CHAPTER 2

Organization of the Peripheral Nervous System

SOME FUNDAMENTAL DICHOTOMIES DEFINED

Central Versus Peripheral Nervous System

The brain and spinal cord compose the **central nervous system** (CNS). All the nerves that emanate from the CNS, their branches, and interconnections constitute the **peripheral nervous system** (PNS). Nerves that exit directly from the brain are said to be **cranial** nerves. The rest of the PNS consists of the spinal nerves (with their branches) and that part of the autonomic nervous system (see further on) associated with spinal nerves.

A detailed consideration of brain and spinal cord structure is the province of neuro-anatomists. Gross anatomists are concerned with the PNS. An understanding of the innervation of specific organs is one of the most clinically important tasks facing a student of medicine.

Efferent Versus Afferent, and Motor Versus Sensory, Portions of the Nervous System

Whereas the distinction between the CNS and the PNS is defined solely on the basis of anatomical location, the difference between the efferent and afferent, or motor and sensory, portions of the nervous system is defined functionally. However, it does have anatomical correlates.

Any nerve fiber that carries information from the CNS out to other tissues of the body is defined as an **efferent** fiber, and along with its cell body it constitutes an efferent neuron. Any nerve fiber that carries information from other tissues of the body into the CNS is defined as an **afferent** fiber, and along with its cell body it constitutes an afferent neuron. Most efferent neurons are concerned with innervating glands and muscles - the motor tissues of the body. This large subset of efferent neurons comprises the motor portion of the peripheral nervous system. Most afferent information coming into the CNS is capable of reaching consciousness. Touch, temperature, pressure, vibration, stretch, and pain are sensory modalities familiar to all of us. The large subset of neurons carrying such information comprises the sensory part of the peripheral nervous system. In the remainder of this text I will concentrate almost exclusively on the motor and sensory components of the efferent and afferent systems. As we shall soon

learn, there are certain nerve bundles that carry only motor fibers, and there are certain regions of the CNS that contain only motor neurons. Similarly, there are certain nerve bundles that carry only sensory fibers, and there are certain regions of the CNS that contain only sensory neurons.

Visceral Versus Somatic Neurons

Among the motor tissues of the body a major distinction can be made between striated voluntary muscle, on the one hand, and smooth muscle, cardiac muscle, and glands, on the other. Striated voluntary muscle composes the so-called **somatic motor tissue** of the body. Smooth muscle, cardiac muscle, and glands constitute the **visceral motor tissue**. More generally, any dissectible structure formed largely of visceral motor tissue is said to be a **visceral structure**. All other structures, whether formed of striated voluntary muscle or simply connective tissue, are said to be **somatic structures**. Most of the body wall is composed of somatic structures, only its vasculature, arrector pili muscles, sweat glands, and sebaceous glands being visceral. On the other hand, all the internal organs of the body are visceral structures.

Nerve fibers that stimulate striated muscle tissue are said to be **somatic motor fibers**. Innervation of smooth muscle, cardiac muscle, and glands is accomplished by **visceral motor fibers**. The entire ensemble of visceral motors fibers is said to compose the **autonomic nervous system**. The sensation that originates in visceral structures is called **visceral sensation**, and it is transmitted along **visceral sensory fibers**. Sensation arising from all other structures is **somatic sensation**, transmitted by **somatic sensory fibers**.

There are certain nerve bundles that carry only visceral nerve fibers. There are certain regions of the CNS that contain only visceral neurons.

DEVELOPMENT AND INNERVATION OF THE BODY WALL

Spinal nerves exist for the purpose of innervating the body wall below the head. In order to understand the organization of spinal nerves, it is necessary to understand the embryonic development of the body wall.

Somites and Their Dermomyotomes

The early embryo becomes internally segmented by division of the paraxial mesoderm (on either side of the neural tube) into somites (Figs. 2-1 and 2-2). A few somites form in the head region alongside the developing brain, but obvious signs of head segmentation are soon lost (see Chapter 6). Most somites form caudal to the head, alongside the developing spinal cord. Here, each somite differentiates into (1) a sclerotome that provides cells for vertebrae and ribs (Fig. 2-1*B*) and (2) a dermomyotome that provides cells for dermis and striated muscle. Each dermomyotome divides into a small dorsal block of cells--the **epaxial** portion of the dermomyotome--and a larger ventral block of cells--the **hypaxial** portion of the dermomyotome (see Fig. 2-1*B*). The epaxial dermomyotome cells migrate to a position beneath the ectoderm of the back and here differentiate into the dermis, connective tissue, and striated muscles of the dorsal body wall. The hypaxial dermomyotome cells migrate ventrally into the somatic layer of the lateral plate mesoderm and there differentiate into the striated muscles of the ventrolateral body wall. The somatic layer of the lateral plate mesoderm itself becomes the dermis and connective tissue of the ventrolateral body wall. **All the structures derived from a single dermomyotome, from the mesoderm into which it migrates and from the ectoderm that overlies this mesoderm, constitute a body wall segment**. On the other hand, each vertebra is derived from two adjacent sclerotomes (Fig. 2-2*C*) and thus vertebrae lie between body wall segments, i.e., are intersegmental. Ribs are nothing but long lateral processes of vertebrae; thus, they too are intersegmental.

On each side, between the developing skull and the first rib-bearing vertebra, there are 8 dermomyotomes (see Fig. 2-2*C*). These obviously are neck, or **cervical**, dermomyotomes. Caudal to each of the 12 rib-bearing vertebrae is a **thoracic** dermomyotome (see Fig. 2-2*C*). Following the 12 thoracic dermomyotomes are 5 **lumbar**, 5 **sacral**, and 1 **coccygeal** dermomyotome, each caudal to a vertebra of

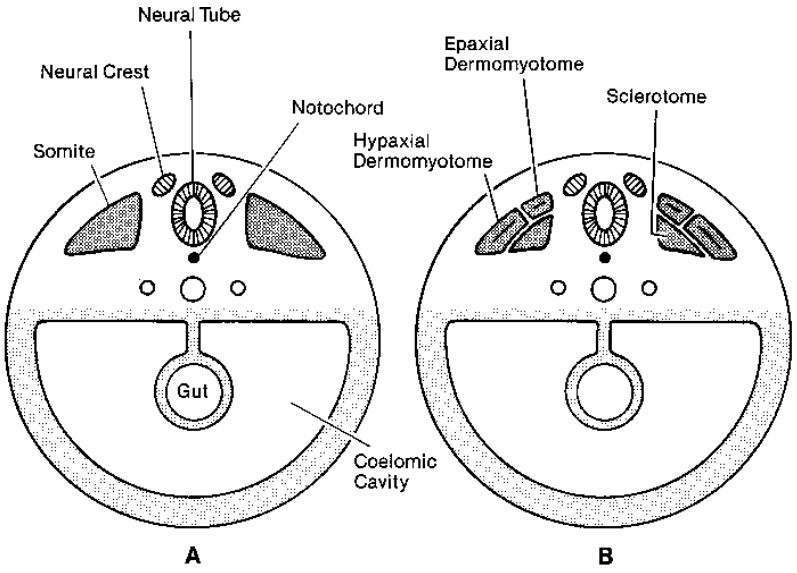

Figure 2–1. Schematic transverse sections through an embryo at two sequential stages in development. *A*, The relationship of somites to the neural tube and notochord. *B*, The division of each somite into a sclerotome that will participate in formation of vertebrae, an epaxial dermomyotome that contributes to formation of both intrinsic back muscles and dermis of the dorsal body wall, and a hypaxial dermomyotome that contributes to formation of the other striated muscles of the trunk and limbs.

the same name and number (see Fig. 2-2*C).* Addition of these numbers reveals that there are a total of 31 dermomyotomes and, consequently, 31 body wall segments on each side. However, caudal to the 1st coccygeal somite are some extra somites that do not produce dermomyotomes. Most of these degenerate completely, but a few produce small sclerotomes that develop into the rudimentary 2nd, 3rd, and 4th coccygeal vertebrae (see Fig. 2-2*C*). If more than the usual number of caudal somites persist to produce sclerotomes, the infant will be born with a short tail.

Segmentation of the Neural Tube

The portion of the neural tube caudal to the head becomes the spinal cord. Its major function is to receive sensory innervation from, and provide motor impulses to, the structures of the body wall. It does this by means of spinal nerves. Since the body wall is composed primarily of somatic structures, spinal nerves are composed primarily of somatic motor and somatic sensory fibers. Let us begin by considering how the spinal cord sends somatic motor instructions out to the body wall and receives somatic sensation from it.

