



Autonomic neurons in the myenteric plexus of the digestive tract

CHAPTER

15

The Autonomic Nervous System and Visceral Reflexes

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Brushing Up

To understand this chapter, it is important that you understand or brush up on the following concepts:

- Innervation of smooth muscle (p. 434)
- Neurotransmitters and synaptic transmission (pp. 464–467)
- Spinal nerves (p. 490)
- The hypothalamus and limbic system (pp. 530, 534)
- Cranial nerves (p. 547)

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We have studied the somatic nervous system and somatic reflexes, and we now turn to the *autonomic nervous system* (ANS) and *visceral reflexes*—reflexes that regulate such primitive functions as blood pressure, heart rate, body temperature, digestion, energy metabolism, respiratory airflow, pupillary diameter, defecation, and urination. In short, the ANS quietly manages a myriad of unconscious processes responsible for the body's homeostasis. Not surprisingly, many drug therapies are based on alteration of autonomic function; some examples are discussed at the end of this chapter.

Harvard Medical School physiologist Walter Cannon, who coined such expressions as *homeostasis* and the *fight or flight* reaction, dedicated his career to the physiology of the autonomic nervous system. Cannon found that an animal can live without a functional sympathetic nervous system, but it must be kept warm and free of stress; it cannot survive on its own or tolerate any strenuous exertion. The autonomic nervous system is more necessary to survival than many functions of the somatic nervous system; an absence of autonomic function is fatal because the body cannot maintain homeostasis. We are seldom aware of what our autonomic nervous system is doing, much less able to control it; indeed, it is difficult to consciously alter or suppress autonomic responses, and for this reason they are the basis for polygraph ("lie detector") tests. Nevertheless, for an understanding of bodily function and health care, we must be well aware of how this system works.

General Properties of the Autonomic Nervous System

Objectives

When you have completed this section, you should be able to

- explain how the autonomic and somatic nervous systems differ in form and function; and
- explain how the two divisions of the autonomic nervous system differ in general function.

The **autonomic nervous system (ANS)** can be defined as a motor nervous system that controls glands, cardiac muscle, and smooth muscle. It is also called the **visceral motor system** to distinguish it from the somatic motor system that controls the skeletal muscles. The primary target organs of the ANS are the viscera of the thoracic and abdominal cavities and some structures of the body wall, including cutaneous blood vessels, sweat glands, and piloerector muscles.

Autonomic literally means "self-governed."¹ The ANS usually carries out its actions involuntarily, without our conscious intent or awareness, in contrast to the voluntary nature of the somatic motor system. This voluntary-involuntary distinction is not, however, as clear-cut as it

once seemed. Some skeletal muscle responses are quite involuntary, such as the somatic reflexes, and some skeletal muscles are difficult or impossible to control, such as the middle-ear muscles. On the other hand, therapeutic uses of biofeedback (see insight 15.1) show that some people can learn to voluntarily control such visceral functions as blood pressure.

Visceral effectors do not depend on the autonomic nervous system to function, but only to adjust their activity to the body's changing needs. The heart, for example, goes on beating even if all autonomic nerves to it are severed, but the ANS *modulates* (adjusts) the heart rate in conditions of rest or exercise. If the somatic nerves to a skeletal muscle are severed, the muscle exhibits flaccid paralysis—it no longer functions. But if the autonomic nerves to cardiac or smooth muscle are severed, the muscle exhibits exaggerated responses (*denervation hypersensitivity*).

Insight 15.1 Clinical Application

Biofeedback

Biofeedback is a technique in which an instrument produces auditory or visual signals in response to changes in a subject's blood pressure, heart rate, muscle tone, skin temperature, brain waves, or other physiological variables. It gives the subject awareness of changes that he or she would not ordinarily notice. Some people can be trained to control these variables in order to produce a certain tone or color of light from the apparatus. Eventually they can control them without the aid of the monitor. Biofeedback is not a quick, easy, infallible, or inexpensive cure for all ills, but it has been used successfully to treat hypertension, stress, and migraine headaches.

Visceral Reflexes

The ANS is responsible for the body's **visceral reflexes**—unconscious, automatic, stereotyped responses to stimulation, much like the somatic reflexes discussed in chapter 14 but involving visceral receptors and effectors and somewhat slower responses. Some authorities regard the visceral afferent (sensory) pathways as part of the ANS, while most prefer to limit the term ANS to the efferent (motor) pathways. Regardless of this preference, however, autonomic activity involves a visceral reflex arc that includes receptors (nerve endings that detect stretch, tissue damage, blood chemicals, body temperature, and other internal stimuli), afferent neurons leading to the CNS, interneurons in the CNS, efferent neurons carrying motor signals away from the CNS, and finally effectors.

For example, high blood pressure activates a visceral *baroreflex*.² It stimulates stretch receptors called *baroreceptors* in the carotid arteries and aorta, and they transmit

¹auto = self + nom = rule

²baro = pressure

signals via the glossopharyngeal nerves to the medulla oblongata (fig. 15.1). The medulla integrates this input with other information and transmits efferent signals back to the heart by way of the vagus nerves. The vagus nerves slow down the heart and reduce blood pressure, thus completing a homeostatic negative feedback loop. A separate autonomic reflex arc accelerates the heart when blood pressure drops below normal.

Divisions of the Autonomic Nervous System

The ANS has two divisions, the sympathetic and parasympathetic nervous systems. These divisions differ in anatomy and function, but they often innervate the same target organs and may have cooperative or contrasting

effects on them. The **sympathetic division** prepares the body in many ways for physical activity—it increases alertness, heart rate, blood pressure, pulmonary airflow, blood glucose concentration, and blood flow to cardiac and skeletal muscle, but at the same time, it reduces blood flow to the skin and digestive tract. Cannon referred to extreme sympathetic responses as the “fight or flight” reaction because they come into play when an animal must attack, defend itself, or flee from danger. In our own lives, this reaction occurs in many situations involving arousal, competition, stress, danger, anger, or fear. Ordinarily, however, the sympathetic division has more subtle effects that we notice barely, if at all. The **parasympathetic division**, by comparison, has a calming effect on many body functions. It is associated with reduced energy expenditure and normal bodily maintenance, including such functions as digestion and waste elimination. This can be thought of as the “resting and digesting” state.

This does not mean that the body alternates between states where one system or the other is active. Normally both systems are active simultaneously. They exhibit a background rate of activity called **autonomic tone**, and the balance between *sympathetic tone* and *parasympathetic tone* shifts in accordance with the body’s changing needs. Parasympathetic tone, for example, maintains smooth muscle tone in the intestines and holds the resting heart rate down to about 70 to 80 beats/minute. If the parasympathetic vagus nerves to the heart are cut, the heart beats at its own intrinsic rate of about 100 beats/min. Sympathetic tone keeps most blood vessels partially constricted and thus maintains blood pressure. A loss of sympathetic tone can cause such a rapid drop in blood pressure that a person goes into shock.

Neither division has universally excitatory or calming effects. The sympathetic division, for example, excites the heart but inhibits digestive and urinary functions, while the parasympathetic division has the opposite effects. We will later examine how differences in neurotransmitters and their receptors account for these differences of effect.

Neural Pathways

The ANS has components in both the central and peripheral nervous systems. It includes control nuclei in the hypothalamus and other regions of the brainstem, motor neurons in the spinal cord and peripheral ganglia, and nerve fibers that travel through the cranial and spinal nerves you have already studied.

The autonomic motor pathway to a target organ differs significantly from somatic motor pathways. In somatic pathways, a motor neuron in the brainstem or spinal cord issues a myelinated axon that reaches all the way to a skeletal muscle. In autonomic pathways, the signal must travel across two neurons to get to the target organ, and it must cross a synapse where these two neurons meet in an autonomic

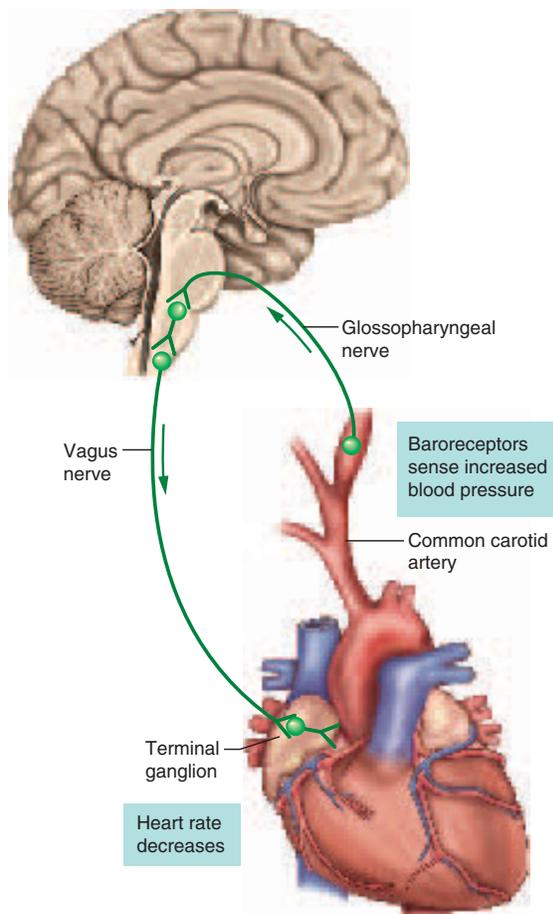


Figure 15.1 Autonomic Reflex Arcs in the Regulation of Blood Pressure. In this example, a rise in blood pressure is detected by baroreceptors in the carotid artery. The glossopharyngeal nerve transmits signals to the medulla oblongata, resulting in parasympathetic output from the vagus nerve that reduces the heart rate and lowers blood pressure.

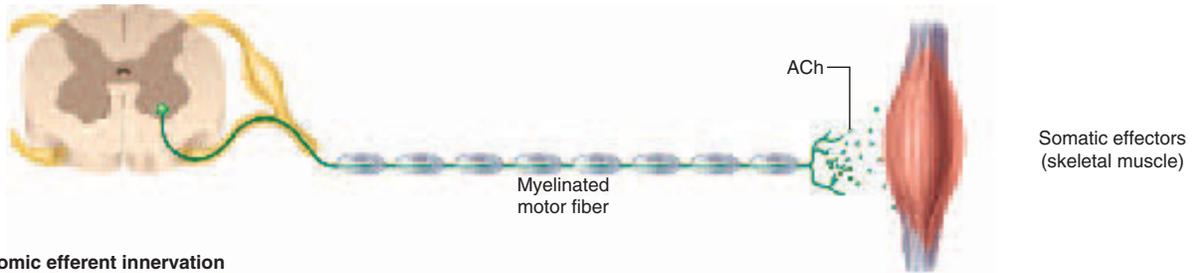
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ganglion (fig. 15.2). The first neuron, called the **preganglionic neuron**, has a soma in the brainstem or spinal cord whose axon terminates in the ganglion. It synapses there with a **postganglionic neuron** whose axon extends the rest of the way to the target cells. (Some call this cell the *ganglionic neuron* since its soma is in the ganglion and only its axon is truly postganglionic.) The axons of these neurons are called the *pre-* and *postganglionic fibers*.

