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Neurons and Sensory Receptors

INTRODUCTION

Virtually all animal cells react in some way to the physics and chemistry of the environments that they inhabit. Some multicellular animals, however, have evolved a special network of cells (neurons) that have the ability to communicate with specific groups of other neurons in a highly precise manner. This cellular communication network is the nervous system. Among the advantages of a nervous system are that it is able to take information about the surrounding environment and process it in some way before the animal reacts. This processing provides the animal with options such as to respond or not respond to a stimulus, or to respond one way or another way. In addition, a nervous system offers the ability to store information about the consequences of a particular response to a particular environmental stimulus; this information can then have an impact on the course of future action when a similar stimulus next occurs. Because of the wide range of chemical and physical events that are of importance to animals, certain neuron or neuron-like cells became specialized for the detection of these stimuli, such as light, pressure, chemical, and temperature detectors. These nervous system specializations, known as receptors, along with specializations of various body parts, permitted animals to enter and exploit new regions of the environment. To the extent that these explorations were successful, they led to further specialization and adaptation.

In this chapter we will examine some of the fundamentals of the anatomy of neurons and receptors as individual elements of the nervous system. In subsequent chapters we explore the organization of these elements into neuronal systems. Among these systems are:

- Sensory systems that acquire information about the external and internal environments.
- Integrative systems that process the incoming information, evaluate this information, often in the context of past experience, and make decisions for action or inaction, depending on the circumstances.
- Motor systems that convert decisions into commands for action (or inaction) by effector organs (muscles and glands).
- Coordinating systems that organize the patterns of commands to the effector organs, especially muscle groups, to assure that the individual effector organs or groups of organs operate on the environment in a smooth, efficient, and orderly way.

THE NERVOUS SYSTEM

The nervous system, like all organs of the body, is made up of cells. Like many organs, the nervous system contains more than one specialized type of cell. Unlike other systems of the body, however, the nervous system has a great variety of cell types and sizes arranged in highly specific ways, which are fundamental to its operation. Indeed, these highly specific relationships between its cellular constituents are what give the nervous system its unique character, which permits us to have automatic central control over our internal organs, to sense the external and internal environments, to remember, to think, to communicate, and so on. These functions depend on precise interconnections between specific cell populations. In no other biological system does the functioning of that system depend on such precise and rapid communication between

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one particular cell and another. Moreover, the sequences in which the cells communicate are fundamental to the way in which the nervous system functions. If, for example, these relationships are interfered with by injury, disease, or developmental malformation, important visceral and behavioral functions that the nervous system performs will be impaired.

Another major difference between the nervous system and other organs is the distance over which many of the cellular components communicate. In large animals such as humans, whales, elephants, and giraffes, the distances over which a single neuron communicates with other neurons can be a meter or more. In addition, in these large creatures, the lengths of the cells that carry information from the body surface to the nervous system and those that carry the nervous system's commands to the muscles can be many meters in length.

The cells of the central nervous system fall into two broad categories: **neurons** and **glia**. The neurons are the communication and information-processing elements of the nervous system. The glia are support elements; they protect and nurture the neurons and may play a subtle role in the processing of information. In addition to its cells, the nervous system contains a rich supply of blood vessels to bring oxygen and nutrients to the cells and to remove waste products.

Neurons communicate with each other by means of signals that are mostly chemical, sometimes electrical, and occasionally a mixture of the two. When the communication must be carried out at a distance, the transmission of the signal along the length of the neuron is carried out by means of an electrochemical process known as the nerve impulse or action potential. Because so much of the mechanism of transmission of the signal from cell to cell is by means of the rapid secretion of chemicals into the minute space between cells, neurons may have evolved from secretory cells that became specialized for secretion to one particular cell rather than to any cells that happen to be in its vicinity. As the nervous system grew in size and neurons became spatially separated, they developed the capability to maintain their specific-cell-to-specific-cell contacts over longer and longer distances.

Because the nervous system is the organ of behavior, it must acquire information about the external world and the condition of internal organs and systems. This information is acquired by means of specialized cells called **sensory receptors**. Many receptors are specialized neurons; others are neuron-like cells that have a number of properties in common with neurons and are innervated by neurons that relay the sensory signals to the central nervous system.

The following sections contain a brief description of some characteristics of neurons and receptors that will be especially useful for readers of this book. We assume that the reader already has a basic familiarity with the structure of neurons, their component parts, and the basic principles of axonal conduction and synaptic transmission. Readers who lack this background or wish to refamiliarize themselves with it will find a separate listing of introductory works on these subjects at the end of this chapter.

NEURONS AND SENSORY RECEPTORS

The main components of the neuron are the cell body, or **soma**, and its processes or outgrowths: the **axon** with its axon terminals and the **dendrites** with their dendritic branches and spines. Each of these components can be found in a seemingly endless variety of configurations. Figure 2-1 shows three examples from the wide variety of neuron types. In each of the examples, the arrows indicate the direction of flow of the nerve impulse. The motor neuron shown in Figure 2-1(A) shows the main components of neurons. The star-shaped, solid black region represents the soma, which consists of a cell membrane that contains cytoplasm and the **nucleus**.

The large extensions or processes that give the soma its star shape are the dendrites. The dendrites themselves may have further processes extending from them and are known as dendritic branches. These branches in turn often subdivide further into smaller and smaller branches until they take on the appearance of a leafless tree in winter. The soma and its dendritic tree are the most frequent points of contact between a neuron and those other neurons that are sending their communication signals to it. The size and shape of the soma can vary enormously among neuron types. The soma may be as small as a few micrometers to more than a millimeter, as in the giant cell of Mauthner, which is discussed in Chapter 8. It may be star shaped, as in the example, or it may have many other forms, such as that of a pyramid (pyramidal cell), a pear (piriform cell), or a spindle (fusiform cell), examples of which are shown in Figure 2-3. Dendrites can vary in length from a fraction of a micrometer to many millimeters.

Also projecting from the soma is the axon, which is the component of the neuron that permits long-distance communication. Often axons also are referred to as "nerve fibers" or simply "fibers." In this book, we will use the terms axons and fibers interchangeably. The axon leaves the soma from a gentle swelling called the axon hillock and travels over distances that

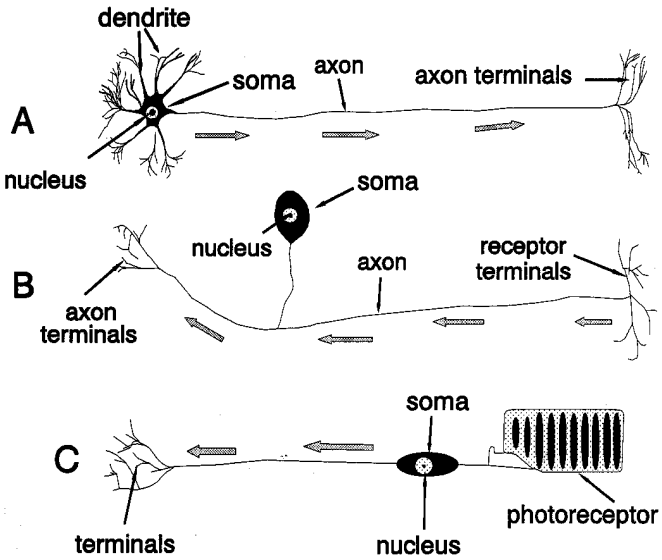

FIGURE 2-1. Examples of three types of neurons. (A) A typical motor neuron with a roughly star-shaped soma, dendrites, axon, and axon terminals. (B) A typical sensory neuron with a pear-shaped soma that is separated from the axon by a stem. This type of neuron does not have dendrites. (C) A receptor neuron, in this case a photoreceptor from the retina, that has neither an axon nor dendrites.

can vary greatly among cell types from a few micrometers to a meter or more. Most axons remain within the central nervous system, but some leave the central nervous system and end on muscles or glands; these axons are called effectors or motor neurons. The neuron illustrated in Figure 2-1(A) is typical of motor neurons that control muscles of the skeleton. Its axon would leave the central nervous system and travel to a muscle where it would divide into a series of branches before terminating on the muscle fibers.

Not all neuron somata (plural of soma) have dendrites. Figure 2-1(B) illustrates a neuron type that has no dendrites in the conventional sense. Its principal source of stimulation is not another neuron at all but rather is some event outside of the central nervous system. It is a sensory receptor neuron, and, like the effector neuron in Figure 2-1(A), it too has most of its process in the environment outside of the central nervous system. In this case, however, the process is actually a very long dendrite. At the right are its receptor branches, which might be under the surface of the skin or wrapped around a small group of muscle fibers to detect muscle stretch. Other such sensory branches might be in contact with specialized receptor cells, such as those that detect light or electric fields, or one of the different types of hair cells that detect the movement of fluids in the auditory or vestibular systems. Mechanical deformation of the receptor branches or activation of the specialized receptor cell activates this sensory or receptor neuron to send a signal along its process and past its cell body, after which point the process is a true axonal fiber, and then to the axon terminals that end on neurons within the central nervous system. Other receptor types detect chemical changes in the external and internal environments.

The soma of this type of neuron typically remains outside of the central nervous system in a sensory **ganglion** and does not participate directly in the process of conduction of the propagated signal. It provides nutritional and metabolic support to the dendritic and axonal parts of its process but is not an active player in the flow of information into the central nervous system. Some sensory neurons, however, have their somata within the central nervous system.

Figure 2-1(C) represents a type of sensory neuron, a photoreceptor, that is specialized for the detection of photons of light. These are the receptors of the eye that convert the energy of light into signals that can be conducted to the brain. The photoreceptor end is activated by photons of light and in some sense can be thought of as a highly specialized dendrite. Activation of the photoreceptor eventually leads to the development of a signal that is conducted along the cell to a terminal where it contacts another neuron that conducts the signal further into the central nervous system.

TRANSPORT WITHIN NEURONS

The soma produces many materials that are important for the maintenance of the internal and external workings of the neuron. These materials include enzymes and other substances that participate in the synthesis of neurotransmitters and neuromodulators; proteins for use in the formation of synaptic vesicles, ion channels, and membrane receptors; and proteins for the maintenance of the neuron's internal skeleton. Still other materials are necessary for maintenance of the cell membrane, which is the boundary between the inside and outside of the cell. Finally, used synaptic vesicles, depleted mitochondria, and other organelles must be returned to the soma for reuse or for digestion in the lisosomes and subsequent "recycling" into new membrane.

The often extreme separation between the soma and the axon terminals and between the soma and the tips of the dendritic branches is too great for simple diffusion to function effectively. Neurons therefore have a kind of intraneuronal circulatory system to move secretion products from the soma to the remote ends of the neuron. There are, in fact, three separate transport systems within the neuron: a fast anterograde (forward moving) transport system that carries materials from the soma towards the axon terminals and dendritic branches, a fast retrograde (backwards moving) transport system in the reverse direction, and a slow axoplasmic transport system.

The fast anterograde transport system, which can move as fast as a meter a day, makes use of one of the neuron's internal skeletal elements, the microtubules, which are slender tubes that run the length of the axon. Rather than flowing through these tubules, which have too narrow a diameter in any case, the organelles are transported along the surface of the tubules by a "motor molecule" called kinesin. The fast retrograde transport, which is involved in the return of used materials to the soma for recycling, moves at a slower speed than the anterograde fast transport. The returning materials are packaged in membranes and are transported along microtubles in a manner similar to that of the fast anterograde system except that a different motor molecule, in this case dynein, moves the membrane packages along the microtubules.

The slowest (1–10 mm/day or slower) of the three transport systems is the slow axoplasmic transport system, which consists of two components: a slow system and a very slow system. The slow system carries proteins that, among other things, coat the synaptic vesicles. The very slow system carries the proteins that maintain the filamentous internal skeleton of the neuron: the microtubules, neurofilaments, and microfilaments. The ability to chemically mark many of the substances being transported within neurons has served as one of the most powerful means of visualizing the connections between neuronal populations. The similarities and differences in the patterns of connections are among the major criteria for determining evolutionary trends within the nervous system.

CLASSIFICATION OF NEURONS

Somata

Neurons may be classified in a variety of ways. Figure 2-2 shows one type of classification. The figure shows a monopolar cell without dendrites on the soma. The bipolar cell has fine dendritic branches at the left and its axon at the right. Such cells are found in the retina of the eye. The multipolar cell is the most common type found in the vertebrate central nervous system; it is shown in Figure 2-2 with many thick dendrites and finer dendritic branches on the left and an axon on the right.

Dendrites

Another system of neuronal classification is presented in Figure 2-3, which shows neurons with several different types

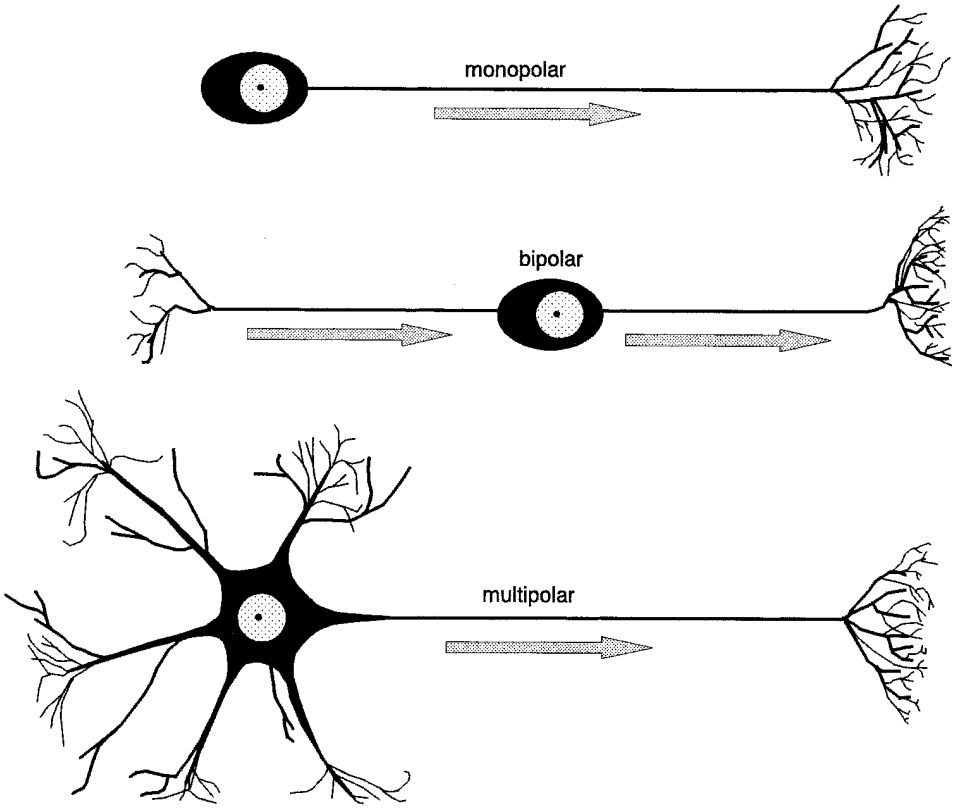

FIGURE 2-2. Three types of neurons classified according to the number of poles. The arrows indicate the direction of conduction of the nerve impulse.