The developing spinal cord gray matter opposite each dermomyotome will be devoted to sending somatic motor impulses to the striated voluntary muscles derived from that dermomyotome, and receiving somatic sensory information from the body wall segment associated with it. Thus, the internal structure of the spinal cord is segmented functionally, if not visually. Each spinal cord segment will become connected to a pair of spinal nerves (one spinal nerve on the right and one on the left) that conduct nerve fibers to and from its corresponding dermomyotomes and body wall segments (see Fig. 2-2*C*). Given what we know about the numbers and names of dermomyotomes, and the fact that each has an associated spinal cord segment, we can deduce that there are 8 cervical, 12 thoracic, 5 lumbar, 5 sacral, and 1 coccygeal spinal cord segments and pairs of spinal nerves. In a fully developed human, the region of the skin innervated by the branches of a single spinal nerve is called a **dermatome**.

Students often have difficulty understanding why there are 8 cervical nerves, but only 7 cervical vertebrae. Of course, the answer is that 8 dermomyotomes form between the skull and the first rib-bearing vertebra, but only 7 vertebrae form in this same region. The first cervical nerve is the one that

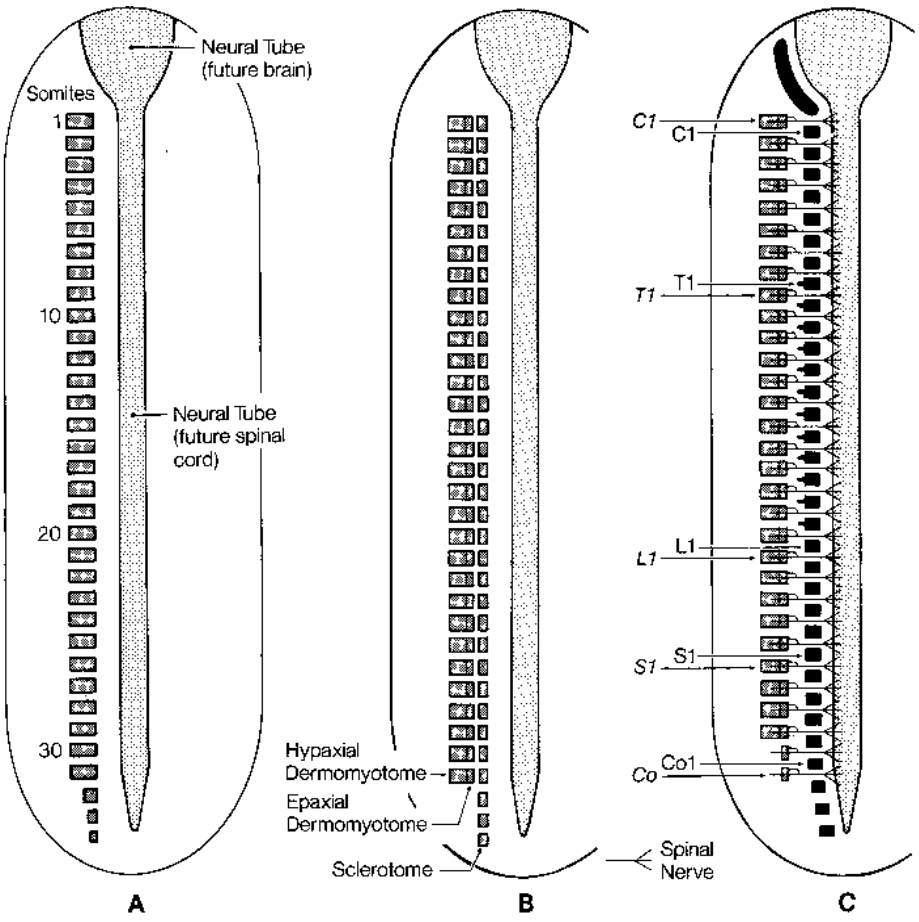

Figure 2–2. Schematic coronal sections through an embryo at three sequential stages in development. *A*, Neural tube with the 34 somites of the trunk (shown only on one side) that contribute to adult structures. *B*, The division of fully formed somites into sclerotomes, epaxial dermomyotomes, and hypaxial dermomyotomes. *C*, The vertebrae (blackened) have been formed as intersegmental structures derived from adjacent sclerotomes. The 1st cervical, 1st thoracic, 1st lumbar, 1st sacral, and 1st coccygeal vertebrae are labelled in Roman type. Dermomyotomes are now named in relation to the vertebral column. The 1st cervical, 1st thoracic, 1st lumbar, 1st sacral, and coccygeal dermomyotomes are labelled in italics. Spinal nerves have grown laterally to reach the dermomyotomes. Each spinal nerve branches into a dorsal ramus for the epaxial portion of the dermomyotome and a ventral ramus for the hypaxial portion of the dermomyotome. The 5th sacral and the coccygeal hypaxial portions degenerate.

passes between the skull and the 1st cervical vertebra to reach the 1st cervical segment of the body wall. The second cervical nerve is cranial to the 2nd cervical vertebra, the 3rd cervical nerve is cranial to the 3rd cervical vertebra, and so on, until one gets to the nerve between the 7th cervical and 1st thoracic vertebrae. It makes no sense to call this the 1st thoracic nerve because it never enters the chest. Rather, like its more superior congeners, it passes from the spinal cord into the neck. Thus, it is the 8th of the cervical nerves. The first nerve to enter the thorax is the nerve caudal to the 1st thoracic vertebra. This and all other nerves are then named by the vertebra to which they are caudal.

Formation of the Spinal Nerve

Within the developing spinal cord the motor neurons and sensory neurons differentiate in separate regions of the spinal gray matter. Sensory neurons are located in the dorsal region of the spinal gray matter, which region is called the **dorsal horn**. Motor neurons lie in the ventral region of the spinal gray matter. That portion of the ventral spinal gray matter containing somatic motor neurons is called the **ventral horn**. Cells within the ventral horn of a single spinal cord segment send out motor axons that grow toward the corresponding dermomyotome. These axons are gathered into several bundles, each of which is called a **ventral rootlet**. Not long after the ventral rootlets from one spinal segment leave the spinal cord, they fuse into a single bundle of motor axons called the **ventral root**. This ventral root, composed of motor axons, continues toward the dermomyotome and then divides into a **dorsal ramus** for the muscles derived from the epaxial portion of the dermomyotome and a **ventral ramus** for the hypaxial muscles.

Lying dorsal to each ventral root, just proximal to the site where it bifurcates into dorsal and ventral rami, is a single clump of nerve cells derived from neural crest (Figs. 2-3 and 2-4). This clump, or **ganglion**, contains the cell bodies of the sensory neurons for the structures of the body wall segment associated with the corresponding dermomyotome. From each cell within the clump arises an axon that immediately divides into a peripheral process, which turns laterally toward the dermomyotome, and a central process, which grows medially toward the dorsal region of the developing spinal cord (Fig. 2-5). The central processes from a single ganglion first travel toward the spinal cord in a single bundle called the **dorsal root**. This soon divides into several separate bundles called **dorsal rootlets**, which in turn enter the appropriate spinal cord segment near the top of the dorsal horn of its gray matter. The peripheral processes of the ganglion cells join immediately with the nearby ventral root and thereby can reach the body wall with that root's ventral and dorsal rami (see Fig. 2-5). The region of juncture between motor axons and the peripheral processes of sensory axons is called the **spinal nerve**. The ventral and dorsal rami must now be considered branches of the spinal nerve (not just the ventral root) and such rami will contain both motor and sensory axons.