In summary, the autonomic nervous system is a division of the nervous system responsible for homeostasis, acting through the mostly unconscious and involuntary

control of glands, smooth muscle, and cardiac muscle. Its target organs are mostly the thoracic and abdominal viscera, but also include some cutaneous and other effectors. It acts through motor pathways that involve two neurons, preganglionic and postganglionic, reaching from CNS to effector. The ANS has two divisions, sympathetic and parasympathetic, that often have cooperative or contrasting effects on the same target organ. Both divisions have excitatory effects on some target cells and inhibitory effects on others. These and other differences between the somatic and autonomic nervous systems are summarized in table 15.1.

Somatic efferent innervation



Autonomic efferent innervation

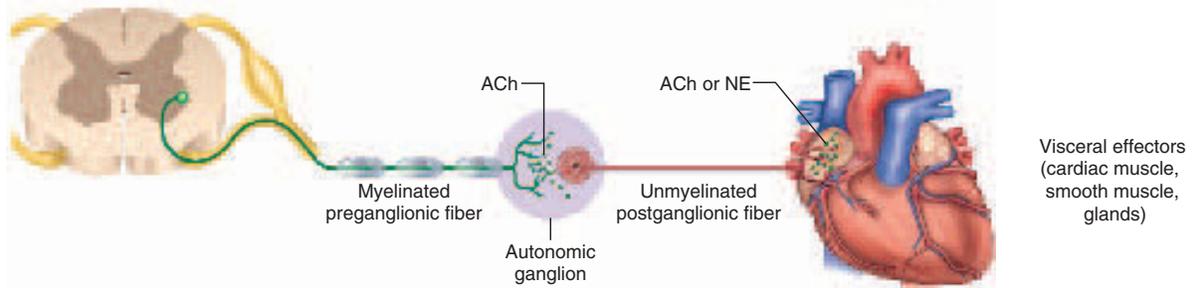


Figure 15.2 Comparison of Somatic and Autonomic Efferent Pathways. The entire distance from CNS to effector is spanned by one neuron in the somatic system and two neurons in the autonomic system. Only acetylcholine (ACh) is employed as a neurotransmitter by the somatic neuron and the autonomic preganglionic neuron, but autonomic postganglionic neurons can employ either ACh or norepinephrine (NE).

Table 15.1 Comparison of the Somatic and Autonomic Nervous Systems

Feature	Somatic	Autonomic
Effectors	Skeletal muscle	Glands, smooth muscle, cardiac muscle
Efferent pathways	One nerve fiber from CNS to effector; no ganglia	Two nerve fibers from CNS to effector; synapse at a ganglion
Neurotransmitters	Acetylcholine (ACh)	ACh and norepinephrine (NE)
Effect on target cells	Always excitatory	Excitatory or inhibitory
Effect of denervation	Flaccid paralysis	Denervation hypersensitivity
Control	Usually voluntary	Usually involuntary

Before You Go On

Answer the following questions to test your understanding of the preceding section:

1. How does the autonomic nervous system differ from the somatic motor system?
2. How do the general effects of the sympathetic division differ from those of the parasympathetic division?

Anatomy of the Autonomic Nervous System

Objectives

When you have completed this section, you should be able to

- identify the anatomical components and nerve pathways of the sympathetic and parasympathetic divisions; and
- discuss the relationship of the adrenal glands to the sympathetic nervous system.

The Sympathetic Division

The sympathetic division is also called the *thoracolumbar division* because it arises from the thoracic and lumbar regions of the spinal cord. It has relatively short preganglionic and long postganglionic fibers. The preganglionic somas are in the lateral horns and nearby regions of the gray matter of the spinal cord. Their fibers exit by way of spinal nerves T1 to L2 and lead to the nearby **sympathetic**

chain of ganglia (**paravertebral³ ganglia**) along each side of the vertebral column (figs. 15.3 and 15.4). Although these chains receive input from only the thoracolumbar region of the cord, they extend into the cervical and sacral to coccygeal regions as well. Some nerve fibers entering the chain at levels T1 to L2 travel up or down the chain to reach these cervical and sacral ganglia. The number of ganglia varies from person to person, but usually there are 3 cervical (*superior*, *middle*, and *inferior*), 11 thoracic, 4 lumbar, 4 sacral, and 1 coccygeal ganglion in each chain.

In the thoracolumbar region, each paravertebral ganglion is connected to a spinal nerve by two branches called *communicating rami* (fig. 15.5). The preganglionic fibers are small myelinated fibers that travel from the spinal nerve to the ganglion by way of the **white communicating ramus**,⁴ which gets its color and name from the myelin. Unmyelinated postganglionic fibers leave the ganglion by way of the **gray communicating ramus**, named for its lack of myelin and duller color, and by other routes. These long fibers extend the rest of the way to the target organ.

Think About It

Would autonomic postganglionic fibers have faster or slower conduction speeds than somatic motor fibers? Why? (See hints in chapter 12.)

³para = next to + vertebr = vertebral column
⁴ramus = branch

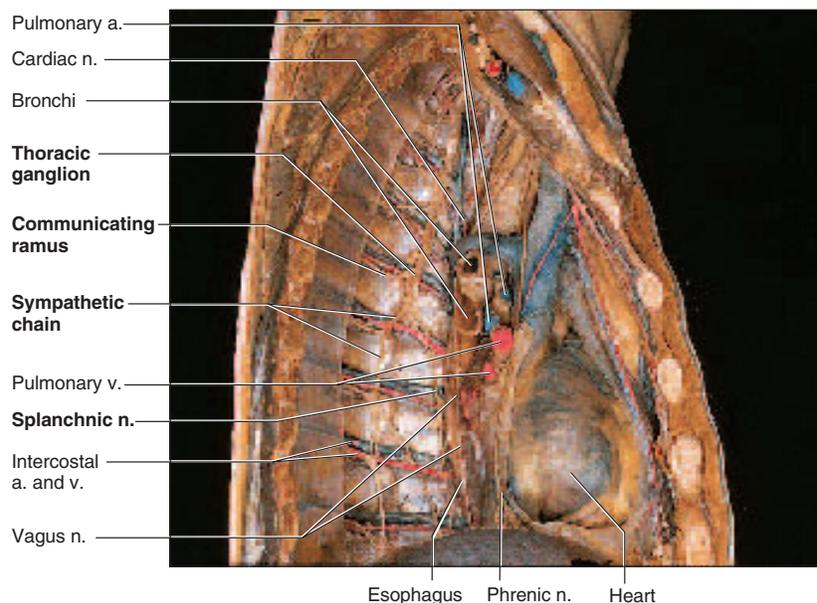


Figure 15.3 The Sympathetic Chain Ganglia. Right lateral view of the thoracic cavity. (*a.* = artery; *n.* = nerve; *v.* = vein.)

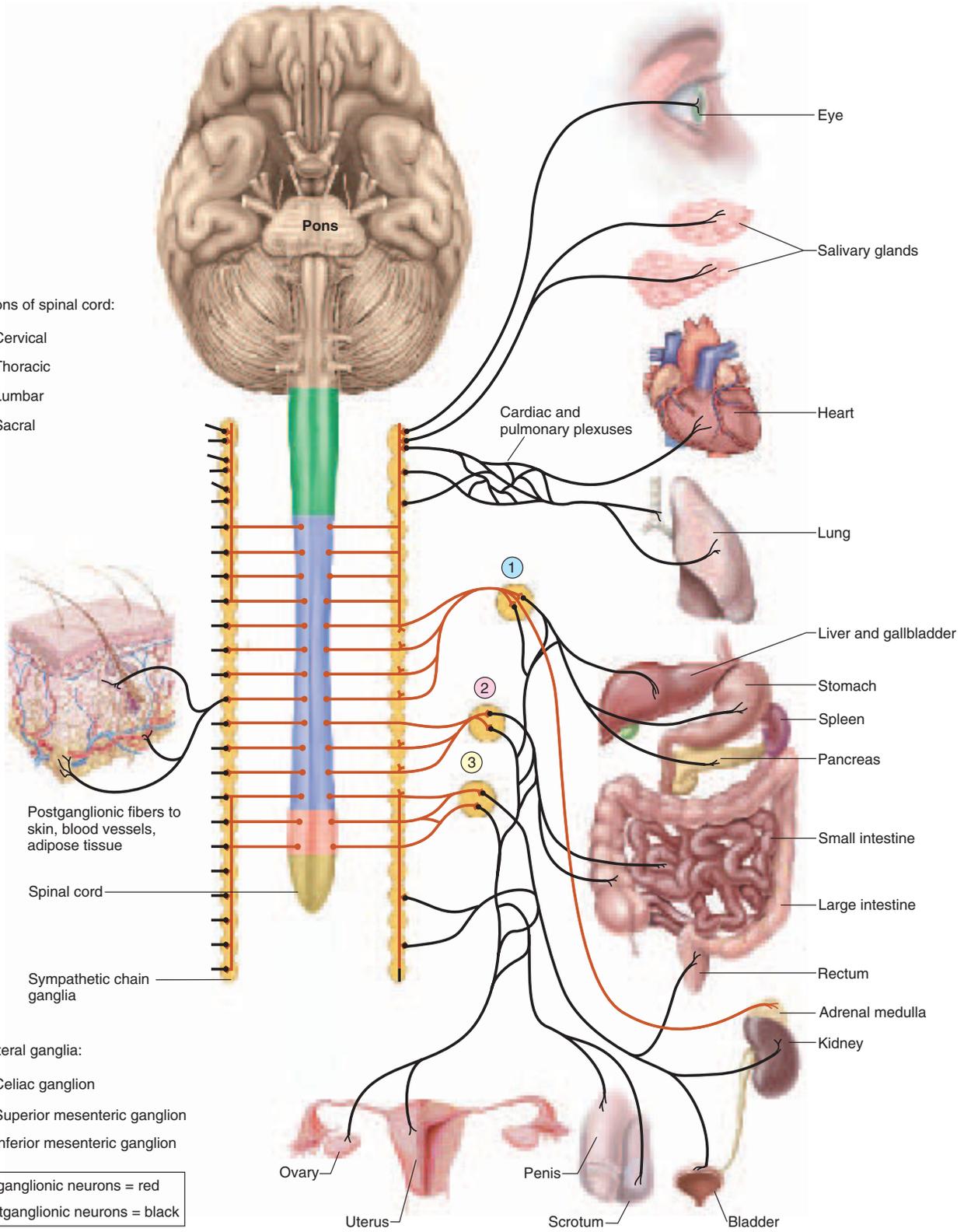


Figure 15.4 Sympathetic Pathways.
Does the sympathetic innervation of the lung cause inhaling and exhaling?