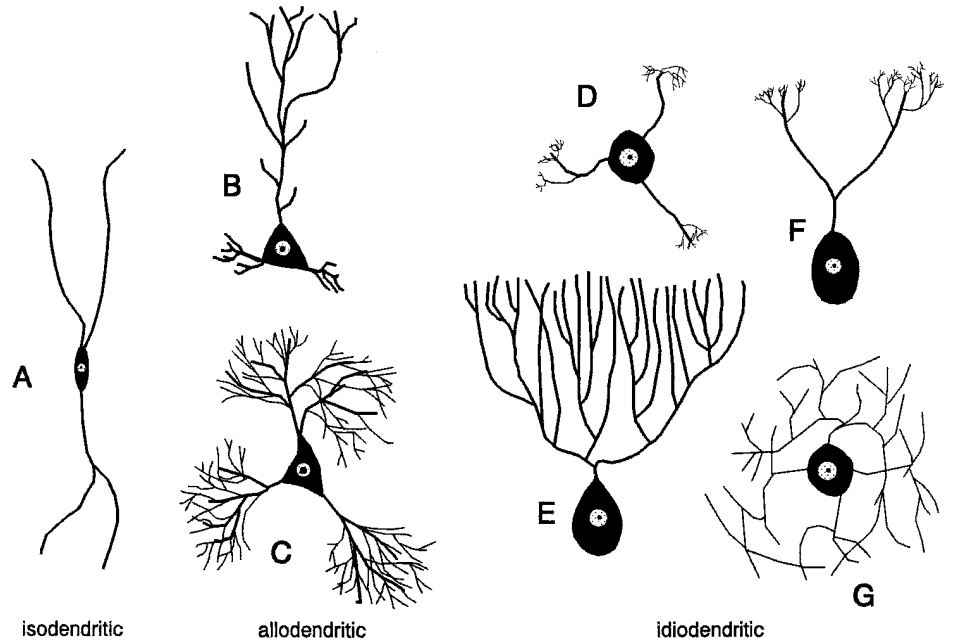

FIGURE 2-3. A classification of neurons according to the type of dendritic tree. Their axons are not shown.

of dendrites. The classification of dendritic types is based on the work of Enrique Ramon-Moliner. The dendrites of the neurons in Figure 2-3(A) are long and slender without many branches and are called **isodendrites**. The neurons in Figure 2-3 (B and C) have branched dendrites and can achieve fairly high degrees of complexity and specialization. These are known as **allodendrites**. The most specialized are called **idiodendrites**, which are represented in Figure 2-3 (D–G), typically are found in regions of the nervous system such as the olfactory bulb or cerebellar cortex.

Figure 2-4 depicts two neurons with their dendrites and a portion of their axons. The cell on the left is known as a pyramidal cell because its soma has the shape of a pyramid; the other is called a piriform cell because its soma is roughly in the form of a pear. In each case, two sets of dendrites are shown: a long dendrite ascending from the peak or apex of the cell (hence called "apical" dendrites) and other dendrites protruding from the base of the cell (the "basal" dendrites). Each of these dendrites subdivides into dendritic branches that increase the dendritic surface area.

Dendrites offer an enormous surface area for axon terminals to end upon. This huge surface provides termination sites for thousands of axon terminals. Some of these terminals are excitatory and contribute to depolarizing the dendrite and soma; others are inhibitory and thus contribute to hyperpolarizing them. Rarely does a single axon terminal have sufficient influence to excite a neuron to produce an action potential or to inhibit it. Summation of the activity of many synapses therefore usually is required in order to influence a neuron's actions. Often the generation or suppression of an action potential is the result of a kind of algebraic summation of the excitatory and inhibitory influences on the cell. If the sum of the excitatory influences outweighs the sum of the inhibitory influences, and if the net excitatory influences are present in sufficient quantity, the action potential or nerve impulse will be generated in the axon hillock and conducted down the axon. Dendrites thus are a battleground on which the opposing forces of excitation and inhibition compete. Because of their varying thicknesses and varying distances from the axon hillock, dendrites serve not merely as the input end of the neuron, but as integrators of neuronal activity. They provide areas in which weak incoming signals can combine to form stronger influences on the ultimate action of the cell.

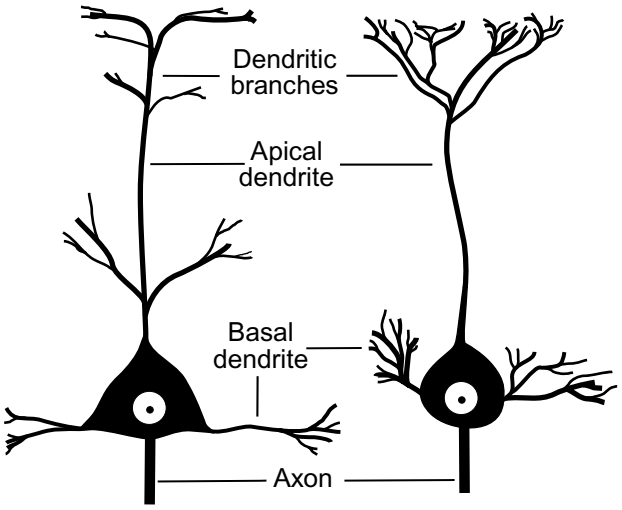

FIGURE 2-4. Examples of dendrites in neurons with different shaped somata. The initial segment of each cell's axon is shown at the bottom.

Axons

Neurons also may be classified according to their axons. At one extreme are the many small neurons that have no axons at all. These axonless neurons are involved only in local neuronal activity that is confined to a circumscribed cell population; since they do not exert an influence on distant cells, they need no axons. At the other extreme are neurons with exceptionally long axons, such as those that travel from the spinal cord down the length of the hind leg of a tetrapod and move its toes. Axons also vary in thickness, from the giant axon of the Mauthner cell to the tiny axons of the olfactory nerve. The effective thickness of an axon depends in part on the diameter of the axon itself, and in part on the diameter of its myelin sheath. The total diameter of the axon (axon plus sheath) is a major determiner of the velocity of conduction of the action potential. In general, larger diameter axons conduct more rapidly, although other factors play a role as well.

SYNAPSES

Chemical Synapses

The surface of the axon terminal where it contacts the neuron is known as the presynaptic membrane; the specialized surface of the neuron that receives the axon terminal is known as the postsynaptic membrane, below which is a specialized region of the dendrite's cytoplasm. The synapse itself is a small extracellular space that is about 20–30 nm across (1 nm is 1/1,000 of a μm). Within the axon terminal are small, membrane-bound packets or "vesicles," which contain chemical substances that are released into the synaptic space by the arrival of the action potential. These chemicals excite or inhibit the postsynaptic membrane and are one of the ways that one neuron can affect the activity of another neuron. Also contained within the axon terminal are one or more mitochondria. The mitochrondria are sources of energy for biological processes and are found in the soma, the synaptic vesicles, and wherever the neuron is highly active. Because the transmission of a signal across the synapse in this case is chemical, this synapse is known as a chemical synapse.

The events that occur in a chemical synapse are shown in Figure 2-5. Figure 2-5(A) shows a synaptic terminal at rest. The axon terminal filled with synaptic vesicles is shown just above the synaptic space. The terminal membrane that faces into the space is the presynaptic membrane. Below the synaptic space is the postsynaptic membrane with protein receptor sites. When the action potential arrives at the terminal, it causes calcium channels to open, which allows an influx of calcium ions. The arrival of the calcium influx in turn results in a forward movement of the vesicles with their contents of **neu-**

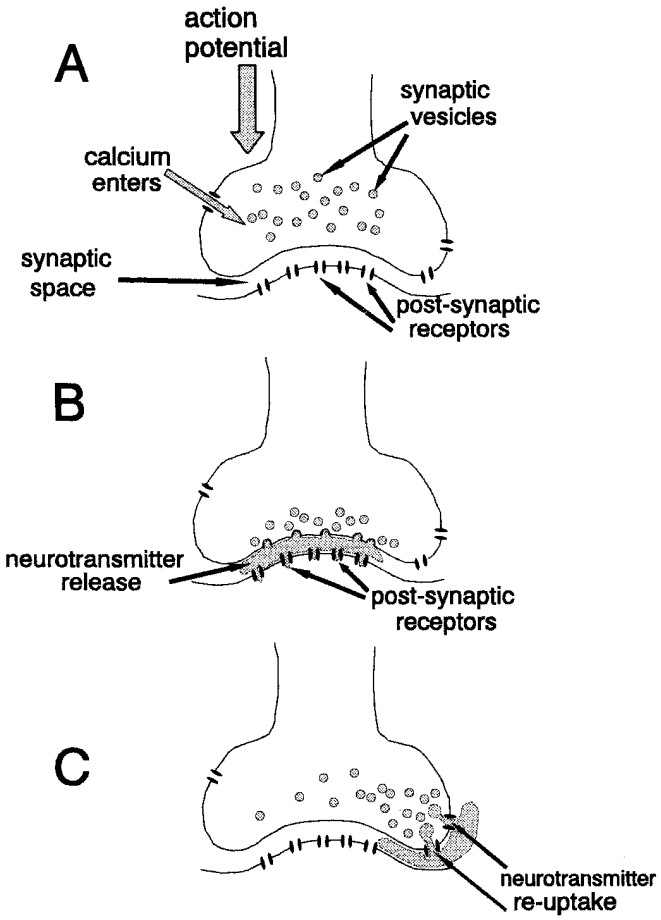

FIGURE 2-5. Transmission in a chemical synapse. (A) Neuroactive chemicals are stored in synaptic vesicles. Calcium enters through a calcium channel. (B) The vesicles move toward the synaptic membrane and fuse with it, thereby releasing their chemical contents into the synaptic space where they are taken up by receptors in the postsynaptic membrane. (C) Reuptake of excess neurotransmitter material from the synaptic space and its reincorporation into vesicles for future use.

rotransmitter substances towards the presynaptic membrane. As shown in Figure 2-5(B), the membranes of the vesicles fuse with the neuronal membrane, allowing the contents of the vesicle to be released into the synaptic space where they can act upon protein receptors in the postsynaptic membrane. If the transmitter substance is excitatory (i.e., depolarizing), it generates an excitatory postsynaptic potential in the postsynaptic membrane. If the substance is inhibitory, its action on the postsynaptic membrane is as if it had increased the polarization of the cell; that is, increased the resting potential thereby making it more difficult to generate an action potential, a phenomenon called hyperpolarization. Figure 2-5(C) shows that excess neurotransmitter material that remains in the synaptic space may be taken back into the terminal by other channels to be reincorporated into vesicles for future use.

Neuroactive Substances

Chemical synapses may be characterized by the chemical compounds present in them. Apart from their functions in synaptic transmission, these compounds are useful to comparative neuroanatomists because they can serve as markers of neuronal pathways and populations in different taxonomic groups. Thus they become another indicator of brain evolution and adaptation to the environment. Table 2-1 lists some of the major neuroactive compounds. These fall into a variety of categories. The two major categories are neurotransmitters and **neuromodulators**. Within each of these categories are several groups of chemicals. The neurotransmitter category contains relatively few compounds; the neuromodulator category has more than 30 compounds, only some of which are listed in the table. The cholinergic neurotransmitter is acetylcholine, which is excitatory or inhibitory. The biogenic-amine neurotransmitters, epinephrine (adrenalin), norepinephrine (noradrenaline), dopamine, serotonin, and histamine may likewise have excitatory or inhibitory actions depending on the type of receptor they encounter. The amino acid neurotransmitters consist of two usually excitatory transmitters, glutamate and aspartate, and two usually inhibitory transmitters, γ-aminobutyric acid (GABA) and glycine.

TABLE 2-1. Some of the Major Neuroactive Substances in the Central Nervous System

Type	Chemical Group	Substance	Function
Neurotransmitters	Cholinergic	Acetylcholine	Excitatory or inhibitory, depending on the type of receptor
	Biogenic amines	Norepinephrine	
		Epinephrine	
		Dopamine	
		Serotonin	
		Histamine	
	Amino acids	Glutamate	Excitatory (usually)
		Aspartate	
		GABA[a]	Inhibitory (usually)
		Glycine	
Neuromodulators	Peptides and hormones	VIP[b]	Modulation of synaptic transmission by affecting transmitter release or reuptake or by changing the sensitivity of the postsynaptic membrane for the transmitter
		Substance P	
		Methionine-enkephalin	
		Leucine-enkephalin	
		Cholecystokinin	
		Somatostatin	
		Neurotensin	
		Bombesin	
		β-Endorphin	
		Angiotensin II	
		Glucagon	
		Bradykinin	
		Calcitonin	
		Neuropeptide Y	
		Anterior pituitary hormones[c]	
		Posterior pituitary hormones[d]	
		Hypothalamic hormones[e]	
		Insulin	
	Second messengers	Cyclic AMP	
		Arachidonic acid Diacycloglycerol Cyclic GMP	

[a] γ-Aminobutyric acid.
[b] Vasoactive intestinal polypeptide.
[c] These include: adrenocorticotrophic hormone (ACTH), prolactin, luteinizing hormone, growth hormone, and thyrotrophic hormone.
[d] Oxytocin and vasopressin.
[e] These include: thyrotropic hormone releasing hormone (THRH), gonadotropic hormone releasing hormone (GnRH), corticotrophic hormone releasing hormone (CHRH), and growth hormone releasing hormone (GHRH).

The neuromodulators generally do not directly affect the depolarization or hyperpolarization of neurons as do neurotransmitters (although some have been reported to have these properties). Instead, the neuromodulators influence the duration or intensity of the action of the neurotransmitters by affecting the reuptake of transmitters, the effectiveness of the enzymes present in the synapse, the rate of transmitter release, and a variety of other phenomena, which make the synapse very different from a simple on-off switch. A vast array of possibilities for subtle and sophisticated modifications of the transfer of information between neurons is made possible by these many substances.

In addition to modulating synaptic transmission, many of these versatile chemical compounds play other roles in the body; indeed many of their names may be familiar to you in other contexts. Some of these peptides are gastrointestinal peptides such as vasoactive intestinal polypeptide (VIP), substance P, cholecystokinin, and neurotensin. Others are hormones that

are secreted by the posterior division of the pituitary (oxytocin and vasopressin) and are involved in the regulation of blood pressure and affect maternal functions and various aspects of social behavior. Others are releasing hormones that are secreted by the hypothalamus, such as thyrotropin releasing hormone (TRH), luteinizing hormone releasing hormone (LHRH), and growth hormone releasing hormone (GHRH). Still others are anterior pituitary hormones, such as adrenocorticotropic hormone (ACTH), growth hormone, and luteinizing hormone. Yet others are naturally occurring opioids, such as methionine-enkephalin, leucine-enkephalin, and β-endorphin. Finally, some second messenger substances, such as cyclic AMP, arachidonic acid, diacycloglycerol, and cylic GMP, which functions in retinal photoreceptors, also have neuromodulator properties.

Electrical Synapses

Not all synaptic junctions make use of chemical substances as the transmitter or modulator. At many synaptic junctions, the transmission is carried out by the passage of electrical current across the synapse. These are known as "electrotonic" or "electrical" junctions or simply "gap" junctions. The synaptic space of an electrotonic junction is only 2–4 nm across, which is only about one-tenth the width of a chemical synapse. Present on each side of the gap are matching pores or ion channels that can be opened and closed by means of a complex of proteins. When these proteins twist, the pore is opened, which allows the ionic current to flow across the gap. Electrical junctions provide for synaptic transmission with virtually no delay because no time is lost as vesicles move to the presynaptic membrane and discharge their chemical transmitters. Electrical junctions also are not subject to "fatigue" as are chemical junctions, which can deplete their supply of vesicles if stimulated too frequently. Most electrical junctions can transmit their electrical signals in either direction, whereas chemical junctions can only transmit from the presynaptic to the postsynaptic membrane. Finally, transmission at electrical synapses is much faster than at chemical synapses.

Electrical synapses are found mostly in invertebrate nervous systems. In spite of their several advantages, they tend to be rather stereotyped in their action and do not lend themselves well to the subtle and varied types of interactions and modulations that are possible in a chemical transmission system. Indeed, the huge variety of possible types of interactions that can occur in a chemical system is a major contributor to the vast array of complexity of behavior that is characteristic of vertebrates and that has played such an important role in their evolution.

Volume Transmission

Many instances of intercellular communication in the nervous system occur via chemical synapses, with the neurotransmitter or neuromodulator release occurring in the immediate vicinity of a postsynaptic dendritic site, or via electrical synapses; however, a different kind of neuronal cell communication, called **volume transmission**, also occurs. Volume transmission, also referred to as nonsynaptic transmission, parasynaptic transmission, or paracrine transmission, was identified and described by Miles Herkenham in 1987, and the reader is referred to his paper as well as to the comprehensive review of this subject by Rudolf Nieuwenhuys, published in 2000, for in depth treatments of this often overlooked phenomenon.