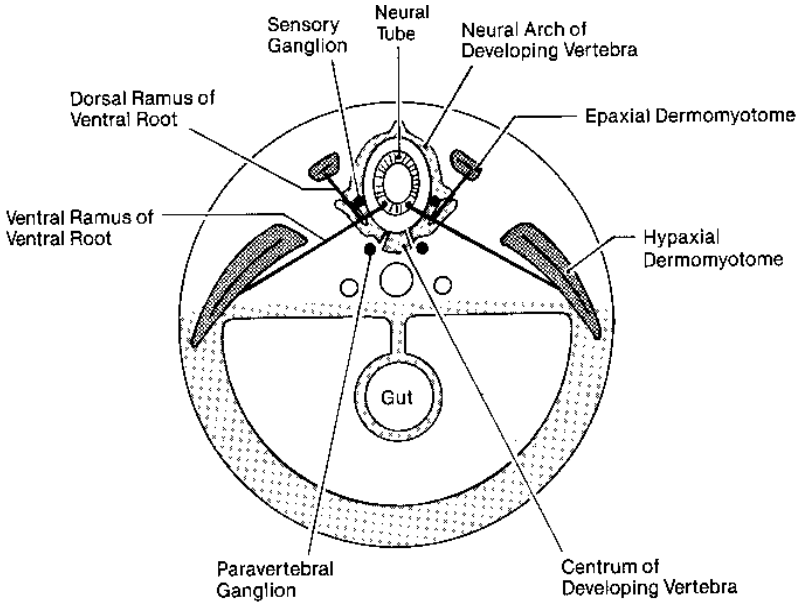

Figure 2–3. A schematic transverse section through an embryo at a stage in development when vertebrae are forming and the ventral roots of spinal nerves have grown out to reach dermomyotomes. Note the presence of an incipient sensory ganglion dorsal to the ventral root, and an incipient paravertebral sympathetic ganglion.

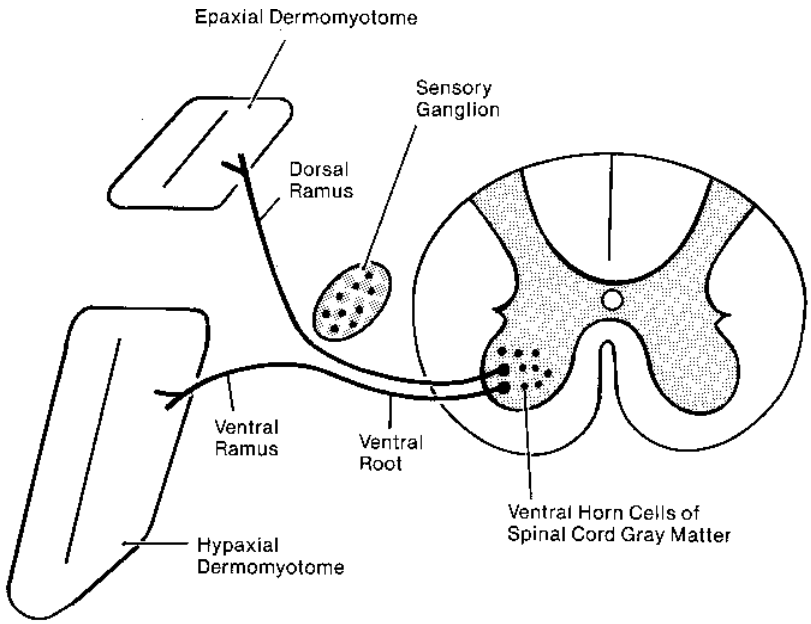

Figure 2–4. A schematic transverse section through the embryonic spinal cord (drawn to resemble the adult structure) showing the formation of the ventral root (of what will later become a spinal nerve) by motor axons growing out from the ventral horn to reach the dermomyotome of one body segment.

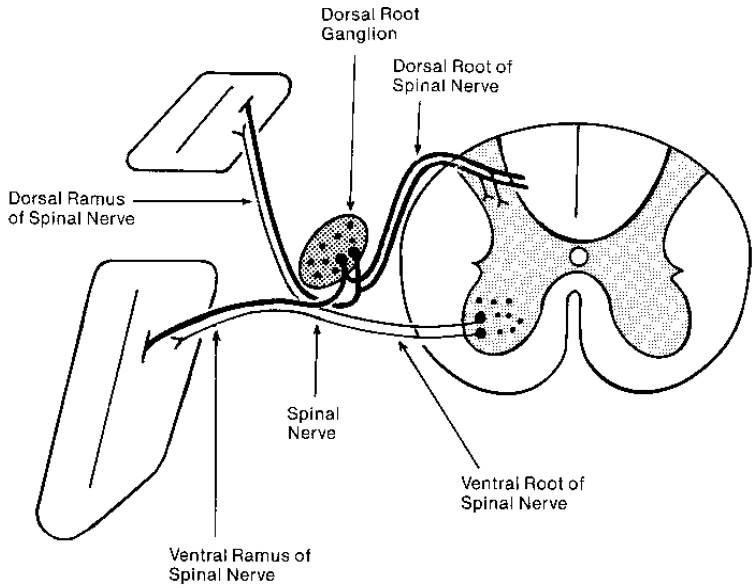

Figure 2–5. A schematic transverse section through the embryonic spinal cord (drawn to resemble the adult structure) showing completion of spinal nerve development by sensory axons growing out from the sensory ganglion. Each sensory axon bifurcates into (1) a peripheral process that joins motor axons to reach the dermomyotome (and structures that later become associated with it) and (2) a central process that grows medially to reach the spinal cord. In this way a spinal nerve with two roots and two rami is formed; the sensory ganglion is said to lie along the path of the dorsal root of the spinal nerve.

I have said that ventral rootlets emerge from the spinal cord, and this is quite correct. On the other hand, dorsal rootlets do not come from the spinal cord, they go to it. Gross anatomists tend to ignore this distinction and to speak as if dorsal rootlets also emerge from each spinal cord segment, then converge into a single dorsal root just before they reach the sensory ganglion. The ganglion is said to lie in the path of this dorsal root on its way to join the ventral root in formation of the spinal nerve. The actual spinal nerve is very short (1 or 2 mm even in the adult), because it branches into dorsal and ventral rami almost immediately after its formation.[1] **The spinal nerve *sensu stricto* is just that short region distal to the dorsal root ganglion where sensory and motor axons interweave so that the ventral and dorsal rami can contain both kinds of axons needed to innervate the body wall**. However, most of us tend to use the term "spinal nerve" loosely so as to include its roots and rami.

The ventral and dorsal rami of a spinal nerve differ primarily in the region of the body wall to which they distribute. Dorsal rami are destined for structures derived from or associated with the epaxial portions of dermomyotomes and will innervate narrow strips of the body wall on either side of the dorsal midline. The ventral rami are for the rest of the body wall (its lateral and ventral portions). The limbs are outgrowths of the lateral body wall, and limb muscles come from cells that have left the hypaxial portions of dermomyotomes. Thus, the limbs are innervated by ventral rami and not dorsal rami. Since so much more of the body wall is innervated by ventral rami than dorsal rami, the former nerve bundles are obviously much larger than the latter.

VISCERAL MOTOR STRUCTURES AND THE AUTONOMIC NERVOUS SYSTEM

As we have stated, the striated muscles derived from dermomyotomes constitute the somatic motor structures of the body. The neurons that innervate them are called somatic motor neurons, and they send their axons out the ventral roots of spinal nerves. The visceral motor tissues of the body--smooth muscle, cardiac muscle, and glands--are not derived from dermomyotomes. Glands are derived either from ectoderm or endoderm. Smooth muscle and cardiac muscle are derived from lateral plate mesoderm. **The part of the nervous system that innervates visceral motor tissues is called the *autonomic nervous system***.

Not only is there a functional distinction between the somatic motor system and the autonomic (i.e, visceral motor) parts of the nervous system, there are equally important anatomical differences. The most important of them is that **the nerve cells whose axons actually go to glands, smooth muscle, and cardiac muscle lie outside the CNS**. Some lie in dissectible clusters called **autonomic ganglia**, others are scattered within the walls of those organs that contain glands, smooth muscle, or cardiac muscle. Independent of whether the cells lie in ganglia or are more diffusely scattered, their axons that travel to glands, smooth muscle, or cardiac muscle are called **postganglionic autonomic axons**. The neurons themselves are called postganglionic autonomic neurons (even though it would make better sense to call them ganglionic neurons).

In order for the CNS to have some control over postganglionic autonomic neurons, there are cells within the CNS that send axons out to them. These are the **preganglionic autonomic neurons**, and their axons are **preganglionic autonomic axons**.

The Subdivisions of the Autonomic Nervous System--Sympathetic and Parasympathetic

There are two subdivisions of the autonomic nervous system (ANS), which differ both functionally and structurally. What binds them together is that they are both visceral motor and that the

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[1] Before it divides into its dorsal and ventral rami, the spinal nerve may give off a small meningeal branch that returns to the vertebral canal for supply of the dura.

axons going to glands, smooth muscle, or cardiac muscle emanate from cells outside the CNS. The two divisions are called **sympathetic** and **parasympathetic**.