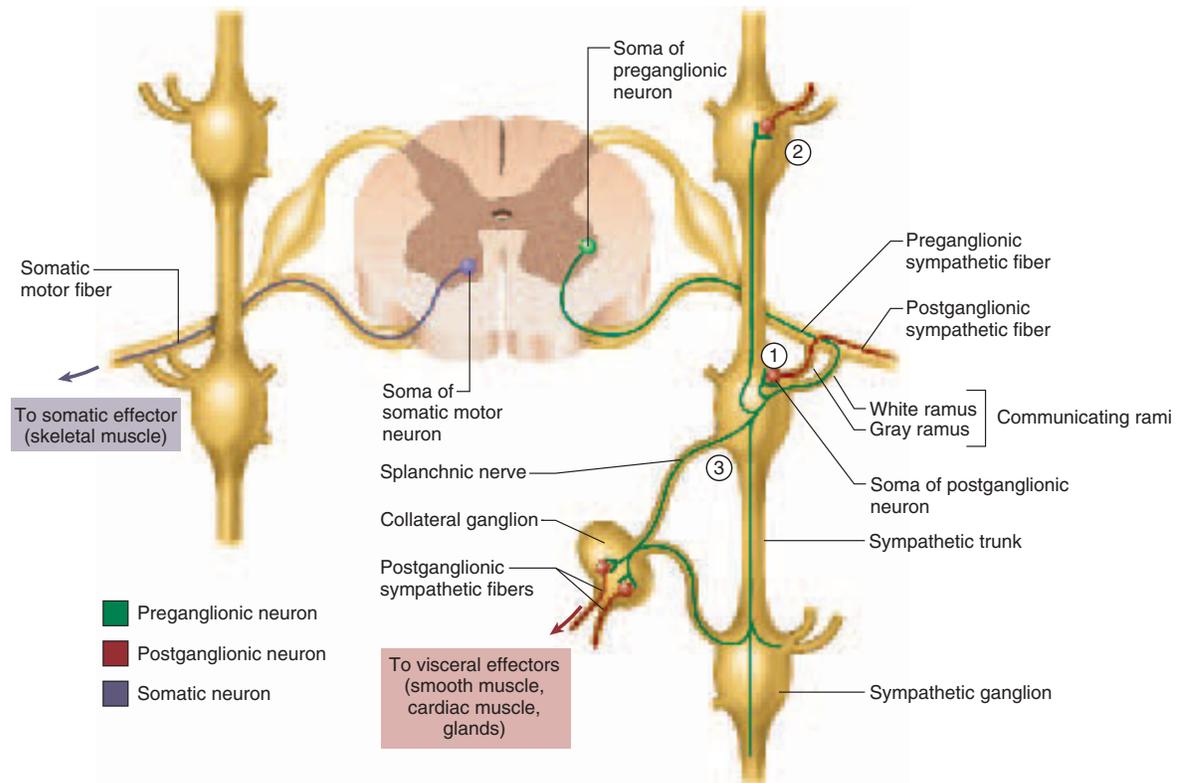


Figure 15.5 Sympathetic Pathways (*right*) Compared to Somatic Efferent Pathways (*left*). Sympathetic fibers can follow any of the three numbered routes: (1) the spinal nerve route, (2) the sympathetic nerve route, or (3) the splanchnic nerve route. Name the parts of the spinal cord where the somas of the sympathetic and somatic efferent neurons are located.

After entering the sympathetic chain, preganglionic fibers may follow any of three courses:

- Some end in the ganglion that they enter and synapse immediately with a postganglionic neuron.
- Some travel up or down the chain and synapse in ganglia at other levels. It is these fibers that link the paravertebral ganglia into a chain. They are the only route by which ganglia at the cervical, sacral, and coccygeal levels receive input.
- Some pass through the chain without synapsing and continue as *splanchnic* (SPLANK-nic) nerves, to be considered shortly.

There is no simple one-to-one relationship between preganglionic and postganglionic neurons in the sympathetic division. For one thing, each postganglionic cell may receive synapses from multiple preganglionic cells, thus exhibiting the principle of *neuronal convergence* discussed in chapter 12. Furthermore, each preganglionic fiber branches and synapses with multiple postganglionic fibers, thus showing *neuronal divergence*. There are about

17 postganglionic neurons for every preganglionic neuron in the sympathetic division. This means that when one preganglionic neuron fires, it can excite multiple postganglionic fibers leading to different target organs. The sympathetic division thus tends to have relatively widespread effects—as suggested by the name *sympathetic*.⁵

Nerve fibers leave the paravertebral ganglia by three routes: spinal, sympathetic, and splanchnic nerves. These are numbered in figure 15.5 to correspond to the following descriptions:

1. **The spinal nerve route.** Some postganglionic fibers exit by way of the gray ramus, return to the spinal nerve or its subdivisions, and travel the rest of the way to the target organ. This is the route to most sweat glands, piloerector muscles, and blood vessels of the skin and skeletal muscles.
2. **The sympathetic nerve route.** Other postganglionic fibers leave by way of **sympathetic nerves** that

⁵sym = together + path = feeling

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extend to the heart, lungs, esophagus, and thoracic blood vessels. These nerves form a plexus around each carotid artery and issue fibers from there to effectors in the head—including sweat, salivary, and nasal glands; piloerector muscles; blood vessels; and dilators of the iris. Some fibers from the superior cervical ganglion form the *cardiac nerves* to the heart.

3. **The splanchnic⁶ nerve route.** This route is formed by fibers that originate predominantly from spinal nerves T5 to T12 and pass through the ganglia without synapsing. Beyond the ganglia, they form greater, lesser, and lumbar **splanchnic nerves**. These

lead to the **collateral (prevertebral) ganglia**, which contribute to a network called the **abdominal aortic plexus** wrapped around the aorta (fig. 15.6). There are three major collateral ganglia in this plexus—the **celiac (SEE-lee-ac) ganglion**, **superior mesenteric ganglion**, and **inferior mesenteric ganglion**—located at points where arteries of the same names branch off the aorta. The postganglionic fibers accompany these arteries and their branches to the target organs. (The term *solar plexus* is regarded by some authorities as a collective designation for the celiac and superior mesenteric ganglia, and by others as a synonym for the celiac ganglion only. The term comes from the nerves radiating from the ganglion like rays of the sun.) Innervation to and from the three major collateral ganglia is summarized in table 15.2.

⁶splanchn = viscera

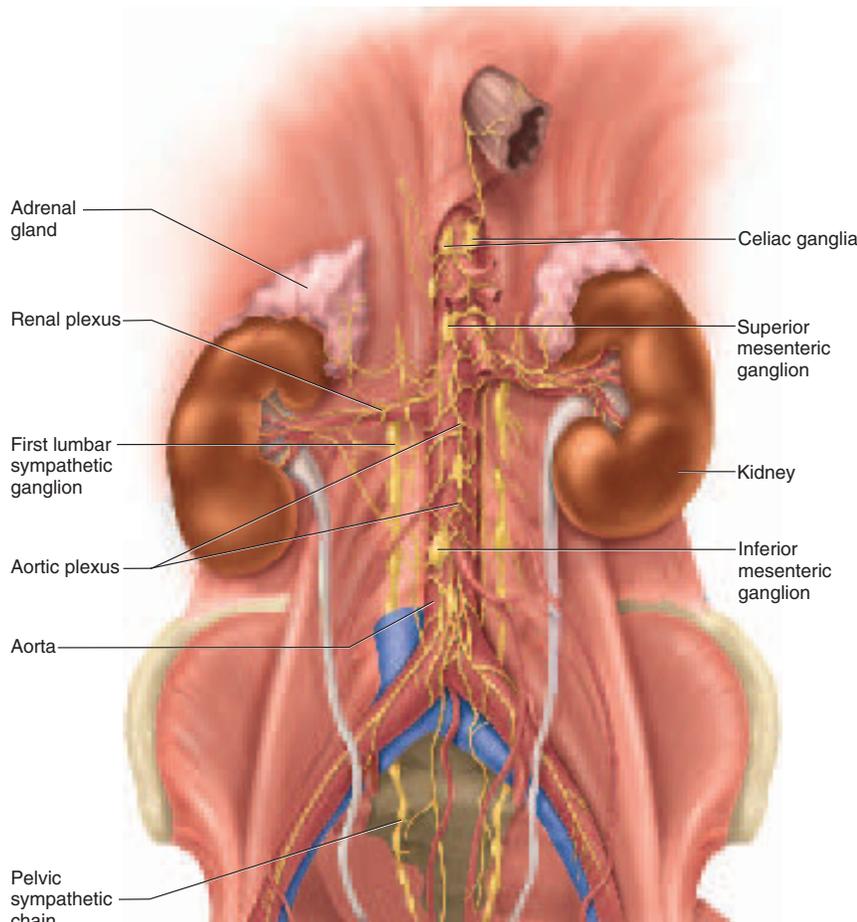


Figure 15.6 Sympathetic Collateral Ganglia and the Abdominal Aortic Plexus.

Table 15.2 Innervation To and From the Collateral Ganglia

Sympathetic Ganglia and Splanchnic Nerve	→ Collateral Ganglion	→ Postganglionic Target Organs
From thoracic ganglia 5 to 9 or 10 via greater splanchnic nerve	Celiac ganglion	Stomach, spleen, liver, small intestine, and kidneys
From thoracic ganglia 9 and 10 via lesser splanchnic nerve	Celiac and superior mesenteric ganglia	Small intestine and colon
From lumbar ganglia via lumbar splanchnic nerve	Celiac and inferior mesenteric ganglia	Distal colon, rectum, urinary bladder, and reproductive organs

In summary, effectors in the body wall are innervated mainly by sympathetic fibers in the spinal nerves; effectors in the head and thoracic cavity by sympathetic nerves; and effectors in the abdominal cavity by splanchnic nerves.