Volume transmission involves the release of neuroactive substances at presynaptic sites that are not positioned close to any postsyanptic sites, thus necessitating diffusion of the released neurochemical to relatively distantly located sites for their activity to be realized. It is common across invertebrates as well as in vertebrates. In the latter, it particularly characterizes the systems that run within the most central portion of the brain and that are involved in emotional and/or visceral types of functions. Nieuwenhuys characterized this central, or medial, part of the brain as a "greater limbic system," referring to various regions of the brain, from the spinal cord through its most rostral levels, that are involved in emotions, learning, memory, and a number of related processes (see Chapter 30) and noted that volume transmission is a particular feature of it. According to this scheme, this medial part of the brain contrasts with the more lateral part, in which the pathways are characterized by chemical synaptic transmission and involved in the more "objective" relay and analysis of incoming sensory information and outgoing motor commands.

NEURONAL POPULATIONS

Anatomists frequently refer to a discrete population (or to two or more populations) of neurons, often situated within a well-circumscribed boundary, as a **nucleus**. The same term is also used to refer to the intracellular structure that contains the DNA of the cell. Fortunately, the potential for confusing these two uses of the term is minimal because the contexts are so different. Examples of such "population nuclei" are the dorsal division of the lateral geniculate nucleus of the visual system, the nucleus ovoidalis of the avian auditory system, and the motor nucleus of the trigeminal nerve, which are structures that will be described in detail in later chapters. In the brain, alternate terms for nuclei include locus (e.g., locus coeruleus), substantia (e.g., substantia nigra), area (e.g., area postrema), and ganglia (e.g., basal ganglia).

One of the hallmarks of nuclei is that the dendrites of the neurons remain within the boundary of the nucleus. A nucleus may consist of several layers, or laminae; however, the dendrites of neurons within each lamina remain within it and do not extend beyond the laminar boundary into the territory of another lamina. In contrast, the term **cortex** is used to denote multiple populations of neurons that are arranged in layers; in most layers, the dendrites of neurons extend across the territory of multiple other layers. The following sections address nuclei, but most of the material in them applies to cortices as well.

Golgi Type I and II Cells

Population nuclei often consist of more than one type of neuron. The nineteenth century Italian anatomist, Camillo Golgi, distinguished two types of cells within the boundary of a nucleus. The **Golgi Type I neuron** tends to have a large soma

and a long, thick, well-myelinated axon. This axon passes outside of the confines of the nucleus and can travel considerable distances; those that pass from nuclei of the brain into the spinal cord of a large animal, such as a giraffe or a whale, can be more than a meter in length. Often the axons of Golgi Type I cells have side branches, called **collaterals**, that permit the axon to contact other nuclear populations en route to its final destination. The various Golgi I axons from the same nucleus typically travel together in bundles (often known as "tracts" or "fiber bundles") as they make their journey to their target neurons.

In contrast, the **Golgi Type II neuron** has a small cell body and short, often unmyelinated axons. These axons rarely pass outside the boundary limits of the nucleus. Some Golgi Type II neurons have no axons at all. Thus their dendrites both receive input from other neurons (axo-dendritic terminations) and make synaptic contact with the dendrites of other neurons (dendro-dendritic contacts). Similar points of contact can be found with the soma. The Golgi Type II neurons are critical for the functioning of the individual population components of the nervous system. They form local circuits within the nucleus that contribute to whatever the function of the particular nucleus might be, such as the processing of information or the patterning of rhythmic events. Golgi Type II neurons are often referred to as **local circuit neurons** or **interneurons**. Figure 2-6 shows Golgi Type I and Golgi Type II neurons.

To understand the differences between the Golgi I and II cells, consider that the Golgi II cells are like a local telephone network that maintains communication within a factory and allows the workers to perform their tasks in an integrated and coordinated manner. The Golgi I cells are like a long-distance telephone network that permits factories that are located at considerable distances from one another to be in contact and to coordinate their activities.

Nuclei and Planes of Section

In order to study the anatomy of the central nervous system, anatomists often cut the neural tissue into very thin slices called "sections" (5–50 μm or thinner), so that they may be examined under a microscope. These sections pass through nuclei and through the axonal bundles or tracts that pass from one nucleus to another. While these sections give an accurate view of the cross-sectional extent of a nucleus or axon bundle, they give no indication of how much of these structures may extend ahead of or behind the plane of the section. Many of the illustrations in this book consist of sections through the brain or spinal cord, and the reader should understand that the ovals, ellipses, circles, and other shapes that appear in the section only represent a single slice through what may be a much larger and much more complex structure. This is diagrammed schematically in Figure 2-7. At the left, represented by the thicker cylinder, is a nucleus with its large Golgi Type I neurons and smaller Golgi Type II neurons. The Golgi Type I axons leave the nucleus and enter an axon bundle, represented by the smaller cylinder. The gray rectangle represents a section through these two structures. To the right of the arrow is the section showing how the nucleus and axon bundle would appear in this single plane. The Appendix describes in detail the planes of section conventionally used in neuroanatomical studies.

Techniques for Tracing Connections Between Nuclei

The second half of the twentieth century was a period of unprecedented new knowledge about connections between neuronal populations in the central nervous system. This explosion of information was largely due to the development of a vast number of new techniques based on a variety of biological principles. Prior to this period, neuroanatomists could only

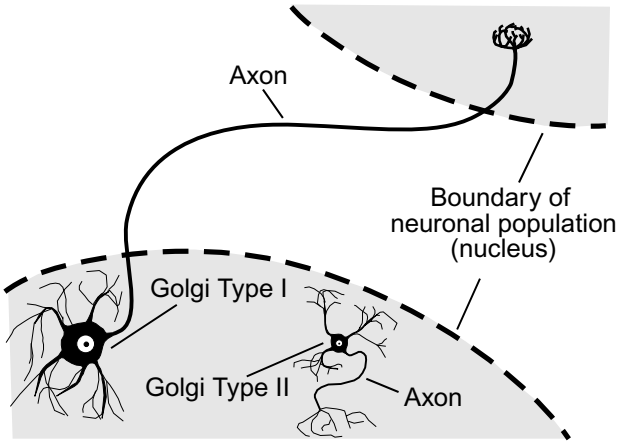

FIGURE 2-6. A Golgi Type II neuron, the axon of which remains within its neuronal population, and a Golgi Type I neuron, which sends its axon to a different neuronal population.

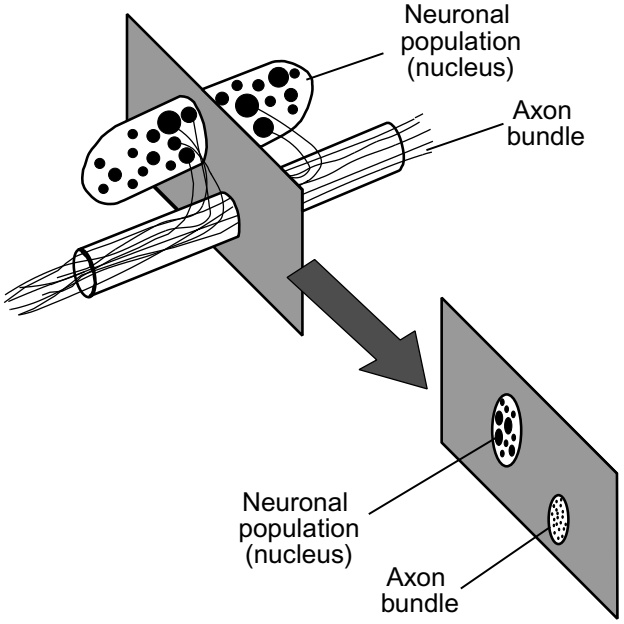

FIGURE 2-7. The appearance of a neuronal population and a nearby axon bundle in a three-dimensional view and in a transverse section through both.

rely on methods that stained neurons in an unpredictable manner. To target a specific population of neurons for study, they could only use methods that were based on the degenerative processes that follow injury of the cell soma or separation of the axon from the soma.

Since the second half of the 19th century, anatomists had been able to visualize neurons or parts of neurons using aniline dyes or metallic deposits. The Golgi technique, in which silver impregnation was used to visualize whole neuronal cell bodies and the full array of their dendritic processes, is an example of one of the metallic impregnation methods. This method is still in use today. Its main drawback as a tracing method is the fact that the one cannot predict ahead of time which neurons will be impregnated by the silver.

The problem was how to target a specific group of axons for study and then to identify them from among the vast number present in the microscopic image as the anatomist went from one section of brain tissue to the next. One of the first tracing methods consisted of injuring the neurons to be studied and then using the resulting degenerative process as a tag or label to trace the course of their axons. Degenerative changes in the soma separated from all or part of its axon (retrograde degeneration) could be observed with the traditional aniline dyes that had been used during the 19th century. The deposited metal could then be reduced so that it appeared black and thus visible under the microscope. The location of the degenerating axoplasm and the terminal endings of the axons could then be traced and charted in serial sections, and the axonal pathway from one point to another within the nervous system could be reconstructed. Degeneration of the separated axon (anterograde degeneration) could be studied by impregnating the degenerated axoplasm with silver or the degenerated myelin with osmium.

The initial phase of the technical revolution of the 1960s and 1970s depended on newer methods of silver impregnation that were developed at that time (the Nauta-Gygax stain and its variants, and the Fink-Heimer stain); these methods allowed for much more precise tracing of connections by suppressing the appearance of silver in normal axons, which made the degenerating axons easier to see, and later by permitting visualization of the actual axon terminals rather than just the axons. These 20th century silver methods also were more effective in both mammalian and nonmammalian vertebrates than previous techniques; they opened the way for a greater exploration of connections in nonmammals than could previously have been attempted.

The techniques currently in use do not require lesions of nervous tissue but instead involve injecting one of a number of tracer substances into a particular site and allowing the intracellular transport processes (axonal transport or axoplasmic flow) to distribute the substance along the length of the axon to its terminals and its cell soma. Histological procedures are then carried out on serially sectioned material, as in the reduced silver methods, and the location of the labeled axons, axon terminals, and cell somas are charted under the microscope. A number of the labeling substances can be visualized at both the light and electron microscopic level. The tracing substances that are most commonly used include tritiated amino acids, horseradish peroxidase (HRP), HRP conjugated to wheat germ agglutinin (WGA), and the plant lectin *Phaseolus vulgaris*-leukoagglutinin (PHA-L).

The large repertoire of axonal transport tracing techniques that has been developed has greatly enhanced our ability to visualize and trace connections. The tracing substances currently available vary widely in how they can be visualized. For example, some can be visualized by histological procedures in which the substance is reacted in various solutions to acquire a color or be tagged with a colored substance that is visible under the microscope. Other tracing substances fluoresce when illuminated with ultraviolet (UV) light. Still other tracing substances are radioactive and can be visualized by applying a thin layer of photographic emulsion over the sections, exposing the emulsion for a certain period of time, and then developing the emulsion just as one would develop a photographic print. The pattern of radioactive emissions then can be charted in serial sections to reveal the course and terminal site of the axonal pathway being studied.

This wide variety of tracing substances and visualization techniques has permitted much sophisticated and elegant experimental work. Double and even triple labeling of different components of a neuronal circuit has been developed to a fine art. For example, one might label one set of afferent axons of a nucleus with one fluorescing tracer, a second set of afferent axons with a different fluorescing tracer that fluoresces under a different wave-length, and the neuronal cell bodies and their dendrites in the nucleus with a retrogradely transported tracer that can be visualized with histological processing. The precise synaptic pattern of the two different sets of afferent fibers on the postsynaptic neurons within the nucleus can thus be worked out.

A number of additional tracing techniques exist that do not depend on axonal transport mechanisms. Some take advantage of the natural fluorescence of some of the neuronal transmitters, such as serotonin and dopamine. Widespread use is also currently made of immunohistochemical methods for antibody labeling of neuroactive substances, such as some of those listed in Table 2-1, which then can be visualized with histological techniques. In addition to axonal tracing methods, techniques allowing *in vivo* and *in vitro* study of particular parts of the brain, whole-brain scanning techniques, extra- and intracellular electrophysiological recording techniques, in situ hybridization techniques for localizing sites of gene expression, and an extensive array of additional such methods allow for a truly comprehensive approach to the study of the organization and function of the central nervous system.

Table 2-2 gives some examples of the more commonly used contemporary methods as well as some of the earlier methods. The table is not intended to be an exhaustive survey but rather gives a sample of the many different methods that you are likely to encounter if you read any of the works listed at the ends of chapters in this book or elsewhere in the neuroanatomy literature.

RECEPTORS AND SENSES

The senses are our windows onto the world—both the world outside and the world within our bodies. We cannot know anything about either of these worlds except through our

TABLE 2-2. Summary of Methods for Tracing Connections in the Central Nervous System

Method Type	Examples	Comments
Retrograde degeneration	Nissl stain	Aniline dye stain of a soma separated from part or all of its axon
Anterograde degeneration	Marchi stain	Impregnation with osmium of degenerating myelin of an axon separated from its soma
Reduced silver	Golgi stain Cajal stain Bielschowsky stain	Impregnation of neurons with reduced silver
	Nauta-Gygax stain	Especially effective on axons that are degenerating due to separation from their somata
	Fink-Heimer stain, de Olmos stain	Especially effective on degenerating axon terminals
Anterograde and/or retrograde axonal transport and/or diffusion along axonal sheaths	Autoradiography	Transported along axons and visualized with photographic emulsion, fluorescence, chromagen (attachment of chemical dye that can be reduced and visualized), or other histological techniques
	Phaseolus vulgaris-leuccoagglutinin (PHA-L)	
	Horseradish peroxidase (HRP)	
	Fluorescent dyes (Evans blue, fast blue, fluorogold, Di-I, Di-O)	
	Rhodamine beads Cholera and other toxins	
	Wheat germ agglutinin-horseradish peroxidase (WGA-HRP), tritiated proline	
Immunohistochemistry	Various neurotransmitters and neuropeptides, mRNA, and related compounds	Antibodies used for visualization with fluorescence or other microscopy methods

sensory systems. Of course we can know a lot about both worlds with the use of scientific instruments, but even this information must come to us via the sensory systems. The senses are our way of detecting energy or chemical substances in the inner and outer worlds. The detectors for the external world are known as **exteroceptors** and those of the inner world are known as **interoceptors**. Exteroceptors are the receptors for vision, taste, smell, touch, warmth, cold, and so on. Interoceptors provide the central nervous system with information about events within the body, such as the distension of the gastrointestinal system and urinary bladder, pressure of the blood in certain blood vessels, and levels of various substances in the blood such as glucose, fat, and various hormones.

The types of energy detected are:

- The electromagnetic spectrum, which includes visible light (i.e., light visible to humans), ultraviolet and infrared portions of the spectrum, and electricity and magnetism.
- Mechanical energy, such as is produced by bending, stretching, shearing, and compressing of the skin or other tissues.
- Chemical energy, which is the energy released by the reactions of chemical substances in the environment with the chemicals that make up the receptor.

How Many Senses?

How many senses are there? When this question is asked, we usually think of five: taste, touch, smell, hearing, and vision. Sometimes we refer to an elusive "sixth sense," by which we really mean "intuition," which is not an energy detector at all. However, there are many more than the proverbial five or even six senses. When we take into account the full range of senses available to vertebrates, we can count something in the neighborhood of 20 senses, depending on how fine one wishes to subdivide the different receptor types. These include the traditional five, plus pain, vestibular sense, temperature, the various types of touch (deep, light, vibration), proprioception (the positions of joints), muscle stretch, etc., the ability to detect electrical fields (lampreys, sharks, some ray-finned fishes, some amphibians, and monotremes), infrared radiation in a manner similar to vision (some snakes), lateral-line sensations (nontetrapods, amphibian larvae, and some adult amphibians), and magnetic fields (some fishes, amphibians, and birds).

