英文原版
医学教材

临床神经解剖学

Clinical Neuroanatomy

- Concise overview of neuroanatomy and of its functional and clinical implications
- Excellent review for the USMLE
- Includes cases and practice exam

Stephen G. Waxman

人民卫生出版社

LANGE

twenty-fifth edition

a LANGE medical book

Clinical Neuroanatomy

twenty-fifth edition

Stephen G. Waxman, MD, PhD
Chairman, Department of Neurology
Professor of Neurology, Neurobiology, & Pharmacology
Yale University School of Medicine
New Haven, Connecticut

Chief, Neurology Service
Yale-New Haven Hospital
New Haven, Connecticut

Visiting Professor of Neurology, Anatomy, & Biology
Institute of Neurology
University College
London, England

人民卫生出版社

人民卫生出版社
McGraw-Hill
A Division of The McGraw-Hill Companies

Clinical Neuroanatomy, Twenty-Fifth Edition

Notice

Medicine is an ever-changing science. As new research and clinical experience broaden our knowledge, changes in treatment and drug therapy are required. The author and the publisher of this work have checked with sources believed to be reliable in their efforts to provide information that is complete and generally in accord with the standards accepted at the time of publication. However, in view of the possibility of human error or changes in medical sciences, neither the author nor the publisher nor any other party who has been involved in the preparation or publication of this work warrants that the information contained herein is in every respect accurate or complete, and they disclaim all responsibility for any errors or omissions or for the results obtained from use of the information contained in this work. Readers are encouraged to confirm the information contained herein with other sources. For example and in particular, readers are advised to check the product information sheet included in the package of each drug they plan to administer to be certain that the information contained in this work is accurate and that changes have not been made in the recommended dose or in the contraindications for administration. This recommendation is of particular importance in connection with new or infrequently used drugs.

图书在版编目（CIP）数据

临床神经解剖学/（美）韦克斯曼（Waxman，S.G.）著. —北京：人民卫生出版社，2003.
ISBN 7-117-05406-9

Ⅰ.临… Ⅱ.韦… Ⅲ.神经系统-人体解剖学-英文 Ⅳ.R322.8

中国版本图书馆 CIP 数据核字（2003）第 011750 号

图字：01-2002-1722

临床神经解剖学（英文版）

编　　著：Stephen G. Waxman，MD，PhD
出版发行：人民卫生出版社（中继线 67616688）
地　　址：（100078）北京市丰台区方庄芳群园 3 区 3 号楼
网　　址：http://www.pmph.com
E - mail：pmph @ pmph.com
印　　刷：北京市安泰印刷厂
经　　销：新华书店
开　　本：787×1092　1/16　　**印张**：25　　**字数**：880 千字
版　　次：2003 年 4 月第 1 版　2003 年12月第 1 版第 2 次印刷
标准书号：ISBN 7-117-05406-9/R·5407
定　　价：60.00 元

Preface

The brain, more complex than any computer that has ever been invented, is a unique and special organ: It is what makes us human. The science of the brain—neuroscience—has emerged as one of the most exciting fields of research and now occupies a central role as a substrate for clinical medicine. At the heart of neuroscience lies the *structure* of the nervous system: neuroanatomy. An understanding of the nervous system and its anatomy is essential not just to researchers and not just to neurologists and psychiatrists but to clinicians in all subspecialties, because they all will encounter patients with disorders involving the brain, spinal cord, and peripheral nerves. Stroke, for example, is the third most frequent cause of death in industrialized societies; mood disorders such as depression affect more than one person in 10; and dysfunction of the nervous system can be seen in 25% of patients in most general hospitals at some time during their hospital stay. The neuroanatomic basis for many of these disorders is already known, and for other disorders it will soon be discovered.

This book provides a concise but comprehensive and easy-to-remember synopsis of neuroanatomy and of its functional and clinical implications. In this new, 25th edition, each chapter has been extensively revised and carefully focused so that it emphasizes the most important concepts, facts, and structures. As a teacher, researcher, and clinician, I have tried to sculpt this book so that it will provide a resource and learning tool for busy medical students, residents, and students in health-related fields such as physical therapy; for graduate students who need an introduction to neuroanatomy; and for clinicians in practice, for whom minutes are precious. This book is not meant to supplant the longer, more encompassing, and comprehensive handbooks of neuroscience and neuroanatomy. On the contrary, it provides a more manageable and concise overview that presents the *essential aspects of neuroanatomy and its functional and clinical correlations.*

This book is unique in including a section entitled "Introduction to Clinical Thinking," which appears early in the text to introduce the reader to the logical processes involved in *using neuroanatomy as a basis for thinking about the disordered nervous system.* Recognizing that some students remember *patients* better than isolated facts, I have included discussions of clinical correlates and clinical illustrations that synthesize the most important characteristics of patients selected from an extensive clinical experience to help the reader interpret and remember neuroanatomic concepts in terms of *function* and *clinical implications.*

Because much of neuroanatomy has a spatial aspect, this book includes numerous figures. The illustrations have been designed to provide clear, explicit, and memorable representations of important pathways, structures, and mechanisms. Many tables are included, and they have been designed to be as clear and easy to remember as possible. These figures and tables incorporate feedback and suggestions from numerous trainees as well as teachers of neuroanatomy.