The Adrenal Glands

The paired **adrenal**⁷ **glands** rest like hats on the superior pole of each kidney (fig. 15.6). Each adrenal is actually two glands with different functions and embryonic origins. The outer rind, the **adrenal cortex**, secretes steroid hormones discussed in chapter 17. The inner core, the **adrenal medulla**, is a modified sympathetic ganglion. It consists of modified postganglionic neurons without dendrites or axons. Sympathetic preganglionic fibers penetrate through the cortex and terminate on these cells.

When stimulated, the adrenal medulla secretes a mixture of hormones into the bloodstream—about 85% epinephrine (adrenaline), 15% norepinephrine (noradrenaline), and a trace of dopamine. These hormones, the *catecholamines*, were briefly considered in chapter 12 because they also function as neurotransmitters. The sympathetic nervous system and adrenal medulla are so closely related in development and function that they are referred to collectively as the *sympathoadrenal system*.

The Parasympathetic Division

The parasympathetic division is also called the *craniosacral division* because it arises from the brain and sacral region of the spinal cord; its fibers travel in certain cranial and sacral nerves. The preganglionic neurons are located in the pons, medulla oblongata, and segments S2 to S4 of the spinal cord (fig. 15.7). They issue long preganglionic fibers which end in **terminal ganglia** in or near the target organ (see fig. 15.1). (If a terminal ganglion is embedded within the wall of a target organ, it is also called an *intramural*⁸ *ganglion*.) Thus, the parasympathetic divi-

sion has long preganglionic fibers, reaching almost all the way to the target cells, and short postganglionic fibers that cover the rest of the distance.

There is some neuronal divergence in the parasympathetic division, but much less than in the sympathetic. The parasympathetic division has a ratio of about two postganglionic fibers to every preganglionic. Furthermore, the preganglionic fiber reaches the target organ before even this slight divergence occurs. The parasympathetic division is therefore relatively selective in its stimulation of target organs.

Parasympathetic fibers leave the brainstem by way of the following four cranial nerves. The first three supply all parasympathetic innervation to the head and the last one supplies viscera of the thoracic and abdominal cavities.

- Oculomotor nerve (III).** The oculomotor nerve carries parasympathetic fibers that control the lens and pupil of the eye. The preganglionic fibers enter the orbit and terminate in the *ciliary ganglion*. Postganglionic fibers enter the eyeball and innervate the *ciliary muscle*, which thickens the lens, and the *pupillary constrictor*, which narrows the pupil.
- Facial nerve (VII).** The facial nerve carries parasympathetic fibers that regulate the tear glands, salivary glands, and nasal glands. Soon after the facial nerve emerges from the pons, its parasympathetic fibers split away and form two smaller branches. The upper branch ends at the *sphenopalatine ganglion* near the junction of the maxilla and palatine bones. Postganglionic fibers then continue to the tear glands and glands of the nasal cavity, palate, and other areas of the oral cavity. The lower branch crosses the middle-ear cavity and ends at the *submandibular ganglion* near the angle of the mandible. Postganglionic fibers from here supply salivary glands in the floor of the mouth.
- Glossopharyngeal nerve (IX).** The glossopharyngeal nerve carries parasympathetic fibers concerned with salivation. The preganglionic fibers leave this nerve soon after its origin and form the *tympanic*

⁷*ad* = near + *ren* = kidney

⁸*intra* = within + *mur* = wall

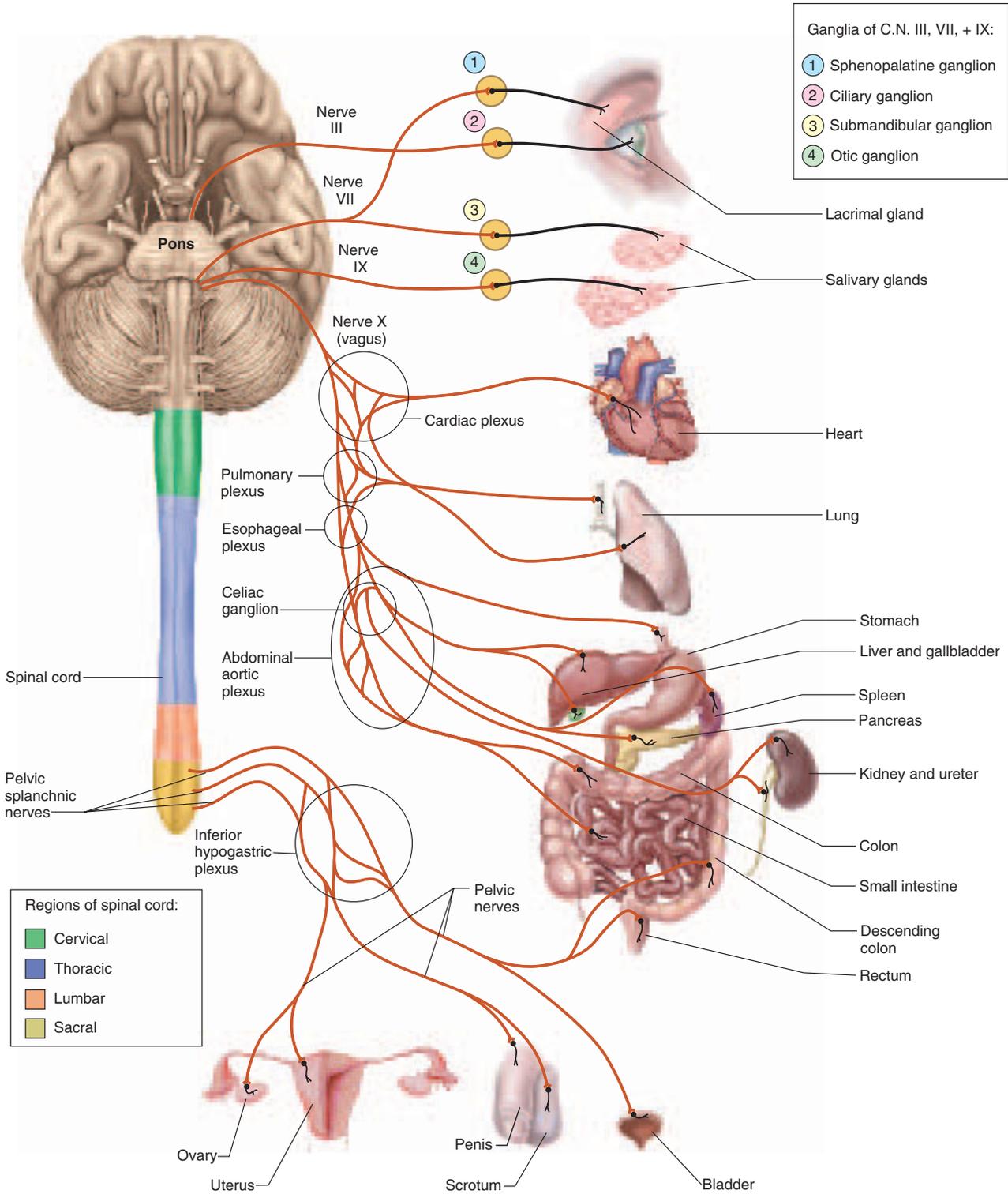


Figure 15.7 Parasympathetic Pathways.
Which nerve carries the most parasympathetic nerve fibers?

nerve, which crosses the eardrum and ends in the *otic*⁹ *ganglion* near the foramen ovale. The postganglionic fibers then follow the trigeminal nerve to the *parotid salivary gland* just in front of the earlobe.

- 4 **Vagus nerve (X).** The vagus nerve carries about 90% of all parasympathetic preganglionic fibers. It travels down the neck and forms three networks in the mediastinum—the **cardiac plexus**, which supplies fibers to the heart; the **pulmonary plexus**, whose fibers accompany the bronchi and blood vessels into the lungs; and the **esophageal plexus**, whose fibers regulate swallowing.

At the lower end of the esophagus, these plexuses give off anterior and posterior **vagal trunks**, each of which contains fibers from both the right and left vagus. These penetrate the diaphragm, enter the abdominal cavity, and contribute to the extensive *abdominal aortic plexus* mentioned earlier. As we have seen, sympathetic fibers synapse here. The parasympathetic fibers, however, pass through the plexus without synapsing and lead to the liver, pancreas, stomach, small intestine, kidney, ureter, and proximal half of the colon.

The remaining parasympathetic fibers arise from levels S2 to S4 of the spinal cord. They travel a short distance in the ventral rami of the spinal nerves and then form **pelvic splanchnic nerves** that lead to the **inferior hypogastric (pelvic) plexus**. Some parasympathetic fibers synapse here, but most pass through this plexus and travel by way of **pelvic nerves** to the terminal ganglia in their target organs: the distal half of the large intestine, the rectum, urinary bladder, and reproductive organs. The parasympathetic system does not innervate body wall structures (sweat glands, piloerector muscles, or cutaneous blood vessels).

The sympathetic and parasympathetic divisions of the ANS are compared in table 15.3.

⁹*ot* = ear + *ic* = pertaining to

Think About It

Would autonomic functions be affected if the ventral roots of the cervical spinal nerves were damaged? Why or why not?

The Enteric Nervous System

The digestive tract has a nervous system of its own called the **enteric**¹⁰ **nervous system**. Unlike the ANS proper, it does not arise from the brainstem or spinal cord, but like the ANS, it innervates smooth muscle and glands. Thus, opinions differ on whether it should be considered part of the ANS. It consists of about 100 million neurons embedded in the wall of the digestive tract—perhaps more neurons than there are in the spinal cord—and it has its own reflex arcs. The enteric nervous system regulates the motility of the esophagus, stomach, and intestines and the secretion of digestive enzymes and acid. To function normally, however, these digestive activities also require regulation by the sympathetic and parasympathetic systems. The enteric nervous system is discussed in more detail in chapter 25.

Before You Go On

Answer the following questions to test your understanding of the preceding section:

3. Explain why the sympathetic division is also called the thoracolumbar division even though its paravertebral ganglia extend all the way from the cervical to the sacral region.
4. Describe or diagram the structural relationships among the following: preganglionic fiber, postganglionic fiber, ventral ramus, gray ramus, white ramus, and paravertebral ganglion.
5. Explain in anatomical terms why the parasympathetic division affects target organs more selectively than the sympathetic division does.
6. Trace the pathway of a parasympathetic fiber of the vagus nerve from the medulla oblongata to the small intestine.