Receptors and Awareness

Events that occur in the internal or external worlds that do not affect our interoceptors or exteroceptors are unknown

to us. For example, many animals can detect light in the ultraviolet portion of the spectrum. No doubt they see it as some sort of color. Because we are unable to detect light energy in this portion of the spectrum, as far as our personal experience is concerned, this part of the spectrum does not exist. We can only know of its existence with the aid of specialized scientific instruments. Similarly, many mammals, including bats, many rodents, and dogs, can hear sounds that are much too highly pitched for us to hear. Even within our own bodies, receptors are at work, participating in the precise regulation of bodily functions such as blood pressure, the flow of materials through the digestive system, the secretion of hormones, all without any awareness on our part because the information from these interoceptors never reaches those brain regions that bring such information to our conscious awareness. For example, a complex series of neural circuits produces a precise regulation of the diameter of the pupil of the eye according to the intensity of light present in the external environment. We are totally unaware of these adjustments, which are being made each time the light level changes. We can become aware of some of our senses if we produce certain types of disturbances of their mechanisms. For example, we are normally unaware of the operation of the vestibular organs in the middle ear, which provide us with information about the pull of gravity, the acceleration of our bodies, the position of our head, and so on, so that the necessary postural adjustments can be made to keep us in our erect posture and prevent us from falling over as we change position or try to walk on an uneven surface. These adjustments are, for the most part, totally transparent to us. If we spin ourselves round and round, however, as most of us did as children, we quickly become aware of a variety of sensations that result from the abnormal stimulation of this sensory system.

Sensory Experience as a Private Mental Event

To return to the detection of ultraviolet light, a feat that we are incapable of, we suggested that those animals that can detect ultraviolet light probably experience it as some sort of color. What color is ultraviolet? We cannot imagine what ultraviolet color looks like any better than we could describe the colors of a sunset or autumn leaves to a person who has been born blind. Sensations are private mental events knowable only to the person or animal having the sensory experience. Indeed, you have no way of knowing for sure that what you experience as red when looking at an apple is what a bird or another mammal experiences when it sees the same apple. This may sound a bit philosophical, but it is of relevance to the fact that we cannot know, nor can scarcely imagine, what the subjective experiences are of animals that have senses very different from our own. For example, birds have more photopigments, which makes them more sensitive to certain regions of the light spectrum than humans, and therefore they almost certainly do not see objects as having the same colors as we do. What does a snake experience when it uses its infrared-detecting pit organs to detect a mouse in total darkness? Possibly it is something akin to vision, but we cannot know what it is like for the snake. Likewise, what does electroreception feel like to an animal that can detect minute changes in the electrical fields present in the surrounding environment? What is it like to have taste receptors all over one's body as do certain fishes? Some birds appear to have the capability to navigate by means of the earth's magnetic fields. What does a magnetic field feel like to them? There is no way for us to know the answers to any of these questions.

Sensory Adaptation

A property of receptors is that they decrease their responsiveness to persistent stimuli. This phenomenon is referred to as **adaptation**. Adaptation is not a voluntary act like a human or an animal shifting its attention to and from specific stimuli at will; rather, it is more like a receptor fatigue phenomenon and only can be reversed by a period of absence of the stimulus or by changing the stimulus. You most likely have experienced adaptation of the olfactory system when you entered a room with a particularly strong odor, but after a few minutes in the room, you no longer notice the odor, even if you try. Some receptors become adapted to a particular level of stimulation and will only respond to a different level. This property sometimes results in strange effects. If you put one hand in very cold water and the other hand in very warm water, leave them for a few minutes, and then put both hands in water that is at room temperature, you will observe that the hand that was in the warm water feels cold and the hand that was in the cold water feels warm, yet both are receiving the same stimulus of room temperature water.

RECEPTOR TYPES

Table 2-3 presents a classification of receptors according to their functional classes, sensory modalities, and receptor types. All of these receptors are neurons or neuron-like cells. As is the case with all neurons, a resting potential is maintained across the cell membrane. When activated by the appropriate energy, the ionic events that maintain the resting potential are disturbed and a receptor potential results. The process by which mechanical, chemical, or electromagnetic energy is converted to neural events (i.e., the electrochemical process that produces receptor potentials) is known as **sensory transduction**.

Receptor potentials are produced by the receptor cells in response to stimulation by the appropriate stimulus. They are like the local potentials of neurons in that they are graded potentials; that is, the magnitude of the potential is proportional to the intensity of the stimulus that is being applied to it. If the receptor potential achieves a sufficient magnitude, an action potential develops in the axon of the sensory neuron. This action potential sweeps down the axon to the terminals located in the brain or spinal cord. These terminals release their neuroactive chemical and the process of sensation has begun.

Some receptor cells are true sensory neurons with either free sensory terminal endings or with specialized sensory terminals. Like other types of neurons, receptor cells with specialized endings have an axon that terminates within the central nervous system. This type of receptor cell is typical of the skin, muscle and joint senses, of touch, pain, stretch, and so on. Some examples of these types of receptors are shown

TABLE 2-3. A Classification of Receptors and Their Senses

Receptor Class	Sensory Modality		Receptor Type
Mechanoreceptor	Touch	Fast adapting	Meissner's corpuscles
		Slow adapting	Merkel's disks
	Tendon stretch		Tendon organs
	Skin stretch		Ruffini endings
	Joint position		Joint receptors
	Muscle length and stretch		Muscle spindles
	Muscle contraction		Golgi tendon organ
	Vibration		Pacinian corpuscles
	Hearing		Hair cells
	Vestibular (gravity, acceleration, head position)		Hair cells
	Lateral line		Hair cells
Radiant-energy receptor	Light (including UV)		Photoreceptors
	Infrared radiation (pit organ)		Pit-organ receptors
	Infrared radiation (skin warmth)		Free nerve endings
	Infrared radiation (skin cold)		Free nerve endings
Chemoreceptor	Taste		Taste buds
	Smell		Olfactory receptors
Electroreceptor	Electric fields		Ampullae
			Tuberous receptors
Nociceptor	Pain		Free nerve endings
	General chemical sensitivity		Free nerve endings
Magnetoreceptor	Magnetic fields		Photoreceptors (?) Ampullae (?) Trigeminal receptors

in Figure 2-8. Other receptor cells, however, are not modified neurons, but rather are specialized receptor cells; they lack axons and must be innervated by sensory neurons in order for their output to be transmitted to the central nervous system. Hair-cell mechanoreceptors, photoreceptors, and chemoreceptors are among those included in this category of receptor cells. These types of receptor cells are illustrated later in this chapter. Unlike other neurons, which have their cell bodies within the central nervous system, the sensory neurons for most sensory systems have their cell bodies outside of the central nervous system. The cell bodies are nearly always clustered together in a **ganglion**, so named because it resembles a "knot." Ganglia are located just outside of the sensory nerve's point of entry into the central nervous system. They are present in both the spinal nerves, which innervate the body, and some cranial nerves, which innervate the head and neck and also contribute to the autonomic regulation of the viscera. A sensory ganglion is illustrated in Figure 2-9.

Mechanoreceptors

Mechanoreceptors are among the most ubiquitous types of receptors. Although they exist in a variety of forms, their common feature is their response to mechanical deformation, such as bending, stretching, or twisting. Some mechanoreceptors are involved in the detection of touch or pressure on the body surface. Others respond to stretching such as those in joints, tendons and muscle spindles, and in the digestive system. Still other mechanoreceptors are located at the bases of surface hairs, feathers, and scales and respond when the position of the surface structure is displaced. You can demonstrate this for yourself by lightly running your finger across the hairs on your arm or head without touching the skin surface. The hairs that make up the facial whiskers or vibrissae of mammals are typical of such hairs. Some mechanoreceptors are illustrated in Figure 2-8.

Mechanoreceptors have been best studied in mammals, which possess a large variety of mechanoreceptor types. We know considerably less about the mechanoreceptors of non-mammalian vertebrates. Some amphibians and reptiles are exceptionally sensitive to vibrations of the substrate on which they are situated; they possess cutaneous mechanorecoptors on their ventral skin. Birds have mechanoreceptors on or near the base of their feathers, possibly indicating whether their feathers are close to the body surface (a thermoregulatory mechanism) and/or possibly indicating air speed.

Mechanoreceptors for touch may be classified in several ways. One way is to categorize them according to the speed at

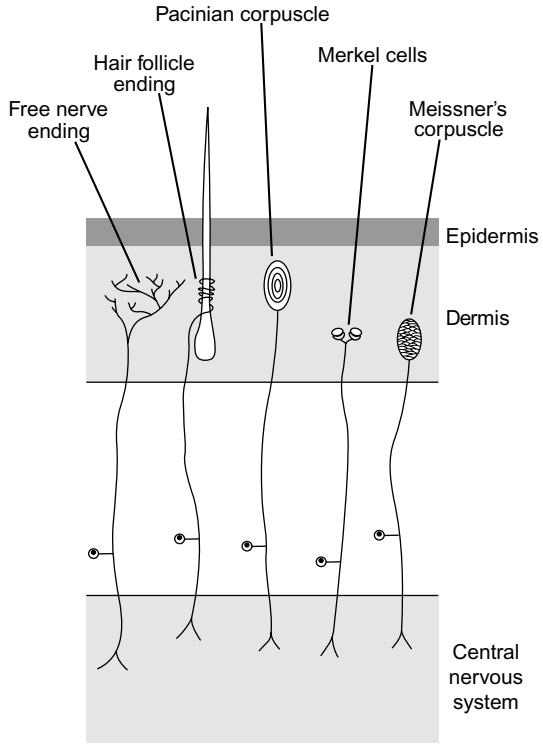

FIGURE 2-8. Examples of somatosensory receptors in the skin.

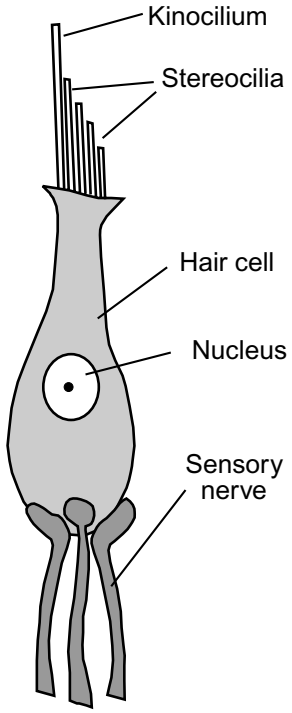

FIGURE 2-10. A hair-cell mechanoreceptor. Hair cells are found in the auditory, lateral line, and vestibular systems.

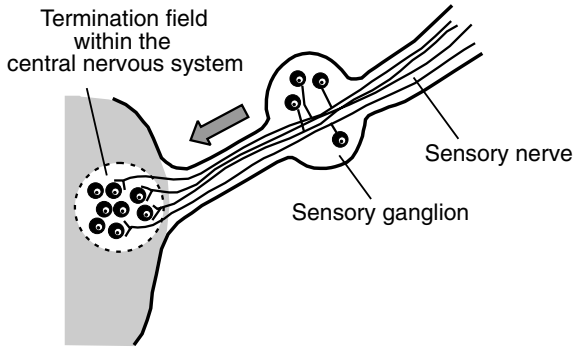

FIGURE 2-9. A sensory ganglion containing the somata of sensory neurons en route to their termination field in the central nervous system. The arrow shows the direction of conduction of the action potentials.

which they adapt to continuous bending or deformation; these are the **fast-adapting** and **slow-adapting** mechanoreceptors. Both types may be further subdivided according to the characteristics of their receptive fields: large with indistinct borders or small with distinct borders.

Hair Cells. A specialized group of mechanoreceptors are the hair cells, which are cells with one or more hairs, or **stereocilia**, protruding from them as well as a longer hair called a **kinocilium**. The stereocilia appear to be involved in the transduction of mechanical energy into a receptor potential, but the kinocilia do not seem to play a direct role in this process. Kinocilia are present in all vertebrates, but in mammals they degenerate during development and hence are not found in adult mammals.

Figure 2-10 shows a typical hair cell. These cells generate receptor potentials in response to bending of their hairs. Hair cells typically are found in fluid-filled chambers, such as the auditory and vestibular organs of the ear and the lateral line organs of the head and the body of aquatic anamniotes. This type of receptor is responsive to displacement waves in the surrounding fluid that have been transmitted from the external environment. The pressure waves that are detected by the lateral line system are of low frequency of the sort that would be produced by the swimming movements of neighboring fish in a school or the bow wave of an approaching predator. Likewise, the hair cells of the vestibular system respond to the low-frequency waves that are set up in the fluids of the vestibular apparatus when the tilt of the head is changed or as the acceleration of the body changes. A third set of hair cells is tuned to respond to the higher frequencies of wave action that occur in the auditory organs when those pressure waves in the external environment that we call "sound" (i.e., pressure waves in the frequency range that we can hear) are transmitted to the fluid in the hearing organ. The external environment may be water, as in the case of fishes, or air, as in the case of terrestrial animals. Indeed, the transition from water to land resulted in dramatic changes in the ear and in hearing mechanisms as a result of the differences in the way sound waves are transmitted through water and air.

The auditory hair cells in tetrapods are located in the inner ear in a structure known as the **basilar papilla**. In mammals, this structure (along with some related structures) is called the **organ of Corti**. The hair cells are arranged in rows in these structures. Some of the hairs are free and others are embedded in an overlying structure. In either case, the pressure of the incoming sound waves ultimately causes these hairs to bend with resulting generator potentials. A more detailed discussion of the mechanics of hearing as well as the variety of hearing organs and their relationships to the animals' environments may be found in the specialized books and articles on this subject listed at the end of the chapter.

Eimer's Organs and the Star-Nosed Mole. The star-nosed mole (*Condylura cristata*) is a mole with a unique sensory adaptation of its snout. The snout consists of a pair of arrays of eleven fleshy, highly mobile, fingerlike protuberances, called rays, that the animal uses to explore the environment (see Box 2-3, Figure 2). Each ray contains thousands of specialized cutaneous mechanoreceptors known as **Eimer's organs**. They are unique to moles and are not found elsewhere among the eulipotyphlans (formerly called insectivores; see Chapter 4)—moles, shrews, and hedgehogs. They are also lacking in moles that live in harsh, very dry climates.

Each Eimer's organ consists of a dome-like swelling of the epidermis below which is located a column of flattened epidermal cells. Contained within the organ are free nerve endings associated with the flattened disks, Merkel mechanoreceptors, and encapsulated corpuscles. The density of Eimer's organs far exceeds the density of touch receptors on even as sensitive a receptor surface as a human hand. This provides the animal with an exceptional somatosensory image of whatever surface the rays are exploring. Because the nasal rays move very quickly, the animals must make very rapid textural discriminations in order to form this tactile picture of the environment immediately in front of its nose.

Lateral Line Organs. An important sense-organ system for aquatic anamniotes are the lateral line organs, which generally are found in the lateral line canals. These canals are located on the head and the body of fishes and larval amphibians. They contain a class of mechanoreceptors known as **neuromasts**, which are hair cell-like receptors. These neuromast receptors are situated in the lateral line organs that line the fluid-filled canals. Some canals are closed and their fluid is internally secreted; others canals have external openings that permit the surrounding water to enter. Neuromasts respond to low-frequency pressure changes in the surrounding water as might

BOX 2-1. Dome Pressure Receptors

The river glides lazily through the dark swamp. Its surface is smooth except for some floating leaves and a half-submerged log. A young deer cautiously approaches the water and begins to drink. Suddenly, the "log" lunges at the deer. Too late the deer sees that the log is a large alligator. How was this predatory attack launched with such surprise and such precision? The answer is with the assistance of a newly characterized but quite ancient sensory receptor called a **dome pressure receptor**. These receptors appear as a series of bumps or small domes on the upper and lower jaws of semi-aquatic alligators and crocodiles above and below the tooth line (see Figure 1) and represent a localized thinning of the animal's body armor.

Daphne Soares discovered that these receptors allow American alligators (*Alligator mississippiensis*) to orient toward their prey, even in total darkness, and without the aid of audition. She observed that single droplets of water dripped onto the surface of the water surrounding the alligator will evoke the orientation response, even in total darkness, as long as the animal's face was positioned at the air-water interface. If the head was above the water's surface, no response occurred. Likewise, if the dome pressure receptors were covered with a plastic elastomer, the alligators failed to respond to the stimulus. Soares reported that the dome pressure receptors are innervated by branches of the trigeminal nerve. (See Box 11-1 for additional sensory receptor types innervated by this versatile nerve.)