The advent of modern neuroimaging has revolutionized the clinical neurosciences, and this book takes full advantage of this technological advance by including numerous computed tomography (CT) and magnetic resonance images (MRIs) of the normal brain and spinal cord, together with functional magnetic resonance images (fMRI) which provides a noninvasive window on brain function. Also included are neuroimaging studies that illustrate common pathological entities that affect the nervous system, including stroke, intracerebral hemorrhage, and tumors of the brain and spinal cord.

As with past editions, I owe a debt of gratitude to many colleagues and friends, especially members of the Department of Neurology at Yale Medical School, who have liberally shared their insights and expertise and have helped to create an environment where learning is *fun*, a motif that I have woven into this book. I hope that readers of this book will join me in finding that neuroanatomy, which provides much of the foundation for both basic neuroscience and clinical medicine, can be enjoyable, memorable, and easily learned.

Stephen G. Waxman, MD, PhD
New Haven, Connecticut
September 2002

Contents

SECTION I
Basic Principles

Fundamentals of the Nervous System

1

The human central nervous system (CNS), smaller and weighing less than most desktop computers, is the most complex and elegant computing device that exists. It receives and interprets an immense array of sensory information, controls a variety of simple and complex motor behaviors, and engages in deductive and inductive logic. The brain can make complex decisions, think creatively, and feel emotions. It can *generalize* and possesses an elegant ability to recognize that cannot be reproduced by even advanced mainframe computers. The human nervous system, for example, can immediately identify a familiar face regardless of the angle at which it is presented. It can carry out all of these demanding tasks in a nearly simultaneous manner.

Given the complexity of the nervous system and the richness of its actions, one might ask whether it can ever be understood. Indeed, neuroscience has begun to provide an understanding, in elegant detail, of the organization and physiology of the nervous system and the alterations in nervous system function that occur in various diseases. This understanding is firmly based on an appreciation of the *structure* of the nervous system and the interrelation between structure and function.

The complexity of the nervous system's actions is reflected by a rich and complex structure—in a sense, the nervous system can be viewed as a complex and dynamic network of interlinked computers. Nevertheless, the anatomy of the nervous system *can* be readily understood. By understanding correlative neuroanatomy (ie, the structure of the nervous system and the implications of that structure for physiology), one can begin to comprehend the myriad actions of the nervous system and the disease processes that interfere with normal function of the nervous system.

GENERAL PLAN OF THE NERVOUS SYSTEM

Main Divisions

A. Anatomy

Anatomically, the human nervous system is a complex of two subdivisions.

1. CNS—The CNS, comprising the brain and spinal cord, is enclosed in bone and wrapped in protective coverings (meninges) and fluid-filled spaces.

2. Peripheral nervous system (PNS)—The PNS is formed by the cranial and spinal nerves (Fig 1–1).

B. Physiology

Functionally, the nervous system is divided into two systems.

1. Somatic nervous system—This innervates the structures of the body wall (muscles, skin, and mucous membranes).

2. Autonomic (visceral) nervous system (ANS)—The ANS contains portions of the central and peripheral systems. It controls the activities of the smooth muscles and glands of the internal organs (viscera) and the blood vessels and returns sensory information to the brain.

Structural Units & Overall Organization

The central portion of the nervous system consists of the **brain** and the elongated **spinal cord** (Fig 1–2 and Table 1–1). The brain has a tiered structure and, from a gross point of view, can be subdivided into the cerebrum, the brain stem, and the cerebellum.

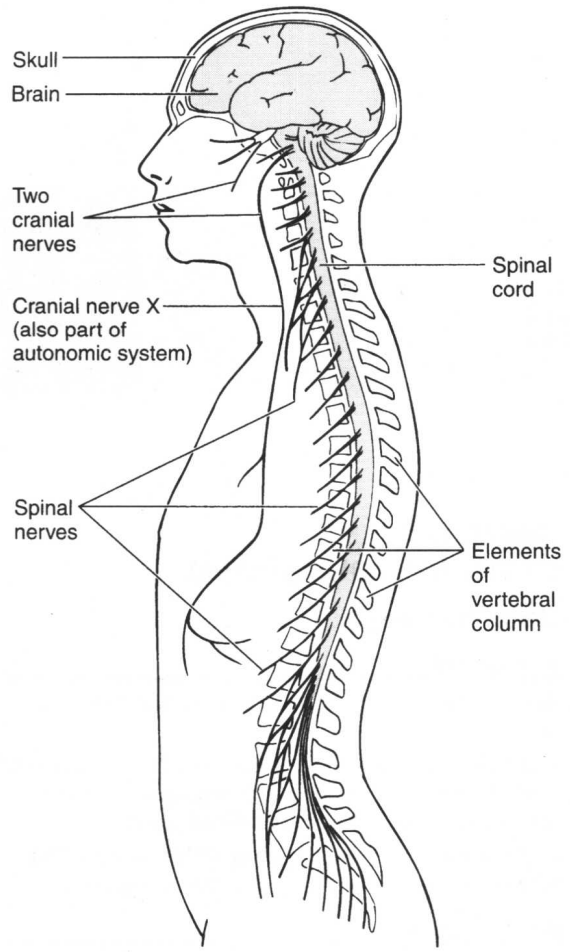

Figure 1–1. The structure of the central nervous system and the peripheral nervous system, showing the relationship between the central nervous system and its bony coverings.