¹⁰*enter* = intestines + *ic* = pertaining to

Table 15.3 Comparison of the Sympathetic and Parasympathetic Divisions

Feature	Sympathetic	Parasympathetic
Origin in CNS	Thoracolumbar	Craniosacral
Location of ganglia	Paravertebral ganglia adjacent to spinal column and prevertebral ganglia anterior to it	Terminal ganglia near or within target organs
Fiber lengths	Short preganglionic Long postganglionic	Long preganglionic Short postganglionic
Neuronal divergence	Extensive (about 1:17)	Minimal (about 1:2)
Effects of system	Often widespread and general	More specific and local

Autonomic Effects on Target Organs

Objectives

When you have completed this section, you should be able to

- name the neurotransmitters employed at different synapses of the ANS;
- name the receptors for these neurotransmitters and explain how these receptor types relate to autonomic effects;
- explain how the ANS controls many target organs through dual innervation; and
- explain how control is exerted in the absence of dual innervation.

Neurotransmitters

The key to understanding the effects of the ANS lies in knowing which neurotransmitters it releases and what kind of receptors occur on the target cells. The ANS has both **cholinergic fibers**, which secrete acetylcholine (ACh), and **adrenergic fibers**, which secrete norepinephrine (NE). Cholinergic fibers include the preganglionic fibers of both divisions, the postganglionic fibers of the parasympathetic division, and a few sympathetic postganglionic fibers (those that innervate sweat glands and some blood vessels). Most sympathetic postganglionic fibers are adrenergic (table 15.4).

The sympathetic nervous system tends to have longer-lasting effects than the parasympathetic. After ACh is secreted by the parasympathetic fibers, it is quickly broken down by acetylcholinesterase (AChE) in the synapse and its effect lasts only a few seconds. The NE released by sympathetic nerve fibers, however, has various fates: (1) Some is reabsorbed by the nerve fiber and either reused or broken down by the enzyme *monoamine oxidase (MAO)*. (2) Some diffuses into the surrounding tissues, where it is degraded by another enzyme, *catechol-O-methyltransferase (COMT)*. (3) Much of it is picked up by the bloodstream, where MAO and COMT are absent. This NE, along with epinephrine from the adrenal gland, circulates throughout the body and exerts a prolonged effect.

ACh and NE are not the only neurotransmitters employed by the ANS. Although all autonomic fibers secrete one of these, many of them also secrete neuropeptides that modulate ACh or NE function. Sympathetic fibers may also secrete enkephalin, substance P, neuropeptide Y, somatostatin, neurotensin, or gonadotropin-releasing hormone. Some parasympathetic fibers relax blood vessels and increase blood flow by stimulating the endothelial cells that line the vessel to release the gas nitric oxide (NO). NO inhibits smooth muscle tone in the vessel wall.

Receptors

Both the sympathetic and parasympathetic divisions have excitatory effects on some target cells and inhibitory effects

on others. For example, the parasympathetic division contracts the wall of the urinary bladder but relaxes the internal urinary sphincter—both of which are necessary for the expulsion of urine. It employs ACh for both purposes. Similarly, the sympathetic division constricts most blood vessels but dilates the coronary arteries, and it achieves both effects with NE. Clearly, the difference is not due to the neurotransmitter. Rather, it is due to the fact that different effector cells have *different kinds of receptors* for it. The receptors for ACh and NE are called **cholinergic** and **adrenergic receptors**, respectively. Knowledge of these receptor types is essential to the field of neuropharmacology (see insight 15.2 at the end of the chapter).

Cholinergic Receptors

Acetylcholine binds to two classes of cholinergic receptors—**nicotinic** (NIC-oh-TIN-ic) and **muscarinic** (MUSS-cuh-RIN-ic) **receptors**—named for plant toxins that were used to identify and distinguish them. Nicotine binds only to the former type, while muscarine, a mushroom poison, binds only to the latter. Other drugs also selectively bind to one type or the other—atropine binds only to muscarinic receptors and curare only to nicotinic receptors, for example.

Nicotinic receptors occur on the postsynaptic cells in all ganglia of the ANS, in the adrenal medulla, and in neuromuscular junctions. Muscarinic receptors occur on all gland, smooth muscle, and cardiac muscle cells that receive cholinergic innervation. All cells with nicotinic receptors are excited by ACh, but some cells with muscarinic receptors are excited while others are inhibited by it. For example, by acting on different subclasses of muscarinic receptors, ACh excites intestinal smooth muscle but inhibits cardiac muscle. All cholinergic receptors work by opening ligand-gated ion channels and changing the postsynaptic potential of the target cell.

Adrenergic Receptors

There are likewise different classes of adrenergic receptors that account for the effects of norepinephrine (NE) on different target cells. NE receptors fall into two broad classes called **alpha-(α -)adrenergic** and **beta-(β -)adrenergic**

Table 15.4 Locations of Cholinergic and Adrenergic Fibers in the ANS

Division	Preganglionic Fibers	Postganglionic Fibers
Sympathetic	Always cholinergic	Mostly adrenergic; a few cholinergic
Parasympathetic	Always cholinergic	Always cholinergic

receptors. The binding of NE to α -adrenergic receptors is usually excitatory, and its binding to β -adrenergic receptors is usually inhibitory, but there are exceptions to both. For example, NE binds to β receptors in cardiac muscle but has an excitatory effect.

The exceptions result from the existence of subclasses of each receptor type, called α_1 , α_2 , β_1 and β_2 receptors. All four types function by means of second messengers. Both β receptors activate the production of cyclic AMP (cAMP), α_2 receptors suppress cAMP production, and α_1 receptors employ calcium ions as the second messenger. Some target cells have both α and β receptors.

The binding of NE to α -adrenergic receptors in blood vessels causes vasoconstriction. The arteries that supply the heart and skeletal muscles, however, have β -adrenergic receptors, which dilate the arteries, thereby increasing blood flow to these organs. NE also relaxes the bronchioles when it binds to β -adrenergic receptors. These effects are obviously appropriate to the exercise state, in which the sympathetic nervous system is most active. The autonomic effects on glandular secretion are often achieved through the adjustment of blood flow to the gland rather than direct stimulation of the gland cells.

Figure 15.8 summarizes the locations of these receptor types. Table 15.5 compares the effects of sympathetic and parasympathetic stimulation on various target organs.

Think About It

Table 15.5 notes that the sympathetic nervous system has an α -adrenergic effect on blood platelets and promotes clotting. How can the sympathetic nervous system stimulate platelets, considering that platelets are drifting cell fragments in the bloodstream with no nerve fibers leading to them?

Dual Innervation

Most of the viscera receive nerve fibers from both the sympathetic and parasympathetic divisions and thus are said to have **dual innervation**. In such cases, the two divisions may have either *antagonistic* or *cooperative* effects on the same organ.

Antagonistic effects oppose each other. For example, the sympathetic division speeds up the heart and the parasympathetic division slows it down; the sympathetic division inhibits digestion and the parasympathetic division stimulates it; the sympathetic division dilates the pupil and the parasympathetic division constricts it. In some cases, these effects are exerted through dual innervation of the same effector cells, as in the heart, where nerve fibers of both divisions terminate on the same muscle cells. In other cases, antagonistic effects arise because each division innervates different effector cells with opposite effects on organ function. In the iris of the eye, for example, sympathetic

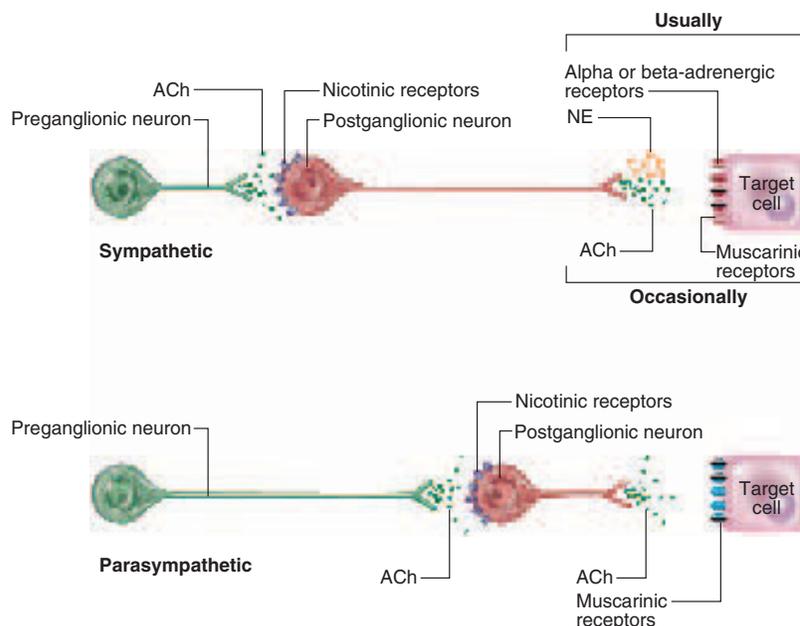


Figure 15.8 Neurotransmitters and Receptors of the Autonomic Nervous System. A given postganglionic fiber releases either ACh or NE, but not both. Both are shown in the *top* illustration only to emphasize that some sympathetic fibers are adrenergic and some are cholinergic.