The sympathetic system was the first part of the ANS to be discovered. Early workers noted its activity during emotional situations. Emotions were called sympathies, hence the name. Later, a second part of the nervous system that was also active during emotional situations was discovered. It was simply called the *para*sympathetic system.

Activity in the **sympathetic** nervous system serves the role of **energy expenditure**. The sympathetic system is activated during moments of great effort. The sweat glands are stimulated in order to dissipate the heat generated by exertion. Arterioles of the skin may be constricted in order to shunt blood to muscles, or dilated to promote dissipation of heat to the environment. Muscular and coronary arterioles dilate to bring more blood to muscles and the heart. Bronchi dilate for increased air flow. The bowel is quieted and its blood vessels constricted; blood is thus shunted away from digestive organs not needed in the effort. The pupils dilate to allow entry of all important visual information. One can deduce almost every action of the sympathetic nervous system by considering what is needed to expend energy.

Activity in the **parasympathetic** system promotes the **intake and conservation of energy**. The pupils and bronchi constrict; the heart slows down, and its vessels constrict. One cannot take in energy without passing foodstuffs through the bowel; thus arteries to the bowel are dilated, peristalsis is activated, and exocrine digestive glands are stimulated to secrete. Room to accommodate new nutrients must be made by the elimination of wastes. Thus, the involuntary sphincter of the anus is relaxed, and the bladder contracts and its sphincter relaxes.

From what has just been said, it is obvious why the sympathetic system is considered the system of "fight or flight." These things involve expenditure of energy. The only disadvantage to a reliance on this mnemonic is that one can mistakenly introduce "fright" into the equation. Fright causes discharge of the entire ANS, hence defecation and urination.

The anatomical differences between the sympathetic and parasympathetic systems may now be enumerated.

1. The sympathetic system innervates visceral motor tissues both in the body wall and within internal organs. The parasympathetic system does not innervate structures in the body wall but is confined to the innervation of internal organs.
2. There are numerous dissectible sympathetic ganglia, but the vast majority of parasympathetic postganglionic cell bodies are scattered in the wall of the organ being innervated.
3. The preganglionic cell bodies of the sympathetic system are confined to the spinal gray matter from the 1st thoracic through the 2nd lumbar segments of the spinal cord (in a region just dorsal to the somatic motor cells). For this reason the **sympathetic** system is said to be the **thoracolumbar** part of the ANS. The parasympathetic preganglionic cell bodies are confined to the brainstem and to the 3rd and 4th sacral segments of the spinal gray matter (occasionally extending, and even then only to a small degree, also into either S2 or S5). For this reason the **parasympathetic** system is said to be the **craniosacral** part of the ANS.

The Sympathetic Nervous System

The Paravertebral Ganglia and Their Primary Role in Innervating Visceral Motor Structures in the Body Wall

One of the things the sympathetic system does is to innervate the sweat glands, arrector pili muscles, and vascular smooth muscle lying in the body wall. Every part of the body wall has such structures, thus every part of the body wall must receive postganglionic sympathetic axons. The question is, how can such axons get to the body wall? The obvious answer is that they can hitch a ride on nerves carrying somatic axons to the body wall, i.e., the ventral and dorsal rami of the spinal nerves.

In embryogenesis, one sympathetic ganglion forms near the ventral ramus of each spinal nerve (see Fig. 2-3). Such ganglia lie just lateral to the developing vertebral bodies and are called **paravertebral** ganglia. Thus, on each side there would be 31 paravertebral ganglia (Fig. 2-6*A*). The cells of any one ganglion send their axons into the ventral ramus of the nearby spinal nerve. The small nerve bundle that carries such postganglionic axons from the ganglion to the ventral ramus is called the **gray ramus communicans** (Fig. 2-7*A*). It is called "gray" because the sympathetic axons are unmyelinated and the bundle lacks the white luster of myelin. Obviously, on each side there are 31 gray rami communicantes, each connecting a paravertebral ganglion to a ventral ramus (see Fig. 2-6*A*). If one of the axons in a gray ramus is destined for a sweat gland or vascular smooth muscle lying in the ventrolateral body wall, it will, after entering the ventral ramus of the spinal nerve, immediately turn distally to distribute with this ventral ramus (see Fig. 2-7*A*). If the postganglionic sympathetic axon is meant for a sweat gland or smooth muscle of the dorsal body wall, the axon will, after entering the ventral ramus, turn proximally and travel to the spinal nerve (*sensu stricto*), whereupon it passes into the dorsal ramus to be distributed with it.

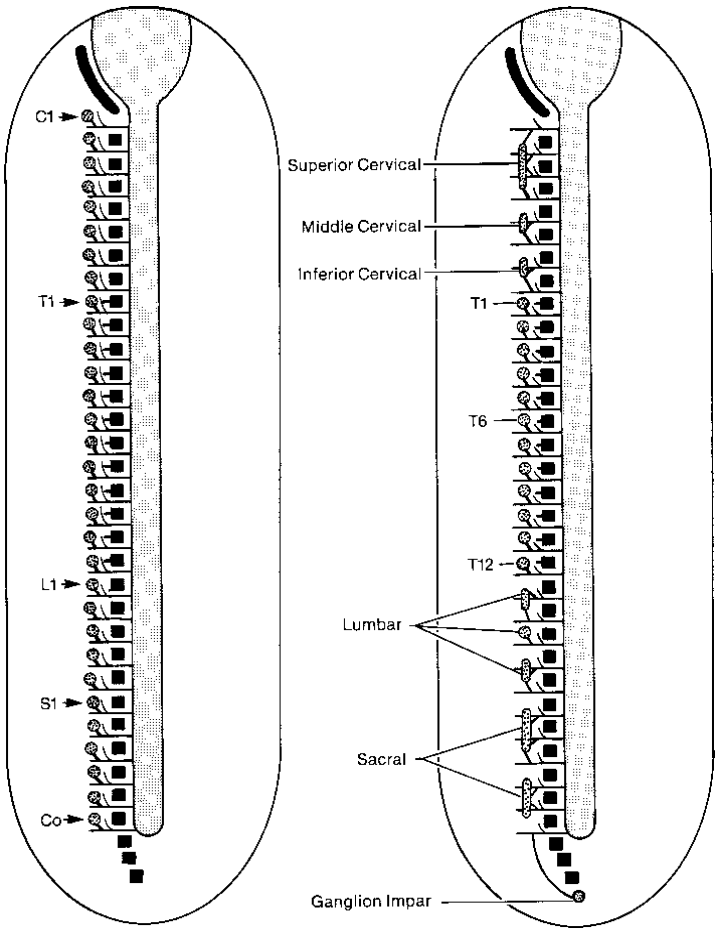

Figure 2–6. Schematic coronal sections through an embryo showing early stages in development of the sympathetic chain. *A*, One paravertebral sympathetic ganglion (stippled) forms for each of the 31 body segments complete enough to require a spinal nerve (i.e., C1–Co). The 1st cervical, 1st thoracic, 1st lumbar, 1st sacral, and coccygeal paravertebral ganglia are labelled. The cells of each ganglion send axons to join the ventral ramus of the corresponding spinal nerve. At each level the bundle formed by these sympathetic postganglionic axons is called a gray ramus communicans. *B*, The paravertebral ganglia in the cervical, lumbar, and sacral regions undergo fusions so that there is no longer one ganglion for each body segment and spinal nerve. The coccygeal paravertebral ganglion of one side migrates to meet that of the opposite side in the midline, forming the ganglion impar. No gray rami have been lost.