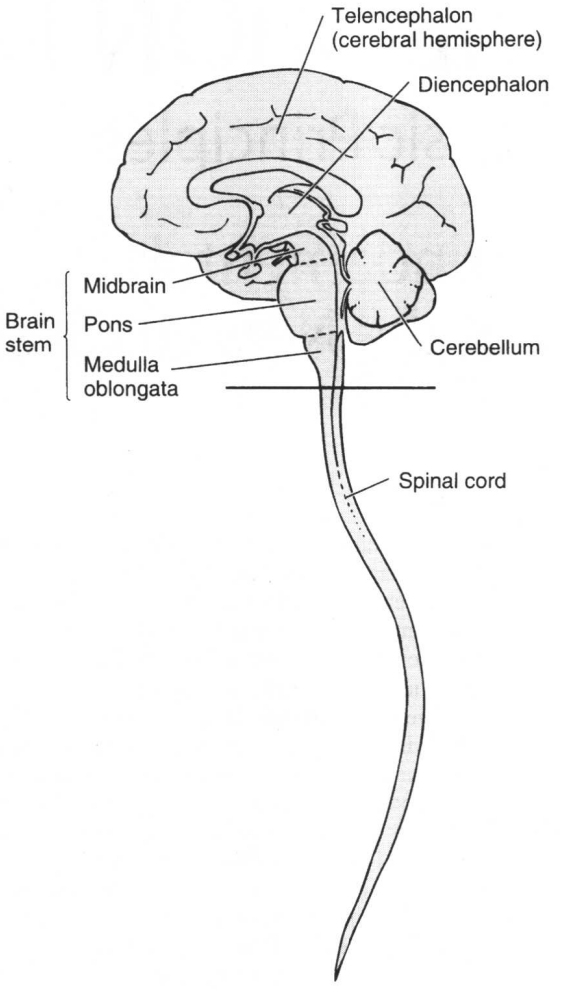

Figure 1–2. The two major divisions of the central nervous system, the brain and the spinal cord, as seen in the midsagittal plane.

The most rostral part of the nervous system (cerebrum, or forebrain) is the most phylogenetically advanced and is responsible for the most complex functions (eg, cognition). More caudally, the brain stem, medulla, and spinal cord serve less advanced, but essential, functions.

The **cerebrum (forebrain)** consists of the **telencephalon** and the **diencephalon;** the telencephalon includes the cerebral cortex (the most highly evolved part of the brain, sometimes called "gray matter"), subcortical white matter, and the basal ganglia, which are gray masses deep within the cerebral hemispheres. The **white matter** carries that name because, in a freshly sectioned brain, it has a glistening appearance as a result of its high lipid-rich myelin content; the white matter consists of myelinated fibers and does not contain neuronal cell bodies or synapses (Fig 1–3). The major subdivisions of the diencephalon are the thalamus and hypothalamus. The **brain stem** consists of the **midbrain (mesencephalon), pons,** and **medulla oblongata.** The **cerebellum** includes the vermis and two lateral lobes. The brain, which is hollow, contains a system of spaces called **ventricles;** the spinal cord has a narrow central canal that is largely obliterated in adulthood. These spaces are filled with cerebrospinal fluid (CSF) (Figs 1–4 and 1–5; see also Chapter 11).

Functional Units

The brain, which accounts for about 2% of the body's weight, contains many billions (perhaps even a trillion)

Table 1–1. Major divisions of the central nervous system.

Brain (encephalon)	Cerebrum (forebrain)	Telencephalon	Cerebral cortex Subcortical white matter Commissures Basal ganglia
		Diencephalon	Thalamus Hypothalamus Epithalamus Subthalamus
	Cerebellum		Cerebellar cortex Cerebellar nuclei
	Brain stem		Midbrain (mesencephalon) Pons Medulla oblongata
Spinal cord	White matter		Dorsal columns Lateral columns Anterior columns
	Gray matter		

of neurons and glial cells (see Chapter 2). The **neurons,** or nerve cells, are specialized cells that receive and send signals to other cells through their extensions (nerve fibers, or **axons**). The information is processed and encoded in a sequence of electrical or chemical steps that occur, in most cases, very rapidly (in milliseconds). Many neurons have relatively large cell bodies and long axons that transmit impulses quickly over a considerable distance. Interneurons, on the other hand, have small cell bodies and short axons and transmit impulses locally. Nerve cells serving a common function, often with a common target, are frequently grouped together into **nuclei.** Nerve cells with common form, function, and connections that are grouped together outside the CNS are called **ganglia.**

Other cellular elements that support the activity of the neurons are the **glial cells,** of which there are several types. Glial cells outnumber neurons 10:1.