In addition to studying the anatomy, physiology, and behavioral functions of the dome pressure receptors, Soares also investigated their phylogeny, as shown in Figure 1, which is a cladogram of crocodyliform reptiles. Examination of the upper jaw, or maxilla, and lower jaw, or mandible, of modern and ancient crocodyliforms revealed a series of small openings, or foramina, through which pass the end branches of the trigeminal nerve. The foramina are arrayed in a hexagonal or "beehive"-shaped pattern. All living semi-aquatic crocodilians possess both the foramina in a beehive pattern and the dome pressure receptors. When Soares examined the skulls of extinct relatives of the modern crocodilians, she found the linear pattern only in those extinct species that are believed to have been adapted to a fully terrestrial environment, such as *Sebecus*. Other ancient crocodilians, such as *Protosuchus*, and modern lizards also all have the foramina in the linear pattern, which supports the idea that the beehive pattern and dome pressure receptors are a unique development of the more recent, semi-aquatic crocodilian lineages. Even the marine iguana, which, like crocodilians, leads a semi-aquatic existence, has the linear pattern and not the beehive pattern of the semi-aquatic crocodilians.

The paleontological evidence, taken along with the behavioral, physiological and anatomical findings suggest that the semi-aquatic crocodilian lineages evolved a unique sensory receptor that enables these large predators to lie in stealth in the water awaiting subtle pressure waves associ-

BOX 2-1. Dome Pressure Receptors—cont'd

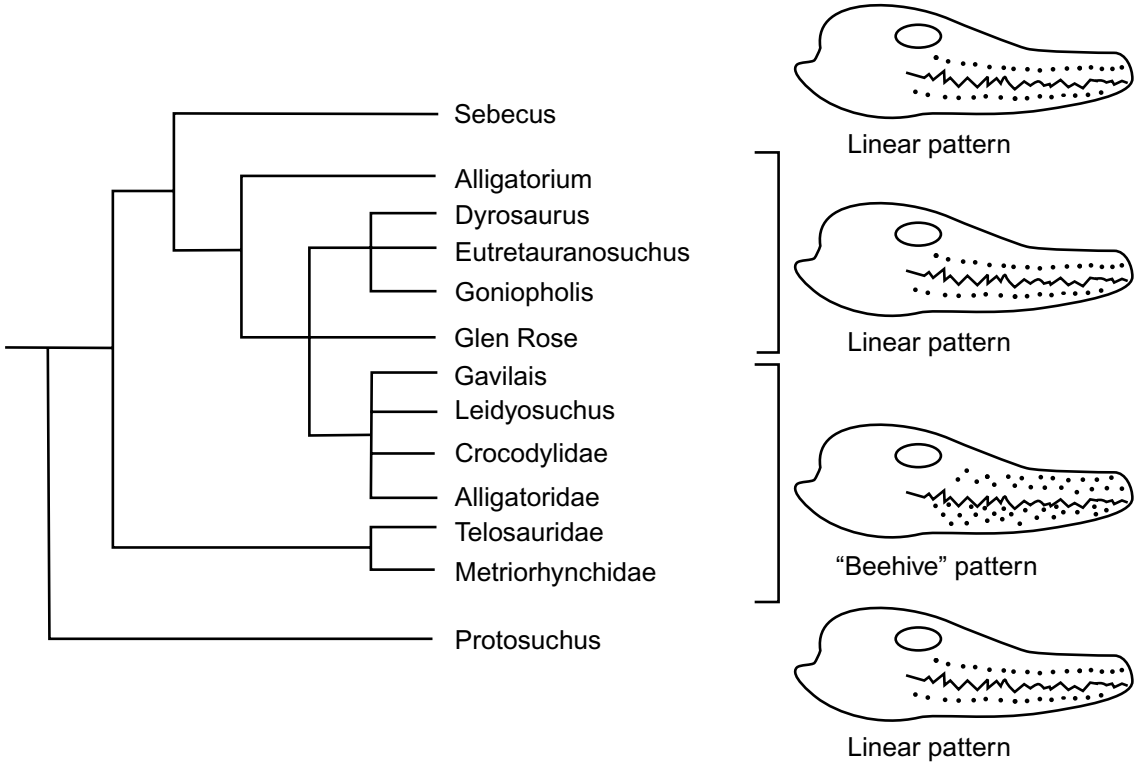

FIGURE 1. A cladogram of crocodyliform reptiles showing evolution of dome pressure receptors, as indicated by the presence of a "beehive" pattern of trigeminal nerve foramina on the upper and lower jaw surrounding the tooth line. The linear pattern is characteristic of the earliest crocodilians and those genera not adapted to the aquatic environment. The linear pattern is also characteristic of lizards, whether or not they are adapted to an aquatic environment. Adapted from Soares (2002) and used with permission.

ated with a disturbance of the water's surface to signal the position and distance of prey, even in total darkness. The ability to process information about the precise location of prey in the water in conjunction with their highly developed locomotor system may have contributed to the long history of success of these animals as predators.

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be produced by the swimming movements of other fish in a school, or by the approach of a predator.

The lateral line canals of a bony fish are shown in Figure 2-11. At least three canals are located on the head, one above the eye (supraorbital canal), one below the eye (infraorbital canal), and one on the lower jaw or mandible (mandibular canal). Additional head canals are present in some fishes. The lateral or trunk canal runs the length of the body.

Radiant-Energy Receptors

Energy that is propagated in the form of electromagnetic waves (or streams of particles called photons) is known as **radiant energy**. A rather narrow portion of the radiant energy spectrum constitutes visible light. Please remember that when we use the term "visible," we mean visible to humans. Various nonhuman animals have no difficulty detecting portions of the

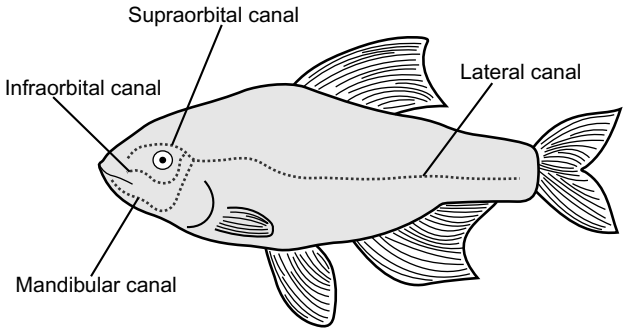

FIGURE 2-11. The lateral line canals of a fish. The main lateral canal runs the length of the body. Three or more canals are located on the head. The figure shows one above the eye (supraorbital), one below the eye (infraorbital), and one on the lower jaw (mandibular).

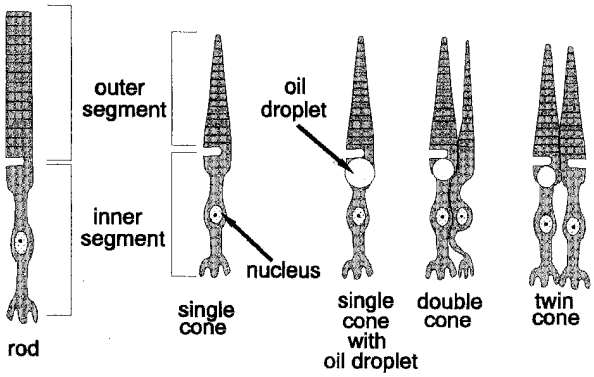

FIGURE 2-12. Photoreceptors of the retina. A rod and several types of cones are shown. The cones of many vertebrates contain colored oil droplets between the inner and outer segments. Vertebrate cones often are paired as may be seen in the double and twin cones.

electromagnetic spectrum that are undetectable to us. Visible light is detected by specialized cells called **photoreceptors**. The two most common types of photoreceptors are the rods and cones of the retina of the eye. These are shown in Figure 2-12. Both types of photoreceptors consist of an inner and an outer segment. The outer segment consists of a series of stacked disks that capture light energy and transduce it into a receptor potential by means of a series of complicated chemical reactions in a group of compounds known as **photopigments**. Each photopigment reacts with light only in a specific range of the spectrum. Rods can be distinguished from cones by the appearance of the stacks of disks; in the rods, the disk diameter remains constant along the length of the outer segment, whereas the diameter of the cone disks becomes progressively smaller so that the cone outer segment tapers to a blunt point. The inner segments of the photoreceptors contain the nuclei and terminal branches of these cells.

In nonmammalian vertebrates, rods and cones can be further differentiated by the presence of oil droplets located between the inner and outer segments of the cones. These droplets may be colorless or they may be yellow, greenish yellow, orange, or red. They appear to function as color filters that serve to restrict the spectral range of light that reaches the outer segment. Thus, a yellow droplet filters out short wavelength (blue) light and a red droplet filters out wavelengths in the range that we call green.

Figure 2-12 also shows some of the varieties of cones, which can include two types of paired cones: double cones and twin cones. These paired cones are characterized by the close proximity of the partners and the absence of pigment epithelium between their outer segments. The partners of these paired cones function in close coordination with each other because they are linked by fast acting, bidirectional electrical synapses. Moreover, they often are found in clusters. Their close proximity thus appears to be a device for increasing the local density of the photoreceptors, which increases the probability of capturing photons. Paired photoreceptors are not found in mammals.

The Retina. Figure 2-13 shows a diagram of the **retina**. Although we often discuss the retina as if it were a simple sensory surface, the retina is, in fact, a highly complex structure with very sophisticated processing capabilities. Indeed, the retina actually is a component of the central nervous system. A full treatment of the anatomy and function of the retina is beyond the scope of this introductory work, and we can only present some of the main features here.

The retina is the innermost layer of the eye. The outermost layer is the **sclera**, which is the tough coat of the eye that gives the eye its globular shape. The next layer is the **choroid**, which is highly vascular and provides the retina with access to the circulatory system. Deep to the choroid lies a layer of **pigment epithelium**. The tips of the photoreceptors are in contact with the pigment epithelium. As its name implies, the pigment epithelium contains dense pigment granules that exclude light. When the light level is high, the pigment epithelium extends down into the spaces between the outer segments to block excess light from reaching the photopigments. When the light level is low, the pigment epithelium retracts to permit the photopigments to have the maximum opportunity to capture photons.

The retina itself consists of several regions. The layer of photoreceptors is the first stage for the processing of light stimulation. As Figure 2-13 indicates, light must pass through all of the other retinal layers before it reaches the photoreceptor outer segments to begin the process of sensory transduction. The layer of photoreceptor nuclei is known as the **outer nuclear layer**. The next region is the middle retina, which consists of **bipolar cells, horizontal cells, amacrine cells**, and **interplexiform cells**. The retinal layer that contains the nuclei of these cells is known as the **inner nuclear layer**. The inner retina consists of the layer of ganglion cells, which are the source of efferent axons from the retina to the brain. These axons converge from all parts of the retina to a single location, known as the **optic nerve head**, to form the **optic nerve**. The bipolar cells connect the photoreceptors to the ganglion cells. The remaining cell types modulate the activity in this pathway from photoreceptors to bipolars to ganglions. The layer of the retina in which the photoreceptor terminals contact the dendrites of the bipolar cells is called the **outer plexiform layer**,

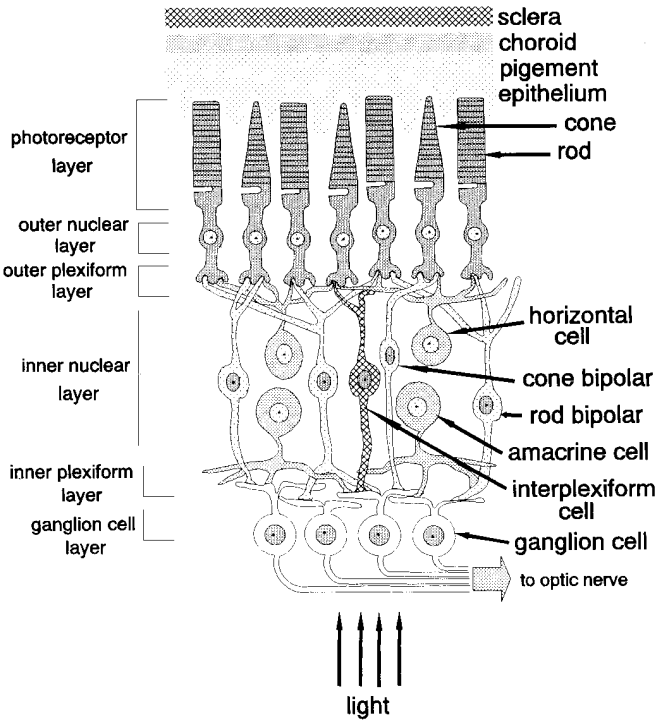

FIGURE 2-13. The retina. The photoreceptors are pointing toward the pigment epithelium, choroid, and sclera. Their outer segments form the photoreceptor layer, their somata form the outer nuclear layer, and their zones of contact with other neurons of the retina form the outer plexiform layer. The inner nuclear layer comprises the somata of the various types of integrative neurons of the retina: the horizontal cells, the bipolar cells, the amacrine cells, and the interplexiform cells. The efferent cells of the retina are the ganglion cells; their dendrites contact the terminals of the integrative cells in the inner plexiform layer. The horizontal cells modulate the activities of the outer plexiform layer, and the amacrine cells modulate the activities of the inner plexiform layer. The two plexiform layers are connected by the bipolar and interplexiform cells. Adapted from Nicholls et al., 1992 and used with permission of Sinauer Associates, with additional information from other sources.

and the layer in which the terminals of the bipolar cells contact the dendrites of the ganglion cells is called the **inner plexiform layer**.

The horizontal cells and amacrine cells provide for lateral interactions within the outer and inner plexiform layers, respectively, while the interplexiform cells link activities between the two plexiform layers. The horizontal cells spread out within the outer plexiform layer to provide a lateral interaction by coupling or uncoupling of the photoreceptors, which permits them to function as groups or as independent detectors of photons. The amacrine cells perform a similar function within the inner plexiform layer. The interplexiform cells provide feedback from the amacrine cells to the horizontal cells and to the bipolar cells.

The Optic Nerve. The bipolar cells project to the **retinal ganglion cells**, which give rise to the axons that form the **optic nerve**. The optic nerve leaves the globe of the eye and passes toward the brain. On route to its terminations in the brain, the optic nerve crosses the midline so that some or most of the axons from the right eye terminate in the left brain and vice versa. This point of crossing is known as the **optic chiasm**. Once the ganglion-cell axons have crossed the midline in the optic chiasm, they are thereafter referred to as the **optic tract**. Not all of the optic nerve axons decussate (cross the midline) in the optic chiasm. Some axons remain ipsilateral (on the same side) to the eye of origin. The proportion that remains ipsilateral varies considerably across vertebrate classes. In general, however, nonmammals tend to have the overwhelming majority of optic axons crossing to the contralateral (opposite) side. In mammals, the proportion of ipsilateral optic axons can be as much as 50%. This will be discussed in greater detail in Chapter 26.

Centrifugal Axons. Not all of the axons in the optic nerve travel from the eye to the brain. In the optic nerve, as in all sensory cranial nerves, centrifugal axons are present that pass from the brain to the receptors. These centrifugal axons generally suppress the activity of the receptors and may play a role in attention mechanisms.

The Median Eye. The eyes that we have been discussing thus far may be considered lateral eyes in that they are located more or less at the sides of the skull. The optics of these eyes

typically are adapted to forming detailed images of the external world on the retina. A considerable amount of this detail is represented in the neural signals that are transmitted to the brain. In addition to these lateral eyes, some vertebrates (but not mammals) have a single, unpaired median eye, located at the top of the skull. This median eye is known as the **pineal eye**. Because the pineal is also known as the **epiphysis**, one could refer to this eye as the **epiphyseal eye**. Unlike lateral eyes, median eyes are not designed to form images, but merely to gather light. The median eye usually consists of a layer of photoreceptors that send their axons directly to the brain. Median eyes do not have the additional neuronal elements that are found in the retina, and therefore are greatly limited in their ability to transmit information about the spatial properties of the visual world. In some vertebrates, a second median eye is present just below the first. The second eye is known as the **parapineal eye** or **paraphysis**. Frequently, the median eye is found below a translucent patch of skin that permits diffuse light to reach the photoreceptors. In some vertebrates, however, a lens-like element occurs that aids in the collection of light.

The median eye synthesizes the hormone and neuroactive substance **melatonin** from serotonin in the absence of light. Melatonin is involved in daily biological rhythms and in seasonal rhythms that depend on the progressive lengthening or shortening of the day, metamorphosis, color change, and sexual development. In birds and mammals, the epiphysis is glandular (the pineal gland) and produces melatonin. It retains its sensitivity to light, even though the light-dark cycle is mostly regulated through central nervous system pathways. Figure 2-14 shows a median eye, from which the axons terminate in the brain.

