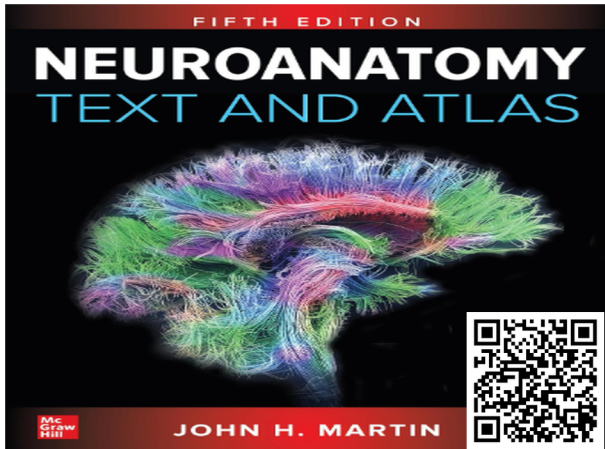


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