Computation in the Nervous System

Nerve cells convey signals to one another at synapses (see Chapters 2 and 3). Chemical transmitters are asso-

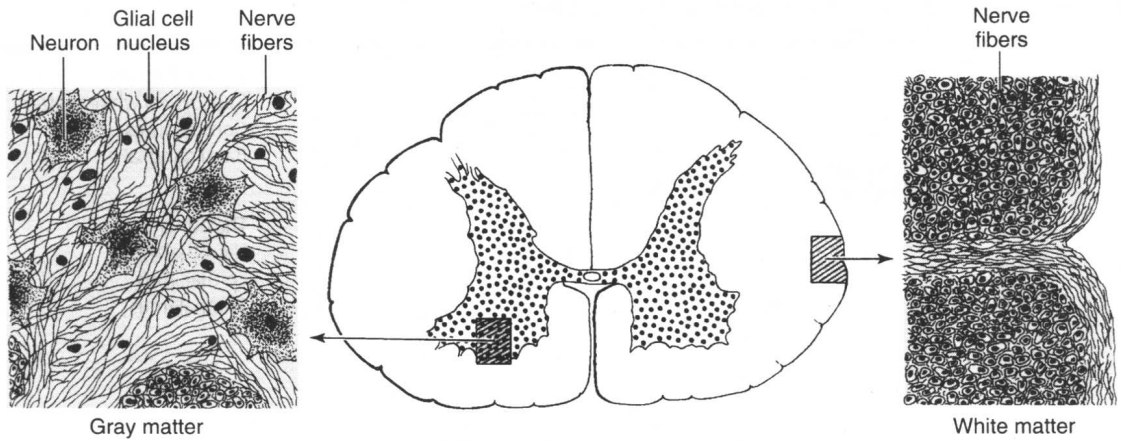

Figure 1–3. Cross section through the spinal cord, showing gray matter (which contains neuronal and glial cell bodies, axons, dendrites, and synapses) and white matter (which contains myelinated axons and associated glial cells). (Reproduced, with permission, from Junqueira LC, Carneiro J, Kelley RO: *Basic Histology,* 9th ed. Appleton & Lange, 1998.)

ciated with the function of the synapse: excitation or inhibition. A neuron may receive thousands of synapses, which bring it information from many sources. By integrating the excitatory and inhibitory inputs from these diverse sources and producing its own message, each neuron acts as an information-processing device.

Some very primitive behaviors (eg, the reflex and unconscious contraction of the muscles around the knee in response to percussion of the patellar tendon) are mediated by a simple **monosynaptic** chain of two neurons connected by a **synapse.** More complex behaviors, however, require larger **polysynaptic** neural circuits in which many neurons, interconnected by synapses, are involved.

Tracts & Commissures

The connections, or pathways, between groups of neurons in the CNS are in the form of fiber bundles, or tracts (**fasciculi**). Aggregates of tracts, as seen in the spinal cord, are referred to as **columns (funiculi).** Tracts may descend (eg, from the cerebrum to the brain stem or spinal cord) or ascend (eg, from the spinal cord

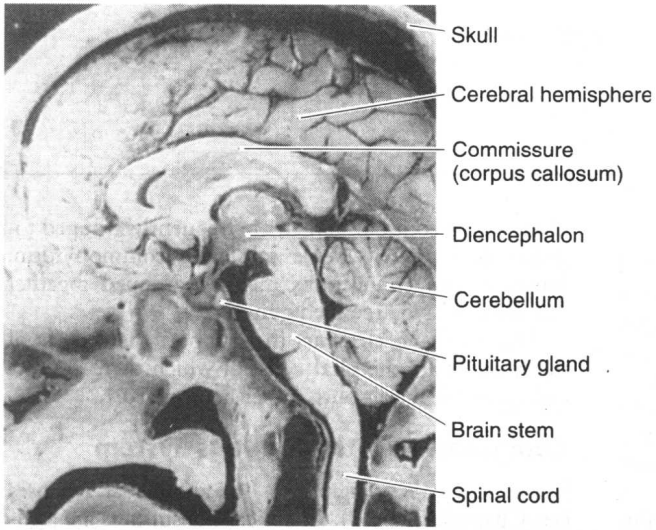

Figure 1–4. Photograph of a midsagittal section through the head and upper neck, showing the major divisions of the central nervous system. (Reproduced, with permission, from deGroot J: *Correlative Neuroanatomy of Computed Tomography and Magnetic Resonance Imagery.* Lea & Febiger, 1984.)

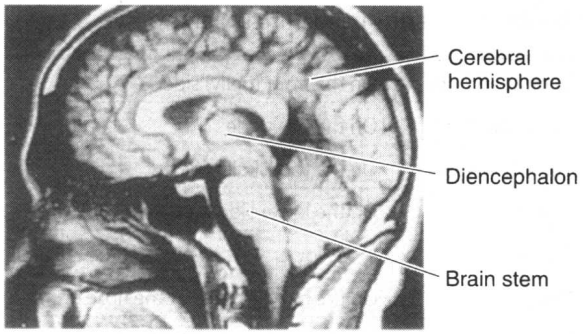

Figure 1–5. Magnetic resonance image of a midsagittal section through the head (short time sequence; see Chapter 22). Compare with Figure 1–2.

to the cerebrum). These pathways are vertical connections that in their course may cross (**decussate**) from one side of the CNS to the other. Horizontal (lateral) connections are called **commissures.**

Multiple tracts connect many parts of the nervous system. For example, multiple ascending and descending tracts connect the PNS and lower spinal centers with the brain. This reflects the fact that the nervous system extracts different aspects of its sensory surround (eg, the shape, weight, and temperature of an object touching the body) and encodes them separately and that it controls specific aspects of motor behavior (posture, muscle tone, delicate movements) using different sets of neurons. The multiplicity of tracts also endows the nervous system with a degree of **redundancy:** After partial destruction of the nervous system, only some functions will be lost; other functions may be retained, increasing the probability that the organism will survive.