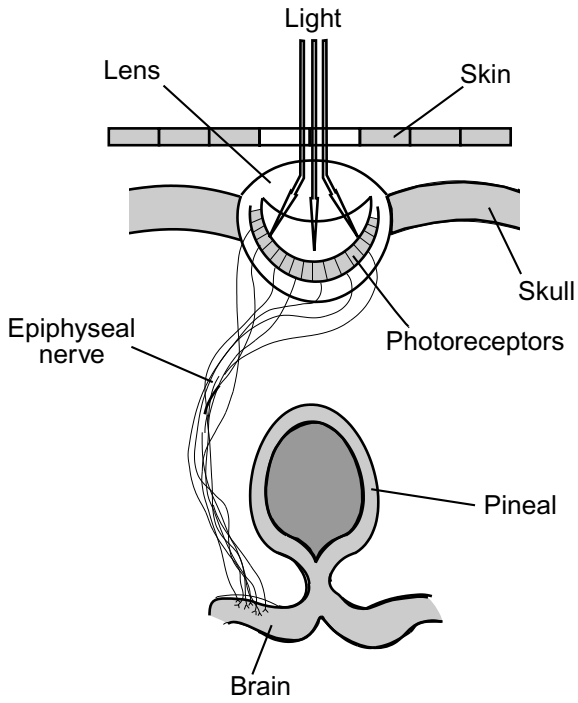

FIGURE 2-14. An example of a median eye. Light impinges on the photoreceptor layer, which is the origin of the epiphyseal nerve that terminates in the epithalamus near the pineal (epiphysis).

Pit Organs. Another type of radiant energy detector is the pit organ, which is found in a group of venomous snakes known as "pit vipers." Rattlesnakes and the other pit vipers have a sensory pit that is located on the snout between the lateral eyes and the nostrils. Certain nonvenomous snakes, such as boas and pythons, have rows of pit organs located on their upper and lower lips. Suspended between the inner and outer cavities of the sensory pit is a membrane that consists of a type of photoreceptor that is sensitive to the infrared range of the electromagnetic spectrum. Infrared is invisible to the human eye, but it can be felt on our skin as heat. In contrast to the heat receptors of the skin, however, the pit membrane is extremely sensitive to subtle differences between the infrared radiation coming from an object (such as a small mammal) and that coming from the background. The pit membrane is innervated by sensory axons of the trigeminal nerve (see Chapter 11). A pit organ is illustrated in Figure 2-15.

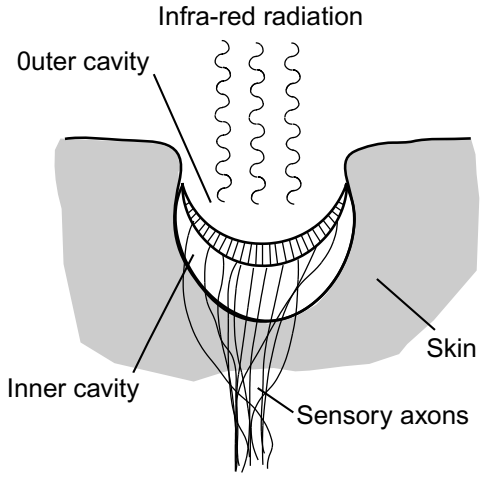

FIGURE 2-15. An IR pit receptor. An IR-sensitive membrane is suspended between the inner and outer cavities of the sensory pit. The membrane is innervated by sensory axons of the trigeminal nerve.

Chemoreceptors

Chemoreceptors sense the chemical properties of the environment. A common feature among chemoreceptors is that they are capable of being stimulated by certain classes of water-soluble chemicals. The two chemosenses that humans are familiar with are gustation (taste) and olfaction (smell). In water, these senses act both as distance receptors (i.e., they can detect stimulus sources that are remote from the receptor, similar to hearing and vision) and as contact receptors (i.e., they detect stimuli that are in direct contact with or very close to a body surface as do touch, temperature, and pain receptors). This occurs because the chemical stimuli must be soluble in the water surrounding the animal. For animals that live in air, however, only the olfactory sense maintains its dual role as both a distance sense and a contact sense. Gustation, on the

other hand, is only a contact sense in land animals because the taste stimuli are only soluble in water, not in air; these stimuli can only produce taste sensations when they dissolve in the epithelial coating of the taste buds within the oral cavity.

Gustation. The gustatory receptors are located within structures known as **taste buds**. In tetrapods, which have tongues, the taste buds are located mainly on the tongue, although some are in the throat as well. The muscular tongue evolved in those branches of the vertebrate lineage that left the water and adapted to life in air where there is no convenient column of sucked-in water to carry food from the mouth to a point where it could be swallowed into the digestive system. The tongue serves this purpose in land animals. In frogs and some reptiles, it serves to grasp prey and bring them quickly into the mouth. In the remaining tetrapods, the tongue serves to manipulate food once it has entered the mouth.

In nontetrapods, taste buds not only are located in the mouth, but also in the throat, on the head, and, sometimes, as in carp, all over the body surface. Some fishes, such as the catfishes, have evolved facial appendages (that give these animals their name) that are studded with taste buds. These appendages, known as **barbels**, are used to sample the gustatory qualities of the environment in the search for edible objects. A catfish typically has more than 100,000 taste buds. Other fishes have fewer but still quite substantial quantities.

The number of taste buds varies among different vertebrate classes. Fishes may have many thousands or even hundreds of thousands of taste buds. Among the land vertebrates, birds have the fewest taste buds and mammals have the greatest numbers. Even within classes, the number varies considerably. Thus, among mammals, humans have approximately 10,000 taste buds (90% of which are on the tongue), in contrast to rabbits and some ungulates (hoofed mammals), which can have two to three times that number.

Figure 2-16 shows a taste bud with its taste receptors. Taste receptors typically are located within a **gustatory papilla**, which can be a raised structure or a pit with a pore opening to the outside. The walls of these papillae contain small, barrel-shaped structures, which are the taste buds. Each taste bud contains dozens of taste receptor cells.

The primary taste qualities of humans are "sweet," "sour," "salt," and "bitter." Other more complex tastes are possible from combinations of these. Taste, however, must be distinguished from *flavor*, which is what most people mean when they refer to the "taste" of something. For example, "this tastes like chocolate" or "this tastes exactly like the way my mother cooked it." These sentences really mean that something had the flavor of chocolate or had the same flavor as Mom's recipe. The reason that this distinction is necessary is because flavor is a different chemosense than taste; the experience of flavor results from a combination of taste and smell. We are all familiar with the loss of the flavor of food when we have a bad cold with a stuffy nose. We may complain that nothing seems to have any "taste" in such a circumstance, but in fact our sense of taste (sweet, sour, salty, and bitter) is perfectly intact. What has occurred is that olfactory stimuli from the mouth (or from the external world, for that matter) cannot reach our olfactory receptors.

BOX 2-2. Another Taste System?

In addition to the classical taste system, which uses gustatory cells within taste buds as the receptors, an additional chemosensory cell type has been reported on skin surfaces, in the mouth, and on the gills of anamniotes, including hagfishes, various teleosts, and amphibians. In the latter, they are located on the ventral skin. These cells are called **solitary chemoreceptor cells**, and they are typically, but not always, found in the company of classical taste buds.

Solitary chemoreceptor cells are particularly well developed in two teleost genera—*Ciliata* (rocklings) and *Prionotus* (sea robins), in which they are located on the fins. In *Ciliata*, these cells respond to fish body mucus and also to fish bile. They thus may serve in the detection of predators and/or competitors. In *Prionotus*, the cells are located on the pectoral fins, which explore the bottom, and may be involved in feeding. They may have other chemosensory functions as well.

Recently, solitary chemosensory cells have been reported in mammals in the gustatory system, the digestive system, and the respiratory system. In newborn rodents, for example, solitary chemosensory cells have been found in the gustatory epithelium. In rats and mice, they have been reported in the nasal epithelium where they form synaptic contacts with endings of the trigeminal nerve. Interestingly, these receptor cells are responsive to substances that produce a bitter taste in humans and very likely activate trigeminal protective reflexes in response to potentially noxious compounds that enter the nasal air stream. The presence of gustatory receptors in association with the trigeminal nerve is yet another example of the extreme versatility of the sensory division of this cranial nerve (see Box 11-1).

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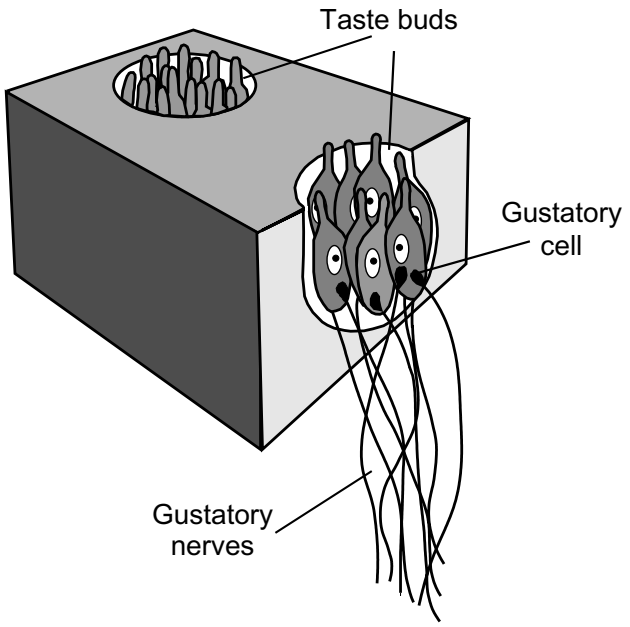

FIGURE 2-16. Taste buds. The cut-away view on the right reveals the structure of the taste bud.

Gustatory neurons in nonhuman land vertebrates respond to the same or similar chemical compounds that produce the human taste qualities; among these are sugars (sweet), acids (sour), salts (salty), and alkaloids (bitter). Gustatory neurons in aquatic vertebrates respond to these same classes of chemical compounds, but in addition respond to a wide range of amino acids. We can only guess at what the subjective gustatory effect of mixing amino acids with the other taste chemicals in varying proportions might be. Whether the subjective experience of these animals to these chemicals is the same as ours, we cannot know, but it is entirely possible that some or all of them may differ. We do know, however, that carbohydrates generally have a sweet taste to us, and both humans and animals will accept carbohydrates as food items. We further know that many plant alkaloids are toxic, that alkaloids evoke a bitter taste in humans, and that animals and humans generally reject bitter tasting food items. Goldfish have been reported to sort out food pellets laced with the bitter (to humans) alkaloids caffeine or quinine from unadulterated pellets using a special oral-particle sorting apparatus (called the palatal organ) contained within their oral cavities.

A fifth taste sensation has been reported in humans; this is known as *umami*. This taste sensation is associated with the food enhancer, monosodium glutamate (MSG). In mice and fishes, taste receptors respond to glutamate, although L-aspartate and other amino acids have been described as evoking umami as well.

Gustatory sensations are not uniformly distributed on the surface of the tongue. Figure 2-17 shows a schematic diagram of a human tongue with the zones that represent the locations of the various taste sensations of humans: sweet (tip), salty (anterior sides), sour (posterior sides), and bitter (back of the tongue). Note the overlap of some of the taste zones. Figure 2-17 also shows the relative distributions of taste buds on the body surface of a catfish. The darker the shading, the greater the density of taste receptors. Note the presence of taste receptors on the fins and the very high concentrations of receptors on the barbels, the head, and the snout.

Olfaction. Olfactory stimuli are very complex. They emanate not only from food objects but from a variety of sources. Because humans are **microsmatic**, which means that we have a relatively poor olfactory system, we cannot appreciate the rich and complex olfactory world of the **macrosmatic** animals, which have well-developed olfactory systems. The canidae, which include dogs, wolves, coyotes, and other dog-like animals, for example, are macrosmatic, and their abilities to identify individuals by smell are well known.

Olfactory receptors are located in cavities within the nose. The openings of the nose (the nostrils, or nares) allow the medium of the external environment (air or water) into the nasal cavity. Within the cavities is the olfactory epithelium that contains the olfactory receptors. These cavities, however, cannot be blind sacs, which would inhibit the continuous flow of the medium from bringing a smooth and continuous sampling of the external environment to the olfactory epithelium. They therefore have both an anterior and a posterior opening. In fishes, the water flows into the anterior naris, through the nasal sac, and out the posterior naris. Figure 2-18 shows the inflow and outflow of the water column through the anterior and posterior naris. Within the nasal sacs of fishes is a highly folded surface that contains the olfactory receptors. This folding greatly increases the receptor surface area permitting a greater number of receptors to be packed into a small space. In tetrapods, however, the air column is pulled into the nares during the inspiration phase of the respiratory cycle and drawn down into the lungs (Figure 2-19). Openings in the ethmoid bone, which forms the roof of the nasal cavity, lead to the olfactory epithelium. Special bones within the nasal cavity called **turbinate bones** ensure a sufficient turbulence of the air column so that the volatile molecules can reach the olfactory epithelium. The olfactory epithelium is coated with mucus into which protrude the olfactory receptors. Olfactory stimuli (or odorants) are chemical substances that can dissolve in the mucus. Unlike the relatively small number of categories of taste stimuli, the number of odorant categories is vast.

The axons of the olfactory receptors terminate in the **olfactory bulb**, which is a specialized olfactory region of the brain that lies directly above the ethmoid bone. Macrosmatic animals have large, well-developed olfactory bulbs; microsmatic animals have small, less-well-developed olfactory bulbs. Figure 2-19 also shows how the olfactory receptor cell axons pass through the ethmoid bone to terminate in the overlying olfactory bulb.

Vomeronasal Organ. An important part of the olfactory world is the social aspect. One facet of this is the recognition of individuals, as mentioned above. Another facet of social olfaction is chemical signaling or communication. Many animals signal danger or readiness to mate or mark their territories by means of a class of chemical-communication substances called **pheromones**. A pheromone is a chemical substance secreted by one animal that produces a specific

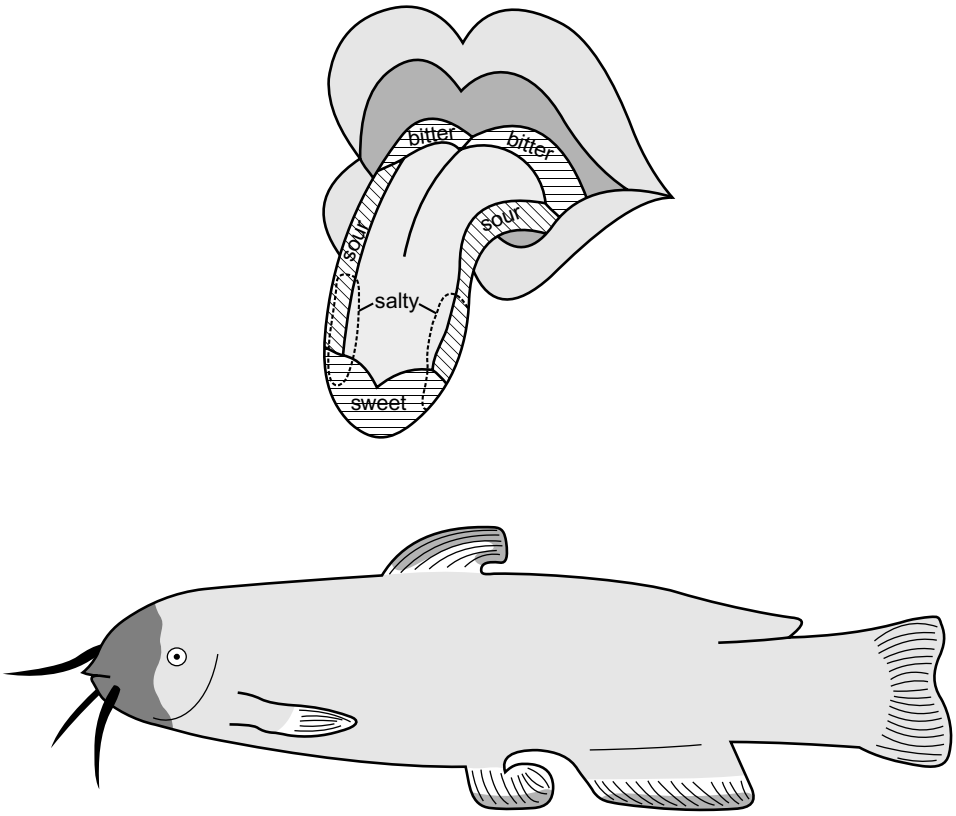

FIGURE 2-17. Top: The taste zones of a human tongue. Receptors that respond primarily to sweet are located at the tip of the tongue. On the sides, just behind the sweet zone, are the salty and sour zones. The bitter zone is located at the rear of the tongue. Note the overlap in the taste regions. Bottom: The relative distribution of taste buds on the body of a catfish. The taste buds are indicated by shading. Greater concentrations of taste receptors are shown by darker shading. Based on data from Atema (1980).