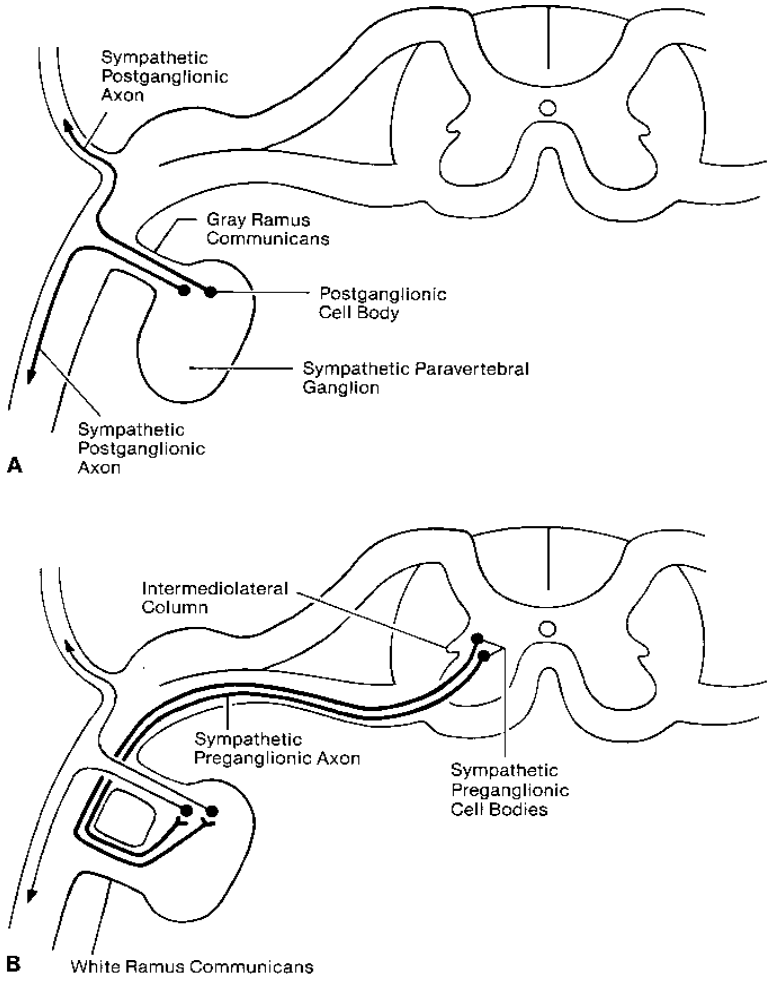

Figure 2–7. Schematic transverse sections through the spinal cord and a spinal nerve showing development of rami communicantes. *A*, Cells in a paravertebral sympathetic ganglion send axons to join the ventral ramus of the nearest spinal nerve and distribute to the body wall with that nerve's dorsal and ventral rami. These sympathetic postganglionic axons form a bundle called the gray ramus communicans. *B*, Cells in a paravertebral ganglion are placed under CNS control by axons that grow from preganglionic cells in the intermediolateral column of the spinal gray matter. These axons pass out the ventral root and through the spinal nerve to reach its ventral ramus. They leave the ventral ramus in a bundle called the white ramus communicans.

The embryonic state of one paravertebral sympathetic ganglion for every spinal nerve is altered only minimally as development progresses (Fig. 2-6*B*). The paravertebral ganglia for cervical nerves 1-4 fuse, producing a single **superior cervical sympathetic ganglion** that sends out four gray rami, one to each of the first four cervical nerves. The paravertebral ganglia for spinal nerves C5 and C6 fuse to produce a **middle cervical sympathetic ganglion** that sends out two gray rami, one to C5 and the other to C6. The paravertebral ganglia for spinal nerves C7 and C8 fuse to form an **inferior cervical sympathetic ganglion** that sends out two gray rami, one to C7 and the other to C8. Sometimes this inferior cervical ganglion itself fuses with the next lower 1st thoracic ganglion; the resulting **stellate** ganglion would emit three gray rami.

Thoracic sympathetic ganglia do not fuse with each other; therefore, in the adult there are 12 thoracic (or one stellate and 11 thoracic) ganglia, each with its own gray ramus going to the ventral ramus of its corresponding spinal nerve.

The original 5 lumbar sympathetic ganglia fuse in a variable manner producing a lesser number of lumbar ganglia in the adult (see Fig. 2-6*B*). There are still 5 lumbar gray rami, but, obviously, which adult ganglion they come from depends on the precise pattern of fusion. The sacral sympathetic ganglia behave as do the lumbar. All that is fixed is the existence of 5 sacral gray rami, one for each sacral ventral ramus. The coccygeal ganglion of the left side fuses with that of the right to form the **ganglion impar** (see Fig. 2-6*B*), which gives off right and left gray rami to the right and left coccygeal nerves.

It may have occurred to the reader that there is one region of the body wall not served by spinal nerves, but which nonetheless has sweat glands, arrector pili muscles, and blood vessels requiring sympathetic innervation. I am speaking of the head. How can postganglionic sympathetic axons get to the visceral motor structures of the head? The problem is solved by having some cells of the superior cervical sympathetic ganglion give off postganglionic axons that surround arteries traveling to the head. Thus, there are plexuses of postganglionic sympathetic axons around the internal and external carotid arteries, which plexuses are derived from branches of the superior cervical ganglion.

Preganglionic Input to Paravertebral Ganglia

Of course, all the cells in the paravertebral ganglia must somehow be under CNS control. In fact, they receive synaptic input from preganglionic neurons that lie within the spinal cord. Because the paravertebral ganglia extend all the way from C1 down to Co, logic would dictate that there would be preganglionic sympathetic cells within every segment of the spinal cord. For some strange reason, however, sympathetic preganglionic neurons are not found at every level of the spinal cord. **All the sympathetic preganglionic cell bodies lie in a column of the ventral spinal gray matter that extends from the 1st thoracic segment through the 2nd lumbar segment**. This column is called the **intermediolateral column**, or sometimes the lateral horn, and it is located just dorsal to the ventral horn that contains somatic motor cell bodies (Fig. 2-7*B*).

Now that we know where the sympathetic preganglionic neurons lie, the question is how do their axons get to paravertebral ganglia? The answer is that these visceral motor axons tag along with the somatic motor axons that are leaving the spinal cord (see Fig. 2-7*B*). Thus, the ventral roots and spinal nerves from T1 through L2 contain both somatic motor and preganglionic sympathetic axons. Because the sympathetic *preganglionic* axons do not wish to distribute with the ventral and dorsal rami of the spinal nerve, they must somehow depart from the path taken by somatic motor axons. They do this by entering the ventral ramus of the spinal nerve and, shortly thereafter, passing out of this ventral ramus in a separate bundle that goes to the nearest paravertebral ganglion (see Fig. 2-7*B*). These preganglionic sympathetic axons are myelinated, and the nerve bundle that leaves the ventral ramus to run to the paravertebral ganglion is white in a fresh specimen. This white nerve bundle that communicates between the ventral ramus and the nearest sympathetic ganglion is called the **white ramus communicans**.

All the ventral roots from T1 through L2 contain preganglionic sympathetic axons, but no other ventral roots do. All spinal nerves and ventral rami from T1 to L2 contain preganglionic sympathetic axons, but no other spinal nerves and no other ventral rami do. **All paravertebral ganglia between T1 and L2 are connected to the nearest ventral ramus by a white ramus communicans, but no other paravertebral ganglion is so connected (Fig. 2-8*A*)**. Since every paravertebral ganglion is connected to the nearest ventral ramus by a gray ramus communicans, it is obvious that there are more gray rami than white rami and that the ganglia corresponding to C1-C8 and L3-Co have solely gray rami. Only the ganglia from T1-L2 have both white and gray rami.