Table 15.5 Effects of the Sympathetic and Parasympathetic Nervous Systems

Target	Sympathetic Effect and Receptor Type	Parasympathetic Effect (all muscarinic)
Eye		
<i>Dilator of pupil</i>	Pupillary dilation (α_1)	No effect
<i>Constrictor of pupil</i>	No effect	Pupillary constriction
<i>Ciliary muscle and lens</i>	Relaxation for far vision (β_2)	Contraction for near vision
<i>Lacrimal (tear) gland</i>	None	Secretion
Integumentary System		
<i>Merocrine sweat glands (cooling)</i>	Secretion (muscarinic)	No effect
<i>Apocrine sweat glands (scent)</i>	Secretion (α_1)	No effect
<i>Piloerector muscles</i>	Hair erection (α_1)	No effect
Adipose Tissue	Decreased fat breakdown (α_2) Increased fat breakdown (α_1, β_1)	No effect
Adrenal Medulla	Hormone secretion (nicotinic)	No effect
Circulatory System		
<i>Heart rate and force</i>	Increased (β_1, β_2)	Decreased
<i>Deep coronary arteries</i>	Vasodilation (β_2) Vasoconstriction (α_1, α_2)	Slight vasodilation
<i>Blood vessels of most viscera</i>	Vasoconstriction (α_1)	Vasodilation
<i>Blood vessels of skeletal muscles</i>	Vasodilation (β_2)	No effect
<i>Blood vessels of skin</i>	Vasoconstriction (α_1, α_2)	Vasodilation, blushing
<i>Platelets (blood clotting)</i>	Increased clotting (α_2)	No effect
Respiratory System		
<i>Bronchi and bronchioles</i>	Bronchodilation (β_2)	Bronchoconstriction
<i>Mucous glands</i>	Decreased secretion (α_1) Increased secretion (β_2)	No effect
Urinary System		
<i>Kidneys</i>	Reduced urine output (α_1, α_2)	No effect
<i>Bladder wall</i>	No effect	Contraction
<i>Internal urethral sphincter</i>	Contraction, urine retention (α_1)	Relaxation, urine release
Digestive System		
<i>Salivary glands</i>	Thick mucous secretion (α_1)	Thin serous secretion
<i>Gastrointestinal motility</i>	Decreased ($\alpha_1, \alpha_2, \beta_1, \beta_2$)	Increased
<i>Gastrointestinal secretion</i>	Decreased (α_2)	Increased
<i>Liver</i>	Glycogen breakdown (α_1, β_2)	Glycogen synthesis
<i>Pancreatic enzyme secretion</i>	Decreased (α_1)	Increased
<i>Pancreatic insulin secretion</i>	Decreased (α_2) Increased (β_2)	No effect

(continued)

Table 15.5 Effects of the Sympathetic and Parasympathetic Nervous Systems (continued)

Target	Sympathetic Effect and Receptor Type	Parasympathetic Effect (all muscarinic)
Reproductive System		
<i>Penile or clitoral erection</i>	No effect	Stimulation
<i>Glandular secretion</i>	No effect	Stimulation
<i>Orgasm, smooth muscle roles</i>	Stimulation (α_1)	No effect
<i>Uterus</i>	Relaxation (β_2) Labor contractions (α_1)	No effect

fibers innervate the pupillary dilator and parasympathetic fibers innervate the constrictor (fig. 15.9).

Cooperative effects are seen when the two divisions act on different effectors to produce a unified overall effect. Salivation is a good example. The parasympathetic division stimulates serous cells of the salivary glands to secrete a watery, enzyme-rich secretion, while the sympathetic division stimulates mucous cells of the same glands to secrete mucus. The enzymes and mucus are both necessary components of the saliva.

Even when both divisions innervate a single organ, they do not always innervate it equally or exert equal influence. For example, the parasympathetic division forms an extensive plexus in the wall of the digestive tract and exerts much more influence over it than the sympathetic division does. In the ventricles of the heart, by contrast, there is much less parasympathetic than sympathetic innervation.

Control Without Dual Innervation

Dual innervation is not always necessary for the ANS to produce opposite effects on an organ. The adrenal medulla, piloerector muscles, sweat glands, and many blood vessels receive only sympathetic fibers. The most significant example of control without dual innervation is regulation of blood pressure and routes of blood flow. The sympathetic fibers to a blood vessel have a baseline sympathetic tone which keeps the vessels in a state of partial constriction called **vasomotor tone** (fig. 15.10). An increase in firing rate causes vasoconstriction by increasing smooth muscle contraction. A drop in firing frequency causes vasodilation by allowing the smooth muscle to relax. The blood pressure in the vessel, pushing outward on its wall, then dilates the vessel. Thus, the sympathetic division alone exerts opposite effects on the vessels.

Sympathetic control of vasomotor tone can shift blood flow from one organ to another according to the

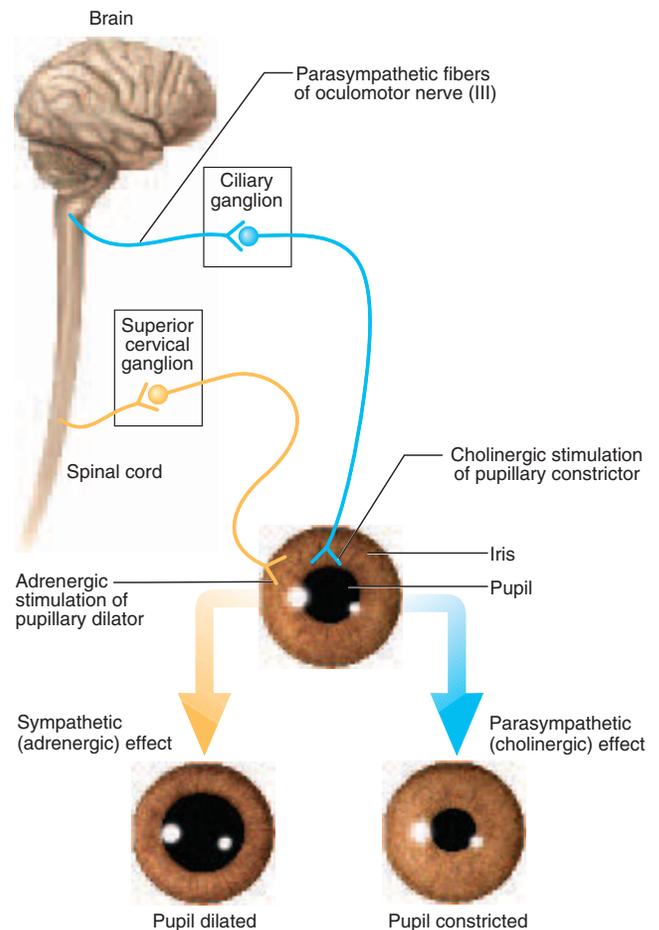


Figure 15.9 Dual Innervation of the Iris. Shows antagonistic effects of the sympathetic and parasympathetic divisions.

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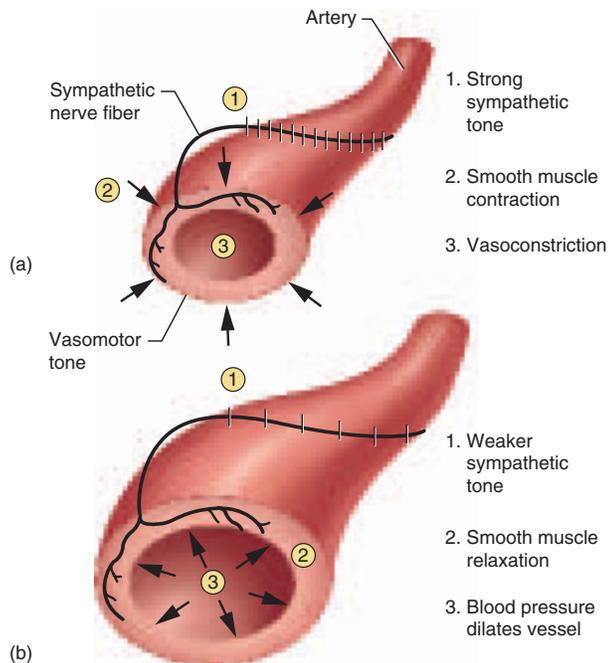


Figure 15.10 Sympathetic Tone and Vasomotor Tone. (a) Vasoconstriction in response to a high rate of sympathetic nerve firing. (b) Vasodilation in response to a low rate of sympathetic nerve firing.

changing needs of the body. In times of emergency, stress, or exercise, the skeletal muscles and heart receive a high priority and the sympathetic division dilates the arteries that supply them. Such processes as digestion, nutrient absorption, and urine formation can wait; thus the sympathetic division constricts arteries to the gastrointestinal tract and kidneys. It also reduces blood flow through the skin, which may help to minimize bleeding in the event that the stress-producing situation leads to injury. Furthermore, since there is not enough blood in the body to abundantly supply all the organ systems at once, it is necessary to temporarily divert blood away from some organs in order to supply an adequate amount to the muscular system.

Before You Go On

Answer the following questions to test your understanding of the preceding section:

7. What neurotransmitters are secreted by adrenergic and cholinergic fibers?
8. Why do sympathetic effects last longer than parasympathetic effects?
9. How can the sympathetic division cause smooth muscle to relax in some organs but contract in others?

10. What are the two ways in which the sympathetic and parasympathetic systems can affect each other when they both innervate the same target organ? Give examples.
11. How can the sympathetic nervous system have contrasting effects in a target organ without dual innervation?

Central Control of Autonomic Function

Objective

When you have completed this section, you should be able to

- describe how the autonomic nervous system is regulated by the brain and somatic nervous system.

In spite of its name, the ANS is not an independent nervous system. All of its output originates in the CNS, and it receives input from the cerebral cortex, hypothalamus, medulla oblongata, and somatic branch of the PNS. In this section we briefly consider how the ANS is influenced by these other levels of the nervous system.

The Cerebral Cortex

Even if we usually cannot consciously control the ANS, it is clear that the mind does influence it. Anger raises the blood pressure, fear makes the heart race, thoughts of good food make the stomach rumble, sexual thoughts or images increase blood flow to the genitals, and anxiety inhibits sexual function. The limbic system (p. 534), an ancient part of the cerebral cortex, is involved in many emotional responses and has extensive connections with the hypothalamus, a site of several nuclei of autonomic control. Thus, the limbic system provides a pathway connecting sensory and mental experiences with the autonomic nervous system.

The Hypothalamus

While the major site of CNS control over the somatic motor system is the primary motor cortex of the cerebrum, the major control center of the visceral motor system is the hypothalamus. This small but vital region in the floor of the brain contains many nuclei for primitive functions, including hunger, thirst, thermoregulation, emotions, and sexuality. Artificial stimulation of different regions of the hypothalamus can activate the fight or flight response typical of the sympathetic nervous system or have the calming effects typical of the parasympathetic. Output from the hypothalamus travels largely to nuclei in more caudal regions of the brainstem and from there to the cranial nerves and the sympathetic preganglionic neurons in the spinal cord.

The Midbrain, Pons, and Medulla Oblongata

These regions of the brainstem house the nuclei of cranial nerves that mediate several autonomic responses: the oculomotor nerve (pupillary constriction), facial nerve (lacrimal, nasal, palatine, and salivary gland secretion), glossopharyngeal nerve (salivation, blood pressure regulation), and vagus nerve (the chief parasympathetic supply to the thoracic and abdominal viscera). These nuclei are part of the reticular formation that extends from the medulla to the hypothalamus.

The Spinal Cord

Such autonomic responses as the defecation and micturition (urination) reflexes are integrated in the spinal cord (see details in chapters 23 and 25). Fortunately, the brain is able to inhibit these responses consciously, but when injuries sever the spinal cord from the brain, the autonomic spinal reflexes alone control the elimination of urine and feces.

Table 15.6 describes some dysfunctions of the autonomic nervous system.

Before You Go On

Answer the following questions to test your understanding of the preceding section:

12. What system in the brain connects our conscious thoughts and feelings with the autonomic control centers of the hypothalamus?
13. List some autonomic responses that are controlled by nuclei in the hypothalamus.
14. What is the role of the midbrain, pons, and medulla in autonomic control?
15. Name some visceral reflexes controlled by the spinal cord.

Insight 15.2 Clinical Application

Drugs and the Nervous System

Neuropharmacology is a branch of medicine that deals with the effects of drugs on the nervous system, especially drugs that mimic, enhance, or inhibit the action of neurotransmitters. A few examples will illustrate the clinical relevance of understanding neurotransmitter and receptor functions.

A number of drugs work by stimulating adrenergic and cholinergic neurons or receptors. *Sympathomimetics*¹¹ are drugs that enhance sympathetic action by stimulating adrenergic receptors or promoting norepinephrine release. For example phenylephrine, found in such cold medicines as Chlor-Trimeton and Dimetapp, aids breathing by stimulating α_1 receptors and dilating the bronchioles and by constricting nasal blood vessels, thus reducing swelling in the nasal mucosa. *Sympatholytics*¹² are drugs that suppress sympathetic action by inhibiting norepinephrine release or by binding to adrenergic receptors without stimulating them. Propranolol, for example, is a *beta-blocker*. It reduces hypertension (high blood pressure) partly by blocking β -adrenergic receptors and interfering with the effects of epinephrine and norepinephrine on the heart and blood vessels. (It also reduces the production of *angiotensin II*, a hormone that stimulates vasoconstriction and raises blood pressure.)

Parasympathomimetics enhance parasympathetic effects. Pilocarpine, for example, relieves glaucoma (excessive pressure within the eyeball) by dilating a vessel that drains fluid from the eye. *Parasympatholytics* inhibit ACh release or block its receptors. Atropine, for example, blocks muscarinic receptors and is sometimes used to dilate the pupils for eye examinations and to dry the mucous membranes of the respiratory tract before inhalation anesthesia. It is an extract of the deadly nightshade plant, *Atropa belladonna*. Women of the Middle Ages used nightshade to dilate their pupils, which was regarded as a beauty enhancement.¹³

The drugs we have mentioned so far act on the peripheral nervous system and its effectors. Many others act on the central nervous system. Strychnine, for example, blocks the inhibitory action of glycine on spinal motor neurons. The motor neurons then overstimulate the muscles, causing spastic paralysis and sometimes death by suffocation.

Table 15.6 Some Disorders of the Autonomic Nervous System

Horner syndrome	Chronic unilateral pupillary constriction, sagging of the eyelid, withdrawal of the eye into the orbit, flushing of the skin, and lack of facial perspiration, resulting from lesions in the cervical ganglia, upper thoracic spinal cord, or brainstem that interrupt sympathetic innervation of the head.
Raynaud disease	Intermittent attacks of paleness, cyanosis, and pain in the fingers and toes, caused when cold or emotional stress triggers excessive vasoconstriction in the digits; most common in young women. In extreme cases, causes gangrene and may require amputation. Sometimes treated by severing sympathetic nerves to the affected regions.

Disorders described elsewhere

Autonomic effects of cranial nerve injuries pp. 550, 554

Mass reflex reaction p. 509

Orthostatic hypotension p. 792

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Sigmund Freud predicted that psychiatry would eventually draw upon biology and chemistry to deal with emotional problems once treated only by counseling and psychoanalysis. A branch of neuropharmacology called *psychopharmacology* has fulfilled his prediction. This field dates to the 1950s when chlorpromazine, an antihistamine, was accidentally found to relieve schizophrenia.

The management of clinical depression is one example of how contemporary psychopharmacology has supplemented counseling approaches. Some cases of depression result from deficiencies of the monoamine neurotransmitters. Thus, they yield to drugs that prolong the effects of the monoamines already present at the synapses. One of the earliest discovered antidepressants was imipramine, which blocks the synaptic reuptake of serotonin and norepinephrine. However, it produces undesirable side effects such as dry mouth and irregular cardiac rhythms; it has been largely replaced by Prozac (fluoxetine), which blocks serotonin reuptake and prolongs its mood-elevating effect; thus it is called a *selective serotonin reuptake inhibitor (SSRI)*. Prozac is also used to treat fear of rejection, excess sensitivity to criticism, lack of self-esteem, and inability to experience pleasure, all of which were long handled only through counseling, group therapy, and psychoanalysis. After monoamines are taken up from the synapse, they are degraded by monoamine oxidase (MAO). Drugs called *MAO inhibitors* interfere with the breakdown of monoamine neurotransmitters and provide another pharmacological approach to depression.

Our growing understanding of neurochemistry also gives us deeper insight into the action of addictive drugs of abuse such as amphetamines and cocaine. Amphetamines ("speed") chemically resemble norepinephrine and dopamine, two neurotransmitters associated with elevated mood. Dopamine is especially important in sensations of pleasure. Cocaine blocks dopamine reuptake and thus produces a brief rush of good feelings. But when dopamine is not reabsorbed by the neurons, it diffuses out of the synaptic cleft and is degraded elsewhere. Cocaine thus depletes the neurons of dopamine faster than they can synthesize it, so that finally there is no longer an adequate supply to maintain normal mood. The postsynaptic neurons make new dopamine receptors as if "searching" for the neurotransmitter—all of which leads

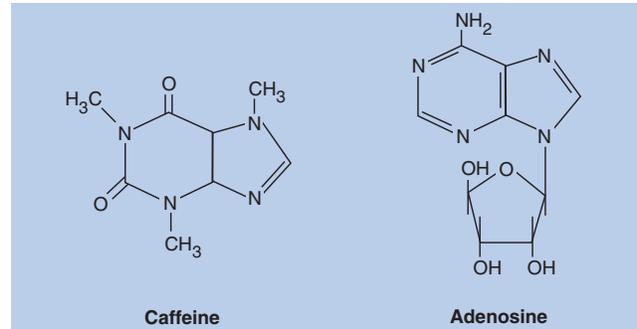


Figure 15.11 Caffeine and Adenosine. Adenosine is an inhibitory neurotransmitter that produces the sense of sleepiness. Caffeine is similar enough in structure to bind to adenosine receptors and block the action of adenosine.

ultimately to anxiety, depression, and the inability to experience pleasure without the drug.

Caffeine exerts its stimulatory effect by competing with adenosine. Adenosine, which you know as a component of DNA, RNA, and ATP, also functions as an inhibitory neurotransmitter in the brain. One theory of sleepiness is that it results when prolonged metabolic activity breaks down so much ATP that the accumulated adenosine has a noticeably inhibitory effect in the brain. Caffeine has enough structural similarity to adenosine (fig. 15.11) to bind to its receptors, but it does not produce the inhibitory effect. Thus, it prevents adenosine from exerting its effect and a person feels more alert.

¹¹*mimet* = imitate, mimic

¹²*lyt* = break down, destroy

¹³*bella* = beautiful, fine + *donna* = woman

Connective Issues

Interactions Between the NERVOUS SYSTEM and Other Organ Systems

- ← indicates ways in which this system affects other systems
- indicates ways in which other systems affect this one

Integumentary System

- ← Nervous system regulates piloerection and sweating; controls cutaneous blood flow to regulate heat loss
- Provides sensations of heat, cold, pressure, pain, and vibration; protects peripheral nerves

Skeletal System

- ← Nervous stimulation generates muscle tension essential for bone development and remodeling
- Serves as reservoir of Ca^{2+} needed for neural function; protects CNS and some peripheral nerves

Muscular System

- ← Somatic nervous system activates skeletal muscles and maintains muscle tone
- Gives expression to thoughts, emotions, and motor commands that arise in the CNS

Endocrine System

- ← Hypothalamus controls pituitary gland; sympathetic nervous system stimulates adrenal medulla
- Many hormones affect neuronal growth and metabolism; hormones control electrolyte balance essential for neural function

Circulatory System

- ← Nervous system regulates heartbeat, blood vessel diameters, blood pressure, and routing of blood; influences blood clotting
- Delivers O_2 and carries away wastes; transports hormones to and from CNS; CSF produced from and returned to blood

Lymphatic and Immune Systems

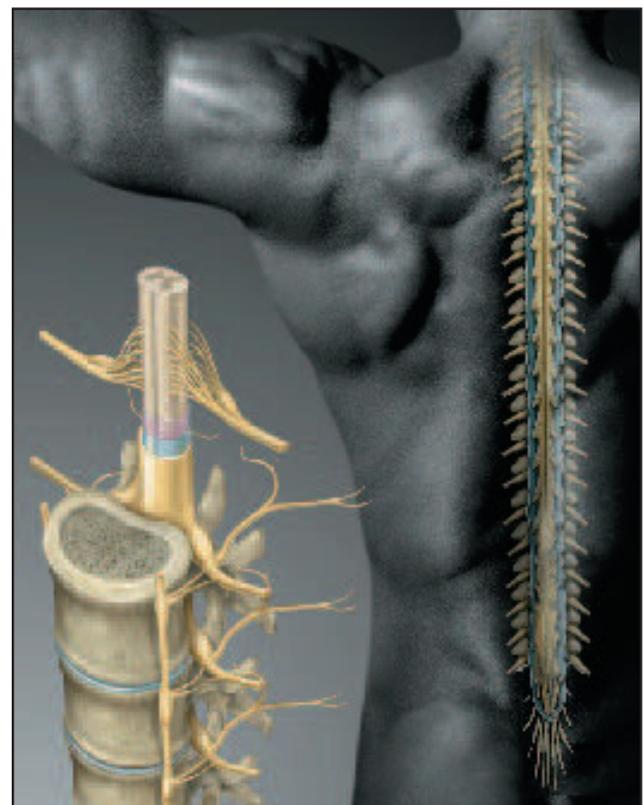
- ← Nerves innervate lymphoid organs and influence development and activity of immune cells; nervous system plays a role in regulating immune response; emotional states influence susceptibility to infection
- Immune cells provide protection and promote tissue repair

Respiratory System

- ← Nervous system regulates rate and depth of respiration
- Provides O_2 , removes CO_2 , and helps to maintain proper pH for neural function

Urinary System

- ← Nervous system regulates renal blood flow, thus affecting rate of urine formation; controls emptying of bladder
- Disposes of wastes and maintains electrolyte and pH balance



Digestive System

- ← Nervous system regulates appetite, feeding behavior, digestive secretion and motility, and defecation
- Provides nutrients; liver provides stable level of blood glucose for neural function during periods of fasting

Reproductive System

- ← Nervous system regulates sex drive, arousal, and orgasm; secretes or stimulates pituitary release of many hormones involved in menstrual cycle, sperm production, pregnancy, and lactation
- Sex hormones influence CNS development and sexual behavior; hormones of the menstrual cycle stimulate or inhibit hypothalamus

Chapter Review

Review of Key Concepts

General Properties of the Autonomic Nervous System (p. 564)

1. The autonomic nervous system (ANS) carries out many visceral reflexes that are crucial to homeostasis. It is a visceral motor system that acts on cardiac muscle, smooth muscle, and glands.
2. Functions of the ANS are largely, but not entirely, unconscious and involuntary.
3. The *sympathetic division* of the ANS prepares the body for physical activity and is especially active in stressful “fight or flight” situations.
4. The *parasympathetic division* has a calming effect on many body functions, but stimulates digestion; it is especially active in “resting and digesting” states.
5. Although the balance of activity may shift from one division to the other, both divisions are normally active simultaneously. Each maintains a background level of activity called *autonomic tone*.
6. The ANS is composed of nuclei in the brainstem, motor neurons in the spinal cord and ganglia, and nerve fibers in the cranial and spinal nerves.
7. Most autonomic efferent pathways, unlike somatic motor pathways, involve two neurons: a *preganglionic neuron* whose axon travels to a peripheral ganglion and synapses with a *postganglionic neuron*, whose axon leads the rest of the way to the target cells.

Anatomy of the Autonomic Nervous System (p. 567)

1. Sympathetic preganglionic neurons arise from thoracic and lumbar segments of the spinal cord, traveling through spinal nerves T1 through L2 to a *sympathetic chain* of ganglia adjacent to the vertebral column.
2. Most preganglionic fibers synapse with postganglionic neurons in one of the ganglia of this chain, sometimes at a higher or lower level than the ganglion at which they enter. Some fibers pass through the chain without synapsing.

3. Sympathetic pathways show substantial neuronal divergence, with the average preganglionic neuron synapsing with 17 postganglionic neurons. Sympathetic stimulation therefore tends to have widespread effects on multiple target organs.
4. Postganglionic fibers leave the sympathetic chain by way of either the spinal nerve route or the sympathetic nerve route. Preganglionic fibers that pass through the chain without synapsing travel by way of *splanchnic nerves* to various more distal *collateral ganglia*, and synapse there with postganglionic neurons.
5. The *adrenal medulla* is a modified sympathetic ganglion composed of anaxonic neurons. These cells secrete mainly epinephrine and norepinephrine into the blood when stimulated.
6. The parasympathetic division issues relatively long preganglionic fibers through cranial nerves III, VII, IX, and X, and spinal nerves S2 through S4, to their target organs. The vagus nerve carries about 90% of all parasympathetic preganglionic fibers.
7. Parasympathetic preganglionic fibers end in *terminal ganglia* in or near the target organ. Relatively short postganglionic fibers complete the route to specific target cells.
8. The wall of the digestive tract contains an *enteric nervous system*, sometimes considered part of the ANS because it innervates smooth muscle and glands of the tract.

Autonomic Effects on Target Organs (p. 574)

1. The autonomic effects on a target cell depends on the neurotransmitter released and the type of receptors that the target cell has.
2. *Cholinergic* fibers secrete acetylcholine (ACh) and include all preganglionic fibers, all parasympathetic postganglionic fibers, and some sympathetic postganglionic fibers. Most sympathetic postganglionic fibers are *adrenergic* and secrete norepinephrine (NE).

3. ACh breaks down quickly and parasympathetic effects are therefore usually short-lived. NE persists longer and sympathetic effects tend to be longer-lasting.
4. Autonomic neurons also employ a broad range of other neurotransmitters and neuromodulators ranging from the peptide enkephalin to the inorganic gas nitric oxide.
5. ACh binds to two classes of receptors called *nicotinic* and *muscarinic* receptors. The binding of ACh to a nicotinic receptor always excites a target cell, but binding to a muscarinic receptor can have excitatory effects on some cells and inhibitory effects on others, owing to different subclasses of muscarinic receptors.
6. NE binds to two major classes of receptors called α and β receptors. Binding to an α -adrenergic receptor is usually excitatory, and binding to a β -adrenergic receptor is usually inhibitory, but there are exceptions to both owing to subclasses of each receptor type.
7. Many organs receive *dual innervation* by both sympathetic and parasympathetic fibers. In such cases, the two divisions may have either antagonistic or cooperative effects on the organ.
8. The sympathetic division can have contrasting effects on an organ even without dual innervation, by increasing or decreasing the firing rate of the sympathetic neuron.

Central Control of Autonomic Function (p. 578)

1. All autonomic output originates in the CNS and is subject to control by multiple levels of the CNS.
2. The hypothalamus is an especially important center of autonomic control, but the cerebral cortex, midbrain, pons, and medulla oblongata are also involved in autonomic responses.
3. Some autonomic reflexes such as defecation and micturition are regulated by the spinal cord.

Selected Vocabulary

autonomic nervous system 564	autonomic tone 565	sympathetic chain 567	adrenergic 574
sympathetic division 565	preganglionic neuron 566	enteric nervous system 573	dual innervation 575
parasympathetic division 565	postganglionic neuron 566	cholinergic 574	vasomotor tone 577

Testing Your Recall

- The autonomic nervous system innervates all of these *except*
 - cardiac muscle.
 - skeletal muscle.
 - smooth muscle.
 - salivary glands.
 - blood vessels.
- Muscarinic receptors bind
 - epinephrine.
 - norepinephrine.
 - acetylcholine.
 - cholinesterase.
 - neuropeptides.
- All of the following cranial nerves except the _____ carry parasympathetic fibers.
 - vagus
 - facial
 - oculomotor
 - glossopharyngeal
 - hypoglossal
- Which of the following cranial nerves carries sympathetic fibers?
 - oculomotor
 - facial
 - trigeminal
 - vagus
 - none of them
- Which of these ganglia is *not* involved in the sympathetic division?
 - intramural
 - superior cervical
 - paravertebral
 - inferior mesenteric
 - celiac
- Epinephrine is secreted by
 - sympathetic preganglionic fibers.
 - sympathetic postganglionic fibers.
 - parasympathetic preganglionic fibers.
 - parasympathetic postganglionic fibers.
 - the adrenal medulla.
- The major autonomic control center within the CNS is
 - the cerebral cortex.
 - the limbic system.
 - the midbrain.
 - the hypothalamus.
 - the sympathetic chain ganglia.
- The gray communicating ramus contains
 - visceral sensory fibers.
 - parasympathetic motor fibers.
 - sympathetic preganglionic fibers.
 - sympathetic postganglionic fibers.
 - somatic motor fibers.
- Throughout the autonomic nervous system, the neurotransmitter released by the preganglionic neuron binds to _____ receptors on the postganglionic neuron.
 - nicotinic
 - muscarinic
 - adrenergic
 - α_1
 - β_2
- Which of these does *not* result from sympathetic stimulation?
 - dilation of the pupil
 - acceleration of the heart
 - digestive secretion
 - enhanced blood clotting
 - piloerection
- Nerve fibers that secrete norepinephrine are called _____ fibers.
- _____ is a state in which a target organ receives both sympathetic and parasympathetic fibers.
- _____ is a state of continual background activity of the sympathetic and parasympathetic divisions.
- Most parasympathetic preganglionic fibers are found in the _____ nerve.
- The digestive tract has a semi-independent nervous system called the _____ nervous system.
- MAO and COMT are enzymes that break down _____ at certain ANS synapses.
- The adrenal medulla consists of modified postganglionic neurons of the _____ nervous system.
- The sympathetic nervous system has short _____ and long _____ nerve fibers.
- Adrenergic receptors classified as α_2 , β_1 , and β_2 act by changing the level of _____ in the target cell.
- Sympathetic fibers to blood vessels maintain a state of partial vasoconstriction called _____.

Answers in Appendix B

True or False

Determine which five of the following statements are false, and briefly explain why.

- The parasympathetic nervous system shuts down when the sympathetic nervous system is active, and vice versa.
- Blood vessels of the skin receive no parasympathetic innervation.
- Voluntary control of the ANS is not possible.
- The sympathetic nervous system stimulates digestion.

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5. Some sympathetic postganglionic fibers are cholinergic.
6. Urination and defecation cannot occur without signals from the brain to the bladder and rectum.
7. Some parasympathetic nerve fibers are adrenergic.
8. Parasympathetic effects are more localized and specific than sympathetic effects.
9. The parasympathetic division shows less neuronal divergence than the sympathetic division does.
10. The two divisions of the ANS have antagonistic effects on the iris.

Answers in Appendix B

Testing Your Comprehension

1. You are dicing raw onions while preparing dinner, and the vapor makes your eyes water. Describe the afferent and efferent pathways involved in this response.
2. Suppose you are walking alone at night when you hear a dog growling close behind you. Describe the ways your sympathetic nervous system would prepare you to deal with this situation.
3. Suppose that the cardiac nerves were destroyed. How would this affect the heart and the body's ability to react to a stressful situation?
4. What would be the advantage to a wolf in having its sympathetic nervous system stimulate the piloerector muscles? What happens in a human when the sympathetic system stimulates these muscles?
5. Pediatric literature has reported many cases of poisoning in children with Lomotil, an antidiarrheic medicine. Lomotil works primarily by means of the morphine-like effects of its chief ingredient, diphenoxylate, but it also contains atropine. Considering the mode of action described for atropine in insight 5.2, why might atropine contribute to the antidiarrheic effect of Lomotil? In atropine poisoning, would you expect the pupils to be dilated or constricted? The skin to be moist or dry? The heart rate to be elevated or depressed? The bladder to retain urine or void uncontrollably? Explain each answer. Atropine poisoning is treated with physostigmine, a cholinesterase inhibitor. Explain the rationale of this treatment.

Answers at the Online Learning Center

Answers to Figure Legend Questions

- 15.4 No; inhaling and exhaling are controlled by the somatic motor system and skeletal muscles.
- 15.5 The soma of the somatic efferent neuron is in the ventral horn and the soma of the autonomic preganglionic neuron is in the lateral horn.
- 15.7 The vagus nerve.

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