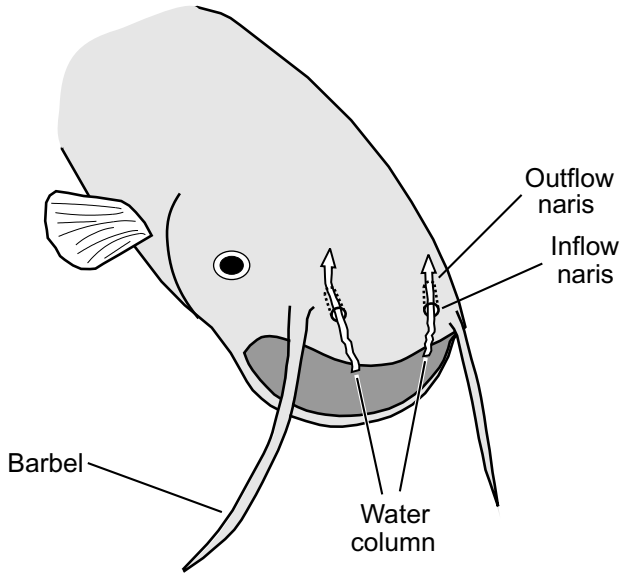

FIGURE 2-18. The nares (nostrils) of a catfish. A column of water enters the anterior naris, passes over the olfactory receptor sheet, and exits through the posterior naris. The barbels of the catfish are covered with taste buds as is much of the rest of its body surface.

behavioral reaction in another animal. Alarm pheromones indicate some dangerous situation, and sex attractant pheromones help males to locate sexually receptive females. Humans normally do not detect sex-attractant pheromones that are secreted by the bodies of other humans, although a few subtle exceptions have been noted. Instead, we rely on a group of chemicals produced by human commercial manufacture known as perfumes.

In some amphibians, some reptiles, and many mammals, the chemoreceptors for pheromones are located in the nasal cavity. However, in a number of vertebrate classes, these chemoreceptors are located in a separate cavity that is in the roof of the mouth and known as the **organ of Jacobson**. Because this cavity is located in a bone known as the vomer, the organ of Jacobson is frequently known as the **vomeronasal organ**. The vomeronasal organ is especially well-developed in snakes and some lizards, but absent in turtles; the rapid flicking in and out of the tongue serves to capture olfactory molecules and to bring them in contact with the vomeronasal organ on the roof of the mouth. Likewise, many ungulates curl their upper lips and inhale air. This behavior, known as the *flehmen* response, serves to draw air over the entrance to the vomeronasal organ. Figure 2-20 shows a vomeronasal organ in a reptile.

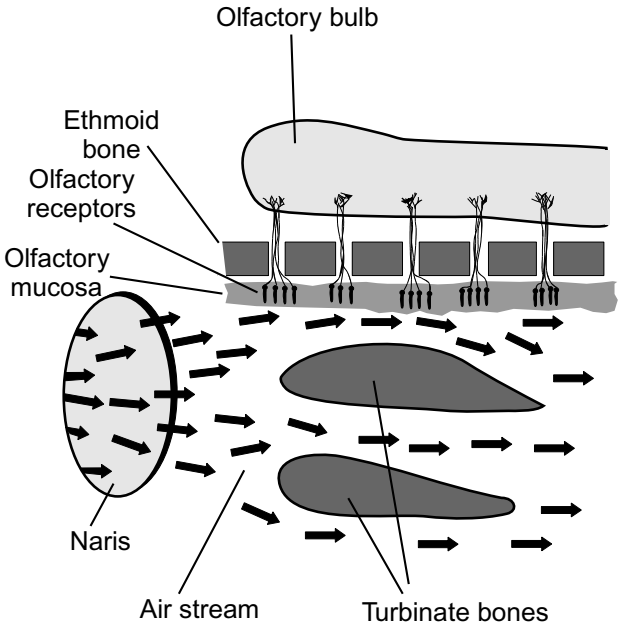

FIGURE 2-19. The olfactory organs of a tetrapod. A stream of air enters the nasal cavity from the outside. The air flows across the turbinate bones and comes in contact with the olfactory receptors located in the mucus layer below the ethmoid bone. The axons of the olfactory receptors pass through openings in the ethmoid bone and terminate in the overlying olfactory bulb.

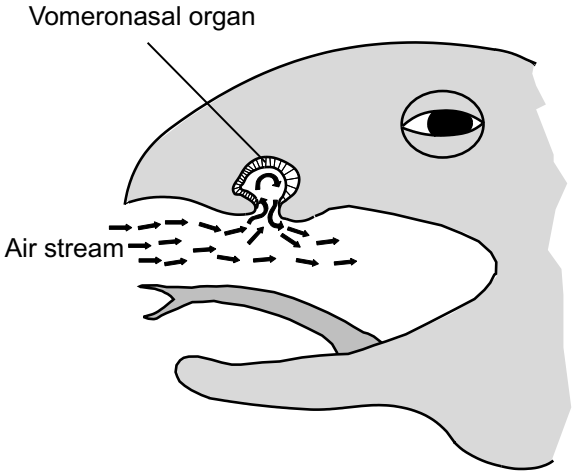

FIGURE 2-20. The organ of Jacobson or vomeronasal organ in a lizard. The flicking of the animal's tongue conducts the air stream into the vomeronasal organ, which is located in the vomer bone of the roof of the mouth. The vomeronasal organ detects pheromones, which are olfactory stimuli that can function as chemical-communication signals.

Primates have a vomeronasal organ during embryological development, but it becomes progressively reduced in size so that by birth it appears to have disappeared. Recent reports, however, indicate that a small vomeronasal organ is present in adult humans. Whether it has neuronal connections to the brain or whether chemical stimulation of it has any behavioral consequences is unknown at present.

Unlike the olfactory receptors of the nasal cavity, those of the vomeronasal organ do not have cilia extending into the mucus that covers the receptor surface. A further difference between the nasal and vomeronasal systems is that they have different terminations within the brain. The nasal receptors terminate in a part of the brain known as the olfactory bulb (or sometimes as the **main olfactory bulb**), whereas the vomeronasal receptors terminate within an **accessory olfactory bulb** located near the main olfactory bulb.

Nervus Terminalis: An Unclassified Receptor

Still another type of receptor, the functions of which have not yet been established, is the **nervus terminalis** or terminal nerve, a microscopically small nerve that innervates the nasal septum. This nerve is present in all jawed vertebrates. Unlike the nasal and vomeronasal systems, the terminal nerve has no specialized receptor endings but rather ends in free nerve endings. Because many of the axons of the terminal nerve contain the hypothalamic hormone, GnRH (gonadotropin releasing hormone), which is involved in a number of reproductive neuroendocrine processes, the terminal nerve may function, among other things, in the detection of pheromones, especially in those vertebrates in which a vomeronasal organ is not present, although this has not been demonstrated experimentally. The terminal nerve also may detect temperature changes or other nonchemical, intranasal stimuli.

Electroreceptors

The detection of electric fields is widespread among vertebrates. Some aquatic predators can detect the electric fields produced by the contractions of the muscles of their prey as they swim. Even the electric fields produced by the contractions of the muscles of respiration may be sufficient for predators to detect at a short distance. Although predatory electroreception is typical in certain groups of cartilaginous fishes and ray-finned fishes, recent investigations report electroreception in lampreys, some amphibians, and in monotreme mammals as well; both platypuses and spiny anteaters have been reported to have electroreceptors in the skin of their snouts.

In addition to detecting the movements of prey, several groups of animals are capable of detecting the self-generated electric fields around their own bodies. These electric fields are much larger than those produced by routine muscle contraction. Rather, they are produced by special organs known as **electric organs**. You probably have heard of the electric eel that is capable of delivering a powerful electric shock to stun or kill prey or animals that threaten it. This powerful electric discharge is produced by electric organs. Other fishes are also capable of powerful electric organ discharges, such as the electric catfish, a ray-finned fish, and the torpedo, a cartilaginous fish from which the undersea weapon gets its name. These fishes, however, do not use their electric-organ discharges only for predation and defense; they also use them to detect objects in the environment around them. They do so by emitting weak

electrical discharges all the time and sensing the distortions of the electric fields surrounding them that result from the presence of nearby objects with high or low electrical conductivity. Objects that conduct electricity well, like other fishes, distort the electric field differently than do poor conductors, such as rocks.

The detection of these weak, self-generated electric fields also is the specialty of several families of ray-finned fishes that are not capable of generating the strong discharges necessary for predation and defense. These animals use their electroreception of changes in the fields around them to locate food, but in a manner quite different from those animals that do not have electric organs; rather than locating prey by the electric fields that emanate from the prey, the weakly electric fishes detect prey by the effects on the electric fields that they generate themselves. In addition to predation, these electric-organ fishes use their electroreception to detect others of their species, to maintain space around themselves, to identify individuals and potential mates, and for other aspects of social behavior. Some electric fishes also can detect the movement-generated electric fields around their prey. Figure 2-21(B) illustrates how stimuli of either high- or low-electrical conductivity affect the lines of the electrical fields actively generated around a weakly electric fish. Figure 2-21(C) shows a shark, which is using its predatory electroreception to detect the electric fields around a fish that it is about to capture.

The electroreceptors themselves fall into two broad categories, each with several subtypes: **ampullary receptors** and **tuberous receptors**. Figure 2-22 shows examples of these two types of receptors. The electroreceptors of fishes are found in the lateral line canals and are innervated by branches of the lateral line nerves. The independently evolved electroreceptors of monotremes are located in the snout region and are innervated by the trigeminal nerve (see Box 11-1).

The ampullary and tuberous receptors differ in their sensitivity and function. The ampullary receptors are responsive to the sorts of low-frequency electric rhythms that would result from the muscular contractions of respiratory or swimming movements (0.1–50 cycles per second). Tuberous receptors, on the other hand, have a much higher frequency range (50–200 cycles per second), which is the frequency range of the electric-organ discharge. Further details about electroreceptors and electroreception may be found among the references at the end of this chapter.

Nociceptors

The term **nociception**, the detection of something unpleasant, is derived from the same roots as the word "noxious" and generally refers to pain "receptors" that usually are free nerve endings. These are activated when the tissue is cut, crushed, or otherwise damaged. Another type of noxious sensation arises from the stimulation of certain irritating chemicals such as strong acids, bases, and a variety of irritants and toxins produced by animals and plants as a defense against predation or as a form of predation, such as insect bites or jellyfish stings. Many of the spicy foods activate general chemical sensitivity in the oral cavity. This sensitivity is not limited to the mouth region, however, as anyone can testify who has been eating highly spiced food with their fingers and then makes the

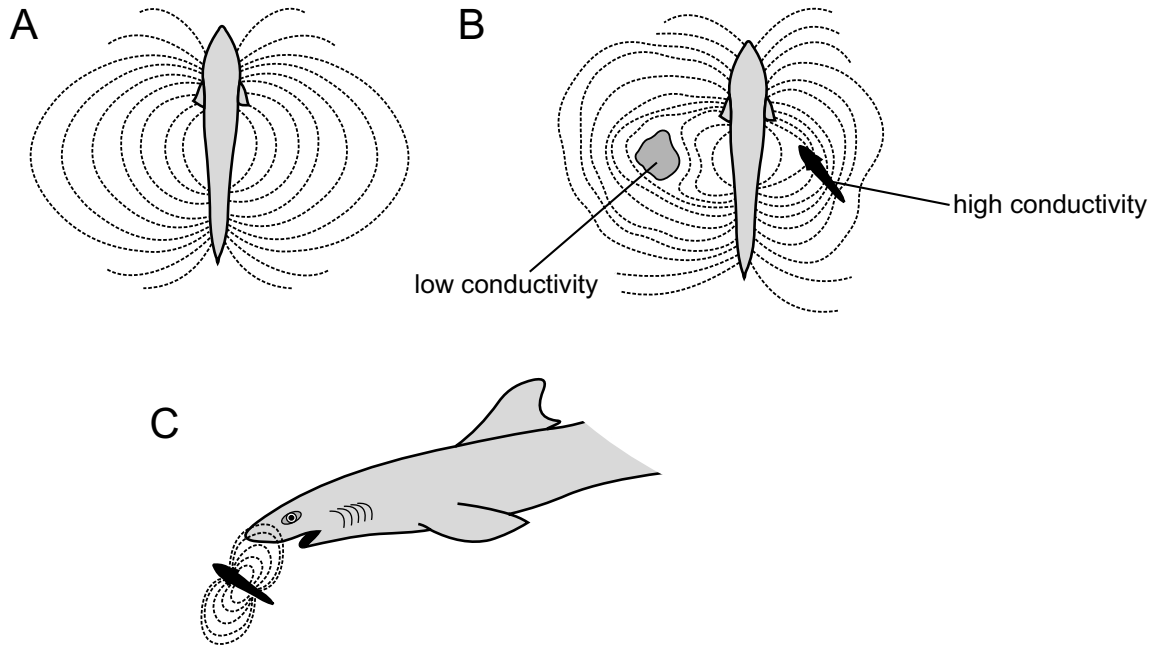

FIGURE 2-21. (A) Actively generated lines of current around a weakly electric fish. (B) Distortion in the current lines as a result of a nearby object of high conductivity (right) and another of lower conductivity (left). Based on Feng (1991) and used with permission of John Wiley & Sons. (C) A predatory electroreceptive shark detects the lines of current around a nearby prey fish. Based on discussion by Kalmijn (1988).

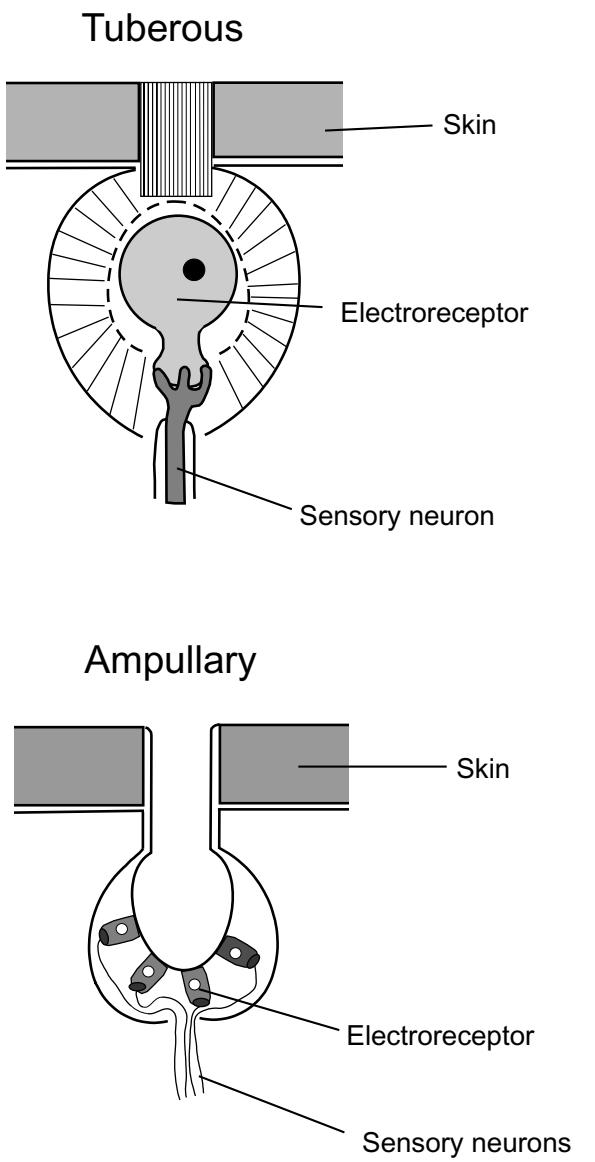

FIGURE 2-22. Two types of electroreceptors: tuberous (top) and ampullary (bottom). Adapted from Feng (1991) and used with permission of John Wiley & Sons.

mistake of rubbing their eyes with their spice-laden fingers. This type of general chemical sensitivity is quite different from chemoreception because receptors are specialized for specific categories of chemical compounds and thus unique sensory experiences resulting from these different compounds do not occur. Like pain, general chemical sensitivity is mediated by free nerve endings located under the surface of the skin and in a number of internal organs.