The Sympathetic Chain

In that each paravertebral ganglion from T1 down to L2 receives a white ramus communicans, the postganglionic cells within these ganglia have no trouble getting preganglionic input. That input is carried to them via the white ramus. The question is, how do cells of the cervical paravertebral ganglia, and those below the 2nd lumbar ganglion, get any preganglionic input? The answer is to be found in the fact that not all preganglionic axons synapse in the ganglion to which they are first brought. Some do, but other preganglionic axons turn either upward or downward to travel to a ganglion that does not have its own white ramus. Sometimes these ascending or descending axons must travel rather far. Thus, some of

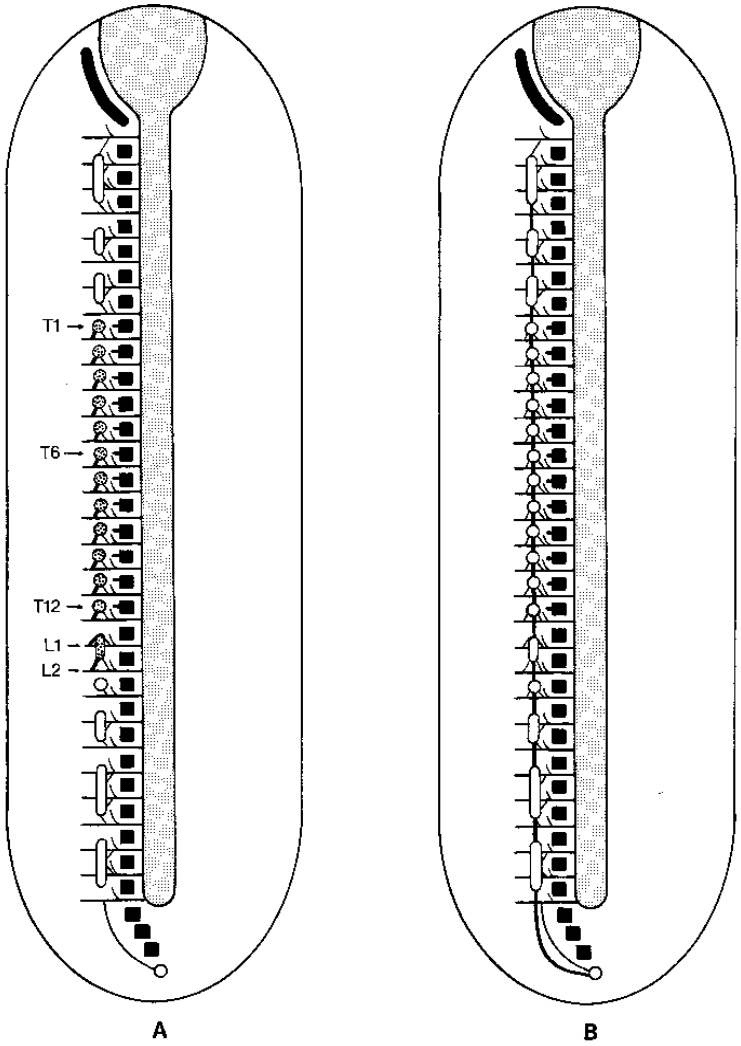

Figure 2–8. Schematic coronal sections through an embryo showing later stages in formation of the sympathetic chain. *A*, The 1st thoracic to 2nd lumbar paravertebral ganglia (stippled) are now connected to their corresponding spinal nerves by white rami communicantes conducting preganglionic axons from the ventral ramus of the spinal nerve to the ganglion. *B*, Preganglionic sympathetic axons pass either upward or downward from the ganglion at which they first arrived, forming bundles that link the paravertebral ganglia into a chain of sympathetic ganglia.

the preganglionic sympathetic axons that travel out the 1st thoracic ventral root into the 1st thoracic spinal nerve, 1st thoracic ventral ramus, 1st thoracic white ramus, and 1st paravertebral ganglion will, without synapse, turn superiorly and run up to the inferior cervical ganglion, pass through it without synapse and run to the middle cervical ganglion, pass through it without synapse and run to the superior cervical ganglion, and only there synapse on postganglionic sympathetic neurons. Most of the cells within the superior cervical ganglion receive their preganglionic input from the axons of preganglionic cells that lie in the 1st thoracic segment of the cord. Recalling that the superior cervical sympathetic ganglion provides axons that innervate visceral motor structures in the head, we can understand that damage to the 1st thoracic spinal cord segment, or the 1st thoracic spinal nerve, will destroy the sympathetic innervation of the head.

Even cells in the middle and inferior cervical ganglia must receive preganglionic input from axons of cells that lie in thoracic segments of the cord, but for these two ganglia the most important cord

levels are the 2nd and 3rd thoracic. Thus, some axons traveling in the 3rd white ramus communicans to the 3rd paravertebral ganglion will turn cranially within this ganglion and ascend to synapse in one of the lower cervical ganglia by passing through all intervening ganglia. Since the sympathetic innervation to the upper limb comes from the middle and inferior cervical ganglia, destruction of the 2nd and 3rd thoracic paravertebral ganglia will interrupt the sympathetic pathways to the upper limb. Surgical destruction of these ganglia is a recognized procedure for treating hyperhidrosis of the palm.

The pattern of preganglionic input to all paravertebral ganglia below the 2nd lumbar is a mirror image of what has just been described. Preganglionic cells lying in the lower thoracic and upper two lumbar levels of the spinal cord send their axons out lower thoracic and the upper two lumbar spinal nerves, through lower thoracic and the upper two lumbar white rami, and then into lower thoracic and the upper two lumbar paravertebral ganglia. While some of these axons synapse in the ganglion to which they are first brought, many other axons descend to lower ganglia until they find the cells on which they are destined to synapse. In so doing, many of these descending axons pass through a number of paravertebral ganglia without synapsing.

Finally, it must be acknowledged that even a ganglion like the 4th thoracic, which in theory could receive all its preganglionic input from axons in the 4th thoracic white ramus and need not rely on axons that have ascended from lower levels or descended from higher levels, does not choose to follow theory. Although many of the cells in the 4th thoracic ganglion receive the synapses of axons that have traveled to it in the 4th thoracic white ramus, some of the synaptic input to the 4th thoracic ganglion does come from preganglionic axons that have either descended from higher levels or ascended from lower levels. The same is true of all other thoracic ganglia. Thus, when one dissects the paravertebral ganglia, it will be seen that each is connected to the ganglion above by one nerve bundle, and to the ganglion below by another nerve bundle. As a result, the paravertebral ganglia do not compose a series of isolated clumps of cells but rather constitute a **chain** of ganglia, the so-called **sympathetic chain** (Fig. 2-8*B*). **A chain ganglion receives preganglionic input from three possible sources: (1) from its corresponding white ramus, (2) from a lower level by ascent, or (3) from a higher level by descent**.

Sympathetic Innervation of Internal Organs

All body wall structures receive their postganglionic sympathetic supply from paravertebral ganglia cells, but where are the postganglionic sympathetic cells that provide innervation to the visceral motor structures within internal organs? The answer is that some are located in paravertebral ganglia and others are not. **All the internal organs of the body superior to the abdominal diaphragm receive postganglionic axons from cells that lie in paravertebral ganglia**. The axons to such organs (e.g., heart, esophagus, bronchus) obviously do not travel in gray rami, because gray rami go to the spinal nerves and spinal nerves do not distribute to internal organs. Instead, the postganglionic axons that innervate internal organs above the diaphragm travel in nerve bundles that go directly from a paravertebral ganglion to the organ (Fig. 2-9). These direct postganglionic sympathetic nerves are named by the organs they go to. Thus, there are **sympathetic cardiac nerves, sympathetic esophageal nerves, sympathetic pharyngeal nerves, sympathetic pulmonary nerves, sympathetic aortic nerves**, and so on, all emanating from one or more paravertebral ganglia. Such nerves may join one another, yielding combination names such as “sympathetic cardiopulmonary nerves”. **Sympathetic "organ" nerves** are found emanating from all paravertebral ganglia above the 6th thoracic.[2] The paravertebral ganglion cells that innervate internal organs receive preganglionic input in precisely the same manner as all other paravertebral ganglion cells, i.e., they receive some preganglionic axons that have entered the ganglion through its white ramus (see Fig. 2-9), other preganglionic axons that have ascended in the chain from lower levels, and yet other preganglionic axons that have descended in the chain from higher levels.

We have discovered that the internal organs above the abdominal diaphragm receive postganglionic sympathetic axons from cells lying in paravertebral ganglia. But where are the

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[2] It also seems that some of the larger arteries of the body wall, e.g., subclavian and common iliac, receive direct postganglionic branches from paravertebral ganglia near their origin.