Symmetry of the Nervous System

The nervous system is constructed with **bilateral symmetry.** This is most apparent in the cerebrum and cerebellum, which are organized into right and left **hemispheres.** On initial consideration, these hemispheres appear symmetric. Some higher cortical functions such as language are represented more strongly in one hemisphere than in the other, but to gross inspection, the hemispheres have a similar structure. Even in more caudal structures, such as the brain stem and spinal cord, which are not organized into hemispheres, there is bilateral symmetry.

Crossed Representation

Another general theme in the construction of the nervous system is **decussation and crossed representation:** The right side of the brain receives information about, and controls motor function pertaining to, the left side of the world and vice versa. Visual information about the right side of the world is processed in the visual cortex on the left. Similarly, sensation of touch, sensation of heat or cold, and joint position sense from the body's right side are processed in the somatosensory cortex in the left cerebral hemisphere. In terms of motor control, the motor cortex in the left cerebral hemisphere controls body movements that pertain to the right side of the external world. This includes, of course, control of the muscles of the right arm and leg, such as the biceps, triceps, hand muscles, and gastrocnemius. There are occasional exceptions to this pattern of "crossed innervation": For example, the *left* sternocleidomastoid muscle is controlled by the *left* cerebral cortex. However, even this exception makes functional sense: As a result of its unusual biomechanics, contraction of the left sternocleidomastoid rotates the neck to the *right.* Even for the anomalous muscle, then, control of movements relevant to the right side of the world originates in the contralateral left cerebral hemisphere, as predicted by the principle of crossed representation.

There is one major exception to the rule of crossed motor control: As a result of the organization of cerebellar inputs and outputs, each cerebellar hemisphere controls coordination and muscle tone on the *ipsilateral* side of the body (see Chapter 7).

Maps of the World Within the Brain

At each of many levels, the brain maps various aspects of the outside world. For example, consider the dorsal columns (which carry sensory information, particularly with respect to touch and vibration, from sensory endings on the body surface upward within the spinal cord). Axons within the dorsal columns are arranged in an orderly manner, with fibers from the arm, trunk, and leg forming a map that preserves the spatial relationship of these body parts. Within the cerebral cortex, there is also a sensory map (which has the form of a small man and is, therefore, called a homunculus), within the sensory cortex. There are multiple maps of the visual world within the occipital lobes and within the temporal and parietal lobes as well. These maps are called retinotopic because they preserve the geometrical relationships between objects imaged on the retina and thus provide spatial representations of the visual environment within the brain. Each map contains neurons that are devoted to extracting and analyzing information about one particular aspect (eg, form, color, or movement) of the stimulus.

Development

The earliest tracts of nerve fibers appear at about the second month of fetal life; major descending motor tracts appear at about the fifth month. **Myelination**

(sheathing with myelin) of the spinal cord's nerve fibers begins about the middle of fetal life; some tracts are not completely myelinated for 20 years. The oldest tracts (those common to all animals) myelinate first; the corticospinal tracts myelinate largely during the first and second years after birth.

Growing axons are guided to the correct targets during development of the nervous system by extracellular **guidance molecules** (including the **netrins** and **semaphorins**). Some of these act as attractants for growing axons, guiding them toward a particular target. Others act as repellants. There are many types of guidance molecules, probably each specific for a particular type of axon, and they are laid down in gradients of varying concentration. In many parts of the developing nervous system, there is initially an overabundance of young axons, and those that do not reach the correct targets are subsequently lost by a process of pruning.

Although the structural organization of the brain is well established before neural function begins, the maturing brain is susceptible to modification if an appropriate stimulus is applied or withheld during a critical period, which can last only a few days or even less.

PERIPHERAL NERVOUS SYSTEM

The **peripheral nervous system (PNS)** consists of spinal nerves, cranial nerves, and their associated ganglia (groups of nerve cells outside the CNS). The nerves contain nerve fibers that conduct information to (afferent) or from (efferent) the CNS. In general, **efferent** fibers are involved in motor functions, such as the contraction of muscles or secretion of glands; **afferent** fibers usually convey sensory stimuli from the skin, mucous membranes, and deeper structures.

