delta$$

where δ is the separation of the plates. Inserting this into Eqn [3.3.A1.7], we have

$$C = \frac{\varepsilon_0 2\pi L}{\ln((r_2 + \delta)/r_2)}$$

$$= \frac{\varepsilon_0 2\pi L}{\ln(1 + (\delta/r_2))}$$

[3.3.A1.9]
$$= \frac{\varepsilon_0 2\pi L}{(\delta/r_2)}$$

$$= \frac{\varepsilon_0 2\pi r_2 L}{\delta}$$

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

This last equation is the formula for the capacitance of a parallel plate capacitor. This relies on the approximation $\ln(1 + \alpha) \approx \alpha$ for small values of α. This approximation is only moderately good for axons in which α might be 1.0, where the thickness of the myelin sheath is as great as the radius of the axon itself.