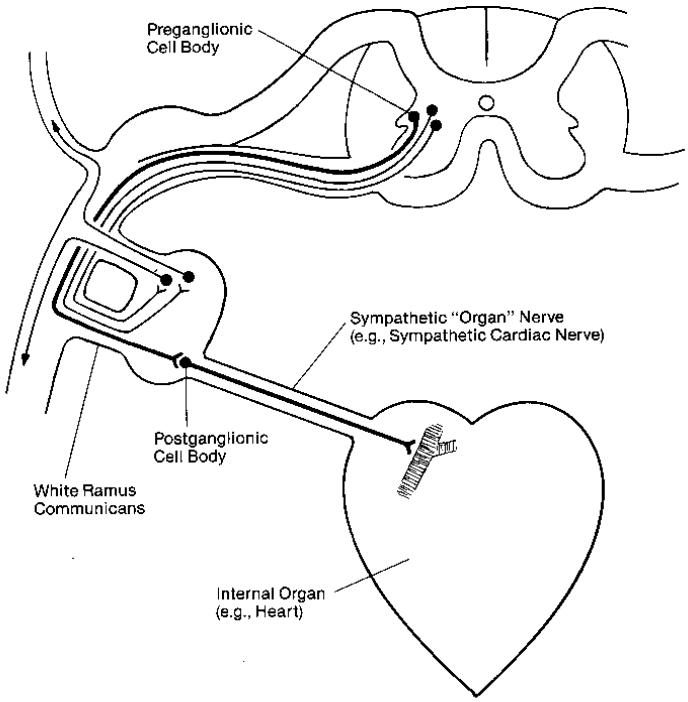

Figure 2–9. Schematic transverse section through the spinal cord and a spinal nerve showing sympathetic pathway to an internal organ superior to the abdominal diaphragm (e.g., the heart).

postganglionic sympathetic neurons for abdominal and pelvic organs? They lie in a few dissectible ganglia, and in a lot of minute ganglia, that are located either on the anterior surface of the abdominal aorta (Fig. 2-10) or, below it, in nerve plexuses that extend down from the aorta into the pelvis. The whole lot of them are best called **subdiaphragmatic ganglia**.[3] Those on the aorta are often called **pre-aortic ganglia**; those inferior to the aorta are called **prevertebral ganglia**. The axons of subdiaphragmatic ganglion cells travel to the organ requiring innervation either directly or along the outside of the arteries that go to that organ. (The adrenal medulla is a perverse sort of subdiaphragmatic ganglion. Its cells do not send axons to smooth muscle or glands but, instead, secrete neurohormones into the bloodstream.)

The subdiaphragmatic ganglia face a special problem getting preganglionic input. Since all preganglionic sympathetic axons are carried to a paravertebral ganglion by a white ramus, some must passthrough this ganglion and leave it in a nerve bundle that runs directly to a subdiaphragmatic ganglion (see Fig. 2-10). When one dissects the sympathetic chain, he or she will see such nerve bundles leaving the paravertebral ganglia from their ventral surfaces and running to the subdiaphragmatic ganglia. These, then, are a third kind of nerve bundle that contains preganglionic sympathetic axons (the first two kinds are the white rami communicantes and the interganglion connections). This third kind of preganglionic sympathetic nerve bundle is called a **splanchnic nerve**. Splanchnic nerves can be seen coming from the 5th through the 12th thoracic paravertebral ganglia, from the lumbar ganglia, and, in women, from the sacral ganglia. Those from thoracic ganglia are called **thoracic splanchnic nerves**; those from lumbar ganglia are called **lumbar splanchnic nerves**; those from sacral ganglia are called **sacral splanchnic nerves**. Obviously, a splanchnic nerve that emanates from any paravertebral ganglion below the 2nd lumbar must carry preganglionic axons that have descended in the chain to reach such a low ganglion (remember, ganglia below L2 have no white rami of their own).

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[3] Pick, J: The Autonomic Nervous System. JB Lippincott, Philadelphia, 1970.

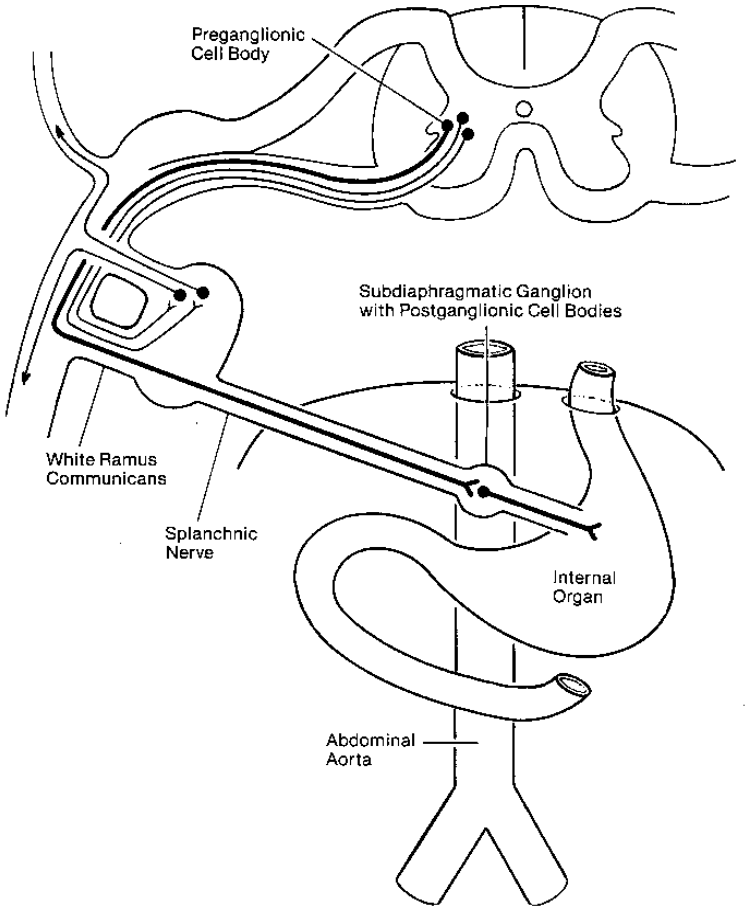

Figure 2–10. Schematic transverse section through the spinal cord and a spinal nerve showing sympathetic pathway to an internal organ inferior to the abdominal diaphragm (e.g., the stomach).

Summary of the Sympathetic System

All preganglionic sympathetic cell bodies lie in the spinal cord from T1 through L2. A preganglionic sympathetic axon reaches the paravertebral ganglion corresponding to its spinal cord segment of origin. These axons may (1) synapse in the ganglion to which they are brought first, (2) ascend and synapse in a higher ganglion, (3) descend and synapse in a lower ganglion, or (4) leave the chain via what is called a splanchnic nerve to synapse in a subdiaphragmatic ganglion (or the adrenal medulla). Postganglionic cell bodies lie either in the paravertebral chain of ganglia or in the subdiaphragmatic ganglia. Some postganglionic axons from each paravertebral ganglion are carried from the ganglion to the ventral ramus of the nearest spinal nerve in a dissectible bundle called the gray ramus communicans. These postganglionic axons are destined to supply sweat glands, arrector pili muscles, and body wall blood vessels. The axons either distribute with the ventral ramus to the ventrolateral body wall, or they backtrack to reach the dorsal ramus and go with it to the dorsal body wall. From the paravertebral ganglia above T6, other postganglionic axons leave directly to go to internal viscera above the abdominal diaphragm. Internal viscera below the diaphragm are innervated by postganglionic axons from the subdiaphragmatic ganglia.

A paravertebral ganglion may have up to six types of nerves attaching to it: (1) a bundle connecting to the next higher ganglion, (2) a bundle connecting to the next lower ganglion, (3) a gray ramus communicans, (4) a white ramus communicans, (5) a direct postganglionic bundle to an internal organ, and (6) a preganglionic bundle to subdiaphragmatic ganglia. All paravertebral ganglia have types

1, 2, and 3. Only the ganglia between T1 and L2 have type 4. The bulk of type 5 bundles come from ganglia C1-T5 (or T6). Below this level, direct postganglionic bundles are small and destined for large vessels. Only the ganglia from T5 and below have type 6 bundles.

The Parasympathetic Nervous System

The parasympathetic nervous system is limited to the innervation of smooth muscle, cardiac muscle, and glands of organs that lie internal to the body wall. Thus, such organs receive dual innervation from both the sympathetic and parasympathetic systems.

The organization of the parasympathetic system is far less complicated than that of the sympathetic system. **All preganglionic parasympathetic cell bodies lie either in the brain and send their axons out with cranial nerves, or lie in the spinal gray matter chiefly confined to the 3rd and 4th sacral levels, sending their axons out the ventral roots of the 3rd and 4th sacral spinal nerves**.