Magnetoreceptors

Behavioral studies have reported that a variety of vertebrates appear to be able to detect various aspects of the earth's magnetic field that they use for orientation and/or navigation; that is, to go in a particular direction and/or to get from one place to another on the surface of the planet. For example, attaching small magnets to the heads of homing pigeons interferes with their ability to find their way home. Although the evidence for magnetoreception is convincing, where these receptors are and what they might be remains a mystery. One recent intriguing possibility that currently is being investigated is that the photopigment molecules of the retinal photoreceptors of birds become magnetized, which permits the bird to "see" the orientation of the magnetic field. Other studies have identified magnetic materials in the beak area of some species of birds and reported that a branch of the trigeminal is responsive to magnetic fields. Some investigators have reported that cartilaginous fishes also can use their electroreceptors to detect the electric fields that are produced in their bodies when they swim through the earth's magnetic field the way that an electric current is produced when a coil of wire is moved around a magnet. (See Boxes 11-1 and 18-1 for additional information about magnetoreception.)

TOPOGRAPHIC ORGANIZATION

Another important feature of sensory systems is **topographic organization**, which means that the spatial organization of the receptor surface, such as the skin, the retina, or the basilar papilla, is preserved within the sensory parts of the central nervous system. In the case of the representation of the body in the central somatosensory system, those neurons that receive sensory information that originates on the body surface are organized in a sequential arrangement that roughly mirrors the sequence in which the individual parts are found on the body surface. Thus, head and forelimb representations are at one end of this area, while pathways that originate in the hind limb and tail areas are located at the other end. Within the body representation, the upper trunk is located near the head and forelimb representations and the lower trunk near the tail and hind limb representations.

Sometimes the topographic organization is crude so that only gross areas are represented; other topographic organizations have a very precise point-to-point mapping of the receptor surface within the brain. For example, in those mammals with facial vibrissae (whiskers), each whisker can have its own region of representation in the head area of the somatosensory brain. In general, the more an animal makes use of a sense to detect the fine details of the environment, whether it be small objects in the visual world, subtle acoustic changes in the auditory world, or microvariations in the objects that are touched, the more likely it is that the central representation of the receptor surface will be topographically organized. Moreover, the greater the degree to which a sense is used by an animal, the greater will be the size of the topographic map.

Special names are used to characterize topographic organization within the various senses: the central representation of the retinal map is known as a **retinotopic** organization, and the central representation of the body map is a **somatotopic** organization. In the auditory system, the spatial distribution of the basilar papilla or cochlea is a representation of the different frequencies of sound that the animal can detect, with the low tones at one end and the high tones at the other. The preservation of this spatial mapping of tones is known as a

tonotopic organization. Figure 2-23 shows examples of two receptor surfaces and their corresponding central representations. In the retinotopic organization, although the tectal map appears to have flipped over (due to optic tract geometry), the individual quadrants of the retinotopic map are in the same relationship to each other as they are on the retina. In highly visual animals, within each quadrant a point-to-point mapping of the retina to the retinotopic map exists. The somatotopic map of the digits and the palm (shown in Box 2-3, Fig. 1B) also is in the correct sequence and forms a virtual map of the surface of the paw. Finally, the order of frequencies present in the auditory receptor surface is preserved within the brain. Topographic organizations may be found in any sensory system in which the ordering of either the position in space or specific sensory qualities is important to the animal's success in its environment. Thus, in animals in which gustation and olfaction are highly developed, evidence for chemotopic maps has been reported. For example, each taste-bud studded barbel (or whisker) of the catfish has its own area of representation within the central gustatory system of this animal. The olfactory bulb, however, appears not to be coded according to olfactory space, but rather is organized according to odor categories. Olfactory space would have to be represented by intensity differences between the two olfactory bulbs, much as auditory space is represented by intensity, time of arrival, and other acoustical differences between the two ears.

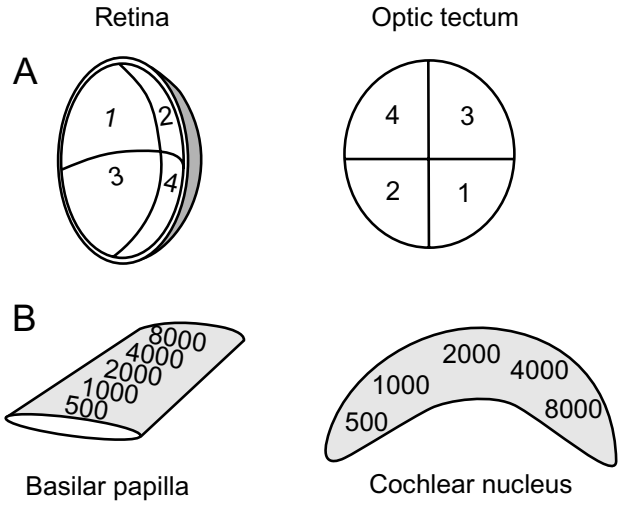

FIGURE 2-23. Topographical organization in the visual and auditory systems. (A) Retinotopic organization: A topographical representation of the retina on the optic tectum in a reptile. (B) Tonotopic organization: A topographical representation of the basilar papilla on one of the cochlear nuclei of a bird.

BOX 2-3. Isomorphic Topographic Maps

An examination of the topographic maps in Figure 2-23 might suggest to the reader that these maps actually form a kind of picture of the sensory surface within the nervous system. In many instances these maps do form an impressive representation of the sensory surface within the brain. Although most of these detailed topographic maps are located in the cerebral cortex of mammals, they also occur in other vertebrate classes as well. Figure 1 shows examples of four such highly precise topographic maps. William Hodos and Ann Butler have termed such precise representations of the sensory surface **isomorphic maps**. Isomorphic maps give the most spatially detailed representation of the sensory surface of any topographic maps. They are the hallmark of a highly developed, sophisticated sensory system.

On the left side of the figure is a cartoon of the sensory surface; on the right side is a map of the neural representation of that sensory surface. In the figure, the left side of part A represents the snout of a rodent with its array of vibrissae (whiskers) and the right indicates the representation of the snout region on the somatosensory cortex of the brain. Within the snout region, each vibrissa has its own representation known as **barrels**, but the overall organization of the barrels within the snout region is a close representation of the location of the vibrissae on the animal's snout.

Part B shows the ventral surface of the paw of a raccoon, an animal with excellent ability for fine manipulation of objects with its paws. In the figure, the digits have been indicated by numbers and the palm pads by letters. Note that the somatosensory representation of the paw matches the sensory surface in an isomorphic manner. Part C represents "whiskers" of another kind, the so-call whiskers of a catfish, which give the animal its name. These structures are unrelated to the vibrissae of mammals, although they do have some functions in common as organs for exploring the close-by environment. Catfish "whiskers" are known as **barbels** and are used for exploring the chemical attributes of the substrate below the fish. This catsfish has four barbels on each side—a nasal barbell adjacent to the naris (NB), a maxillary barbel on the upper jaw (MX), and two mandibular barbells, a lateral (LM) and a medial (MM), on the lower jaw. The axons associated with the barbel gustatory receptors terminate in a region of the fish's hindbrain known as the **facial lobe**. Within the facial lobe is an isomorphic representation of these barbels. The region labeled TTL indicates the area devoted to the representation of the taste buds from the rest of the body.

Finally, we come to an extreme example of isomorphic mapping of a sensory surface. Part D of the figure shows a cartoon of the snout region of a star-nosed mole. A sketch of the entire animal is shown in Figure 2. As reported by Kenneth Catania and Jon Kaas, each half of the rostral end of the animal's snout contains 11 fleshy finger-like protuberances known as **nasal rays**. The two black spots in the

BOX 2-3. Isomorphic Topographic Maps—cont'd

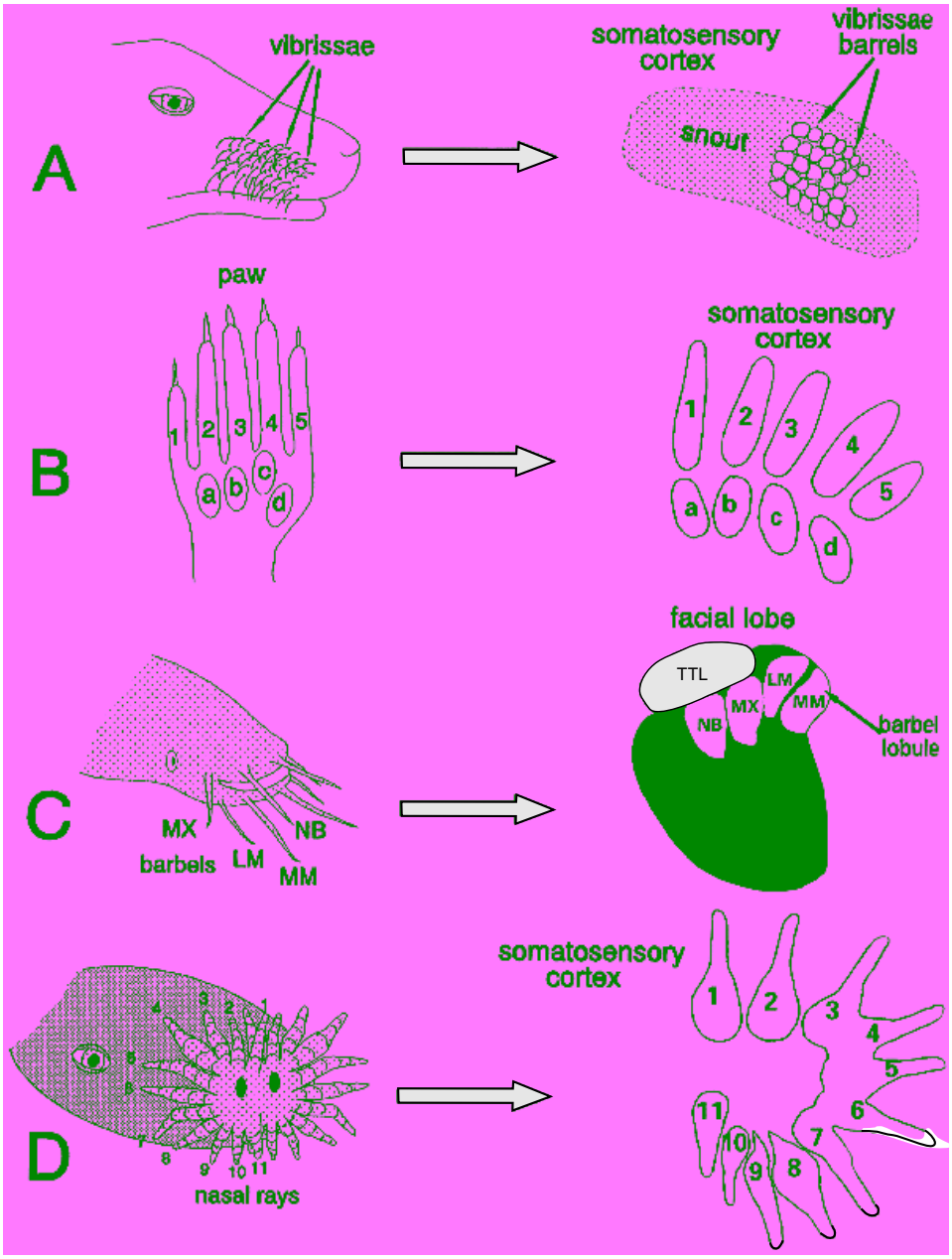

FIGURE 1. Isomorphic representations of peripheral sensory structures within the central nervous system. A: The vibrissae of a rodent and their representation in the somatosensory cortex. B: The ventral surface of the paw of a rodent showing the digits (numbers) and palm pads (letters) and their corresponding somatosensory cortical representation. C: The barbels of a catfish and their isomorphic mapping of each barbel's gustatory receptors within the animal's facial lobe. The region labeled TTL indicates the representation of the gustatory receptors for the rest of the animal's body. D. The 22 nasal rays on the snout of a star-nosed mole. The 11 nasal rays of the animal's right side shown represented with corresponding numbers on its somatosensory cortex. Adapted from Hodos and Butler (1997).

BOX 2-3. Isomorphic Topographic Maps—cont'd

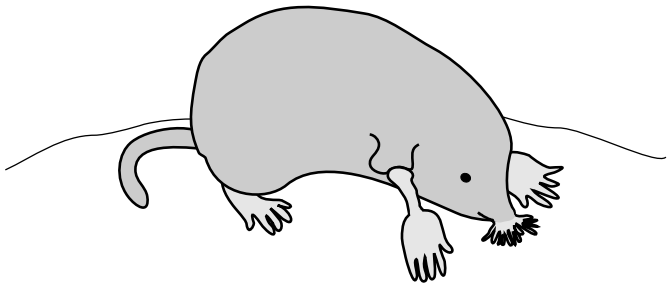

FIGURE 2. A star-nosed mole (*Condylura cristata*).

center of the snout represent the nares. These rays are used to probe the moist earth for earthworms and other prey. Each nasal ray is represented in the animal's somatosensory cortex in an amazing likeness of the peripheral structure's size and location.

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RECEPTIVE FIELDS

In those senses in which either the body surface or the surrounding environment is mapped in a topographic manner, the notion of the **receptive field** has proved quite useful. A receptive field is that area of a sensory surface that must be stimulated in order to influence the activity of a particular sensory neuron in the central nervous system. In the case of vision, the receptive field is that area in visual space in which a stimulus must be presented in order for a neuron in the central visual system to respond. Similarly, a somatosensory receptive field is that region of the body that must be stimulated in order for a central somatosensory neuron to discharge. The existence of discrete receptive fields is the basis of retinotopic and somatotopic organization. The size of the receptive field represents the sum of the excitatory and inhibitory influences present in the sensory pathway that converge on the central sensory neuron. These excitatory and inhibitory influences may be from receptor cells, central sensory neurons, or some combination of both.

THE SENSES AND EVOLUTION OF THE CENTRAL NERVOUS SYSTEM

The diversity of the sensory worlds of animals is matched only by the diversity of the environments that they inhabit. Those animals that achieved the capability to extend their exploration of the sensory world, either by sudden mutation or by more gradual changes in their structure, were able to invade and exploit new adaptive zones to the benefit of themselves and their offspring. These benefits led to further adaptive pressures for increased sensitivity or broader range of responsiveness or altered ranges. In the majority of instances, the development of new sensory adaptations was the wedge that opened the way to new sources of food, new systems for early warning of the approach of predators, more efficient methods for care of the young, better communication with conspecifics, easier detection of the location of potential mates and recognition of their sexual receptivity, and a host of other behavioral adaptations that have promoted both the survival of

existing lineages and the development of new ones. These new sensory adaptations have included increased complexity and organization of topographic maps within the sensory system, the development of multiple topographic maps of the system within the telencephalon, and the emergence of entirely new receptors and/or modification of existing receptors, both of which utilize existing neural pathways. The extreme versatility and adaptability of sensory receptors and their central connections and pathways has been a critical factor in the ability of the central nervous system to evolve and to play a key role in the ability of species to better exploit their present environments or to successfully invade new ones.

INTRODUCTORY NEUROSCIENCE TEXTBOOKS

These books will be useful for readers with little background in cellular neuroscience and other neuroscience topics or for those who need to refresh their knowledge at an introductory level.

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