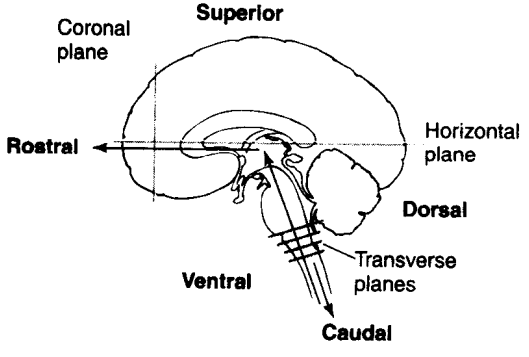

Figure 1–6. Planes (coronal, horizontal, transverse) and directions (rostral, caudal, etc.) frequently used in the description of the brain and spinal cord. The plane of the drawing is the midsagittal.

Table 1–2. Terms used in neuroanatomy.

Ventral, anterior	On the front (belly) side
Dorsal, posterior	On the back side
Superior, cranial	On the top (skull) side
Inferior	On the lower side
Caudal	In the lowermost position (at the tail end)
Rostral	On the forward side (at the nose end)
Medial	Close to or toward the middle
Median	In the middle, the midplane (midsagittal)
Lateral	Toward the side (away from the middle)
Ipsilateral	On the same side
Contralateral	On the opposite side
Bilateral	On both sides

PLANES & TERMS

The planes of section and terms used in neuroanatomy are shown in Figure 1–6 and Table 1–2.

REFERENCES

Barr ML, Kierman JA: *The Human Nervous System,* 4th ed. Harper & Row, 1983.

Brodal A: *Neurological Anatomy,* 3rd ed. Oxford Univ Press, 1981.

Carpenter MC, Sutin J: *Human Neuroanatomy,* 8th ed. Williams & Wilkins, 1983.

Damasio H: *Human Brain Anatomy in Computerized Images.* Oxford Univ Press, 1996.

Finlay BL, Darlington RB: Linked regularities in the development and evolution of mammalian brains. *Science* 1995;268:1570.

Geschwind N, Galaburda AM: *Cerebral Lateralization.* Harvard Univ Press, 1986.

Kandel ER, Schwartz JN, Jessell T: *Principles of Neural Science,* 3rd ed. Appleton & Lange, 1991.

Martin JH: *Neuroanatomy Text & Atlas,* 2nd ed. Appleton & Lange, 1996.

Netter FH: *Nervous System (Atlas and Annotations).* Vol 1: The CIBA Collection of Medical Illustrations. CIBA Pharmaceutical Company, 1983.

Nicholls JG, Martin AR, Wallace BG: *From Neuron to Brain,* 3rd ed. Sinauer, 1992.

Romanes GJ: *Cunningham's Textbook of Anatomy,* 18th ed. Oxford Univ Press, 1986.

Shepherd GM: *Neurobiology,* 2nd ed. Oxford Univ Press, 1988.

Nervous Tissue and Its Cells

2

CELLULAR ASPECTS OF NEURAL DEVELOPMENT

Early in the development of the nervous system, a hollow tube of ectodermal neural tissue forms at the embryo's dorsal midline. The cellular elements of the tube appear undifferentiated at first, but they later develop into various types of neurons and supporting glial cells.

Layers of the Neural Tube

The embryonic neural tube has three layers (Fig 2–1): the **ventricular zone,** later called the **ependyma,** around the lumen (central canal) of the tube; the **intermediate zone,** which is formed by the dividing cells of the ventricular zone (including the earliest radial glial cell type) and stretches between the ventricular surface and the outer (pial) layer; and the external **marginal zone,** which is formed later by processes of the nerve cells in the intermediate zone (Fig 2–1B).

The intermediate zone, or mantle layer, increases in cellularity and becomes gray matter. The nerve cell processes in the marginal zone, as well as other cell processes, become white matter when myelinated.

Differentiation & Migration

The largest neurons, which are mostly motor neurons, differentiate first. Sensory and small neurons, and most of the glial cells, appear later, up to the time of birth. Newly formed neurons may migrate extensively through regions of previously formed neurons. When glial cells appear, they can act as a framework that guides growing neurons to the correct target areas. Because the axonal process of a neuron may begin growing toward its target during migration, nerve processes in the adult brain are often curved rather than straight. The newer cells of the future cerebral cortex migrate from the deepest to the more superficial layers. The small neurons of the incipient cerebellum migrate first to the surface and later to deeper layers, and this process continues for several months after birth.

NEURONS

Neurons vary in size and complexity. For example, the nuclei of one type of small cerebellar cortical cell (granule cell) are only slightly larger than the nucleoli of an adjacent large Purkinje cell. Motor neurons are usually larger than sensory neurons. Nerve cells with long processes (eg, dorsal root ganglion cells) are larger than those with short processes (Figs 2–2 and 2–3).

Some neurons project from the cerebral cortex to the lower spinal cord, a distance of less than 2 ft in infants or 4 ft or more in adults; others have very short processes, reaching, for example, only from cell to cell in the cerebral cortex. These small neurons, with short axons that terminate locally, are called **interneurons.**

Extending from the nerve cell body are usually a number of processes called the **axon** and **dendrites.** Most neurons give rise to a single axon (which branches along its course) and to many dendrites (which also divide and subdivide, like the branches of a tree). The receptive part of the neuron is the **dendrite,** or **dendritic zone** (see Dendrites section). The conducting (propagating or transmitting) part is the axon, which may have one or more collateral branches. The downstream end of the axon is called the **synaptic terminal,** or **arborization.** The neuron's cell body is called the **soma,** or **perikaryon.**

Cell Bodies

The cell body is the metabolic and genetic center of a neuron (see Fig 2–3). Although its size varies greatly in different neuron types, the cell body makes up only a small part of the neuron's total volume.

The cell body and dendrites constitute the receptive pole of the neuron. Synapses from other cells or glial processes tend to cover the surface of a cell body (Fig 2–4).

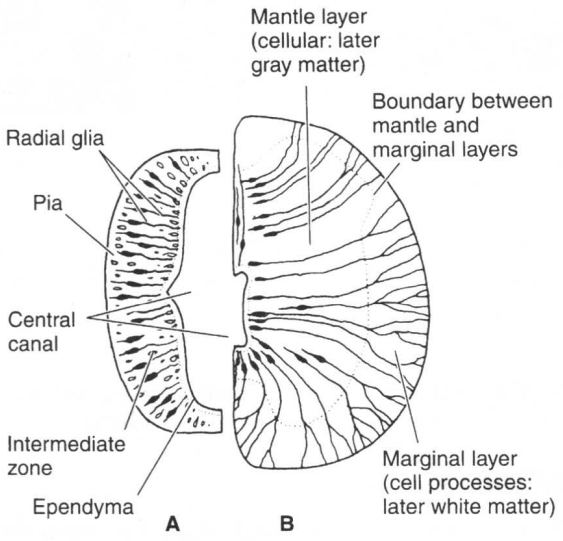

Figure 2–1. Two stages in the development of the neural tube (only half of each cross section is shown). **A:** Early stage with large central canal. **B:** Later stage with smaller central canal.

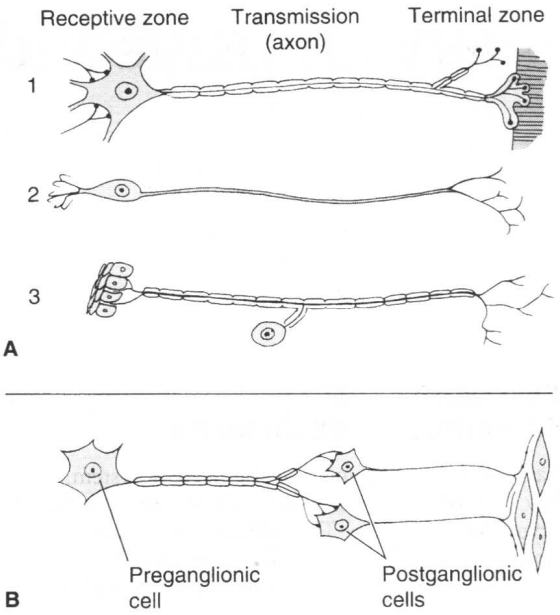

Figure 2–2. Schematic illustration of nerve cell types. **A:** Central nervous system cells: (1) motor neuron projecting to striated muscle, (2) special sensory neuron, and (3) general sensory neuron from skin. **B:** Autonomic cells to smooth muscle. Notice how the position of the cell body with respect to the axon varies.

Dendrites

Dendrites receive incoming synaptic information and thus, together with the cell body, provide the receptive pole of the neuron. Most neurons have many dendrites (see Figs 2–2, 2–3, and 2–5). The receptive surface area of the dendrites is usually far larger than that of the cell body. Because most dendrites are long and thin, they act as resistors, isolating electrical events, such as postsynaptic potentials, from one another (see Chapter 3). The branching pattern of the dendrites can be very complex and determines how the neuron integrates synaptic inputs from various sources. Some dendrites give rise to **dendritic spines,** which are small mushroom-shaped projections that act as fine dendritic branches and receive synaptic inputs.

Axons

A single **axon** arises from most neurons. The axon is a cylindrical tube of cytoplasm covered by a membrane, the **axolemma.** A **cytoskeleton** consisting of **neurofilaments** and **microtubules** runs through the axon. The microtubules provide a framework for fast axonal transport (see Axonal Transport section). Specialized molecular motors (**kinesin** molecules) bind to vesicles containing molecules (eg, neurotransmitters) destined for transport and "walk" via a series of adenosine triphosphate (ATP)-consuming steps along the microtubules.

The axon is a specialized structure that conducts electrical signals from the initial segment (the proximal part of the axon, near the cell body) to the synaptic terminals. The **initial segment** has distinctive morphological features; it differs from both cell body and axon. The axolemma of the initial segment contains a high density of sodium channels, which permit the initial segment to act as a **trigger zone.** In this zone, action potentials are generated so that they can travel along the axon, finally invading the terminal axonal branches and triggering synaptic activity, which impinges on other neurons. The initial segment does not contain Nissl substance (see Fig 2–3). In large neurons, the initial segment arises conspicuously from the **axon hillock,** a cone-shaped portion of the cell body. Axons range in length from a few microns (in interneurons) to well over a meter (ie, in a lumbar motor neuron that projects from the spinal cord to the muscles of the foot) and in diameter from 0.1 μm to more than 20 μm.

A. Myelin

Many axons are covered by **myelin.** The myelin consists of multiple concentric layers of lipid-rich membrane produced by Schwann cells in the peripheral nervous system (PNS) and by oligodendrocytes (a type of glial cell) in the central nervous system (CNS) (Figs 2–6 to 2–9). The myelin sheath is divided into seg-

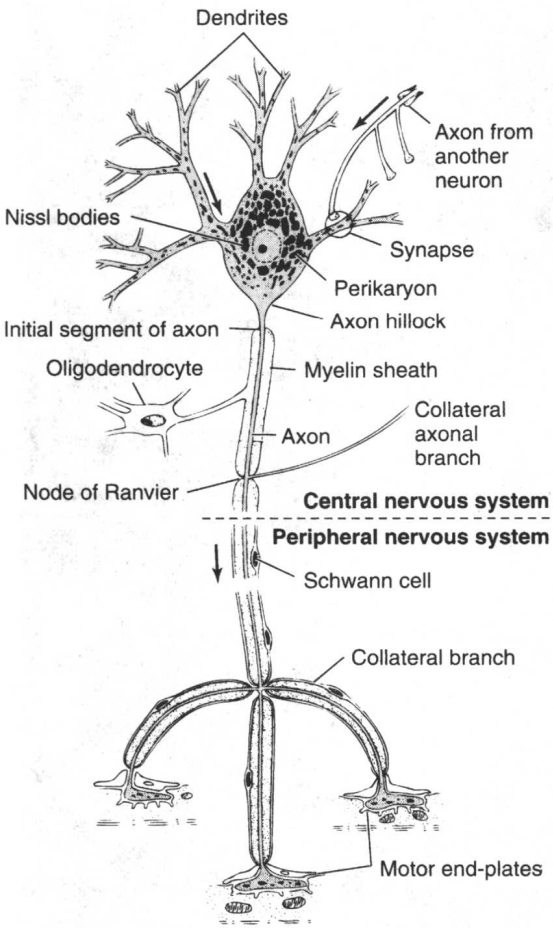

Figure 2–3. Schematic drawing of a Nissl-stained motor neuron. The myelin sheath is produced by oligodendrocytes in the central nervous system and by Schwann cells in the peripheral nervous system. Note the three motor end-plates, which transmit the nerve impulses to striated skeletal muscle fibers. **Arrows** show the direction of the nerve impulse. (Reproduced, with permission, from Junqueira LC, Carneiro J, Kelley RO: *Basic Histology,* 9th ed. Appleton & Lange, 1998.)

ments about 1 mm long by small gaps (1 μm long) where myelin is absent; these are the **nodes of Ranvier.** The smallest axons are unmyelinated. As noted in Chapter 3, myelin functions as an insulator. In general, myelination serves to increase the speed of impulse conduction along the axon.

B. Axonal Transport

In addition to conducting action potentials, axons transport materials from the cell body to the synaptic terminals (**anterograde transport**) and from the synaptic terminals to the cell body (**retrograde transport**). Because ribosomes are not present in the axon, new protein must be synthesized and moved to the axon. This occurs via several types of axonal transport, which differ in terms of the rate and the material transported. Anterograde transport may be fast (up to 400 mm/d) or slow (about 1 mm/d). Retrograde transport is similar to rapid anterograde transport. Fast transport involves microtubules extending through the cytoplasm of the neuron.

An axon can be injured by being cut or severed, crushed, or compressed. After injury to the axon, the neuronal cell body responds by entering a phase called the **axon reaction,** or **chromatolysis.** In general, axons within peripheral nerves can regenerate quickly after they are severed, whereas those within the CNS do not tend to regenerate. The axon reaction and axonal regeneration are further discussed in Chapter 22.

Synapses

Communication between neurons usually occurs from the axon terminal of the transmitting neuron (presynaptic side) to the receptive region of the receiving neuron (postsynaptic side) (Figs 2–5 and 2–10). This specialized interneuronal complex is a **synapse,** or **synaptic junction.** As outlined in Table 2–1, some synapses are located between an axon and a dendrite (**axodendritic** synapses, which tend to be excitatory), whereas others are located between an axon and a nerve cell body (**axosomatic** synapses, which tend to be inhibitory). Still other synapses are located between an axon terminal and another **axon;** these **axoaxonic** synapses modulate transmitter release by the postsynaptic axon. Synaptic transmission permits information from many presynaptic neurons to converge on a single postsynaptic neuron. Some large cell bodies receive several thousand synapses (see Fig 2–4).

Impulse transmission at most synaptic sites involves the release of a chemical transmitter substance (see Chapter 3); at other sites, current passes directly from cell to cell through specialized junctions called **electrical synapses,** or **gap junctions.** Electrical synapses are most common in invertebrate nervous systems, although they are found in a small number of sites in the mammalian CNS. Chemical synapses have several distinctive characteristics: synaptic vesicles on the presynaptic side, a synaptic cleft, and a dense thickening of the cell membrane on both the receiving cell and the presynaptic side (see Fig 2–10). Synaptic vesicles contain neurotransmitters, and each vesicle contains a small packet, or **quanta,** of transmitter. When the synaptic terminal is depolarized (by an action potential in its parent axon), there is an influx of calcium. This calcium influx leads to phosphorylation of a class of