The parasympathetic outflow through cranial nerves will be discussed in detail later in the text. It is sufficient now to state that cranial nerves III (oculomotor), VII (facial), IX (glossopharyngeal), and X (vagus) carry preganglionic parasympathetic axons. The parasympathetic axons in cranial nerves III, VII, and IX are concerned solely with innervating structures in the head and the superior region of the neck. There are one or more dissectible parasympathetic ganglia associated with each of these three cranial nerves. **The vagus carries all the preganglionic parasympathetic axons for internal organs of the thorax, and for abdominal organs derived from the embryonic foregut and midgut. No dissectible parasympathetic ganglia are associated with the vagus; the postganglionic cell bodies lie embedded in the organ to be innervated**.

The preganglionic parasympathetic cells lying in the sacral levels of the spinal cord send their axons out the ventral roots of the spinal nerves S3 and S4 (occasionally, and even then only to a small extent, also either S2 or S5). These axons are carried to the S3 and S4 spinal nerves and leave such nerves through their ventral rami. Shortly after entering the ventral rami of S3 and S4, the parasympathetic preganglionic axons leave as dissectible nerves called **pelvic splanchnic nerves**. **The pelvic splanchnic nerves pass directly to the hindgut and to the pelvic organs. There are no dissectible parasympathetic ganglia associated with the pelvic splanchnic nerves. The postganglionic cells either lie embedded in the organ to be innervated or are found in some minute parasympathetic ganglia within the pelvic nerve plexuses** (see further on). It should be emphasized that preganglionic parasympathetic axons from sacral cord levels 3 and 4 have nothing whatsoever to do with sacral sympathetic ganglia at these levels.[4] The pelvic splanchnic nerves are **not** white rami, neither do they pass through sympathetic ganglia.

THE VISCERAL SENSORY SYSTEM

Just as the motor system is functionally and anatomically divided into two subsets, a somatic and a visceral, so is the sensory system. **Structures receiving visceral motor input give rise to a kind of sensation called visceral sensation**. Thus, the structures of the body that give rise to visceral sensation are the vasculature of the body wall and all the internal organs. (One should also be aware that there is a considerable nonsensory afferent feedback from visceral structures. This information is used for reflex control of glands, smooth muscle, and cardiac muscle.)

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[4] However, in has been reported for some mammals that postganglionic sympathetic axons are found in pelvic splanchnic nerves. Presumably they are derived from cells in sacral paravertebral ganglia, and traveled via gray rami communicantes to the S3 an S4 ventral rami, then accompanied the far more numerous parasympathetic preganglionic axons as they leave to form pelvic splanchnic nerves.

Visceral sensation is different in quality from somatic sensation. The latter may be painful or not, and when painful is generally sharp and well-localized. Visceral sensation is always uncomfortable or painful, but at the same time is dull and poorly localized. Stimuli for somatic pain include touch, temperature, cutting, ischemia (inadequate blood supply), and inflammation. The stimuli for visceral pain are ischemia, inflammation, distension or stretching, and sustained smooth muscle contraction (cramping). Visceral pain is not elicited by squeezing, burning, or cutting. Thus, visceral organs are insensitive to many of the injuries that cause intense somatic pain.

We have traced somatic sensory fibers from the body wall through dorsal and ventral rami of spinal nerves, back to the dorsal root ganglia and spinal cord. The cell bodies of visceral pain neurons also lie in dorsal root ganglia, scattered between the somatic sensory cell bodies. However, since neither dorsal nor ventral rami distribute to internal organs of the body, pain fibers from internal organs must return to the dorsal root ganglion by a different path than do somatic sensory fibers. It is not obvious, but equally true, that even visceral pain from body wall vasculature does not travel the same path as does somatic sensation from the rest of the body wall.

Visceral sensory fibers from blood vessels of the body wall and from all internal organs travel centrally toward the spinal nerve within the same nerve bundles that carry sympathetic supply out to these structures. If you know the sympathetic outflow path, you know the visceral sensory inflow path. Many of these paths will be traced later in the text, but three generalizations are immediately obvious: (1) All such visceral sensory fibers must reach the sympathetic chain before they go to the spinal nerve; (2) all such visceral sensory fibers must travel from the chain to the spinal nerve via the white ramus communicans (since all sympathetic outflow passed from the spinal nerve to the chain via a white ramus); and (3) all such visceral sensation will enter dorsal roots only between T1 and L2.

An exception to the rule just stated concerns visceral sensation arising as the result of distension of pelvic organs. The axons carrying this pain do *not* travel centrally with bundles carrying sympathetic outflow. Instead, they travel centrally with bundles carrying parasympathetic outflow. Thus, such axons will pass centrally in pelvic splanchnic nerves to reach the ventral rami of S3 and S4. From here the pain fibers pass backward into the spinal nerves and dorsal roots of S3 and S4. Such fibers have no connection with sympathetic ganglia, white rami, or gray rami.

The central processes of visceral pain axons travel back from the dorsal root ganglion to the spinal cord in dorsal roots (rootlets). The dorsal horn contains two kinds of cell bodies: one receives input from somatic sensory axons, the other receives input from both somatic sensory pain axons and visceral sensory axons.

REFERRED PAIN

As stated previously, visceral pain is dull and poorly localized. Sometimes when visceral pain impulses from a diseased organ reach the CNS, a "mistake" in interpretation is made, and what reaches consciousness is not only the dull, poorly localized, true visceral pain, but also a sharp, well-localized pain from a region of the body wall innervated by the same segments of the spinal cord as first received the visceral impulses. This mistake probably occurs because the spinal cord dorsal horn cells that receive input from visceral sensory axons also get it from somatic pain fibers. If one knows the spinal cord level supplying autonomic innervation to an organ, then one knows the spinal cord level receiving visceral pain from that organ. If one knows the spinal cord level receiving visceral pain from an organ, then one knows what part of the body wall will experience referred pain if such arises. For example, the heart receives its sympathetic supply from spinal cord segments T1-T5. Its visceral pain returns to these same segments. The skin and deeper structures of the body wall supplied by T1-T5 may experience pain during an ischemic episode of the heart. The uterine cervix receives its parasympathetic supply from S3 and S4, and visceral pain arising from distension of the

cervix returns to these levels. Such pain, as occurs during labor, is referred to the dorsal aspect of the sacrum.

INTERESTING SIDELIGHTS

Enteric Nervous System

Many authors now recognize a third, neither sympathetic nor parasympathetic, portion of the autonomic nervous system. It is called the **enteric nervous system** because its cell bodies lie within the wall of the bowel (alongside parasympathetic postganglionic neurons) and are responsible for the induction of reflex peristalsis without the need for commands from the brain or spinal cord. Some of the cells of the enteric nervous system are sensory, responding to change in bowel shape. Others are simply interneurons that receive input from the sensory cells (and also from sympathetic postganglionic and parasympathetic preganglionic axons) and project to parasympathetic postganglionic cell bodies. Finally, although the sensory cells of the enteric nervous system have axons that synapse on such interneurons, collateral branches of these axons likely proceed to synapse on subdiaphragmatic or paravertebral sympathetic ganglionic cells, or even travel into the CNS.

Possible Roles for Sympathetic Neurons in Other Than Visceral Motor Functions

Although there is much to be said for viewing the sympathetic nervous system as being concerned solely with the innervation of smooth muscle, cardiac muscle, and glands, recent studies point to roles that do not fall into the visceral motor category. Thus, Barker and Saito[5] provide evidence that noradrenergic sympathetic postganglionic axons destined for the supply of vasculature within striated voluntary muscles actually send off branches that go to the striated muscle fibers themselves. No motor endplate (nor any other specialized ending) is formed, causing the authors to suggest that the release of norepinephrine in the near vicinity of a striated muscle fiber has an effect either on its active state or on cholinergic transmission across the motor endplate.

A second atypical function of sympathetic neurons is indicated by the work of Hohmann and colleagues.[6] This study found that, among the nerves innervating periosteum, there are postganglionic sympathetic fibers having vasoactive intestinal peptide as their neurotransmitter. This peptide is known to promote resorption of bone, leading one to postulate a sympathetic influence on bone metabolism and growth. Such sympathetic neurons, as well as those that end near striated muscle cells (see previous paragraph) , are classified as nonmotor visceral efferent.

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[5] Barker, D, and Saito, M: Autonomic innervation of receptors and muscle fibres in cat skeletal muscle. Proc R Soc Lond B, 212:317-332, 1981.

[6] Hohmann, EL, Elde, RP, Rysavy, JA, Einzig, S, and Gebhard, RL: Innervation of periosteum and bone by sympathetic vasoactive intestinal peptide-containing nerve fibers. Science 232:868-871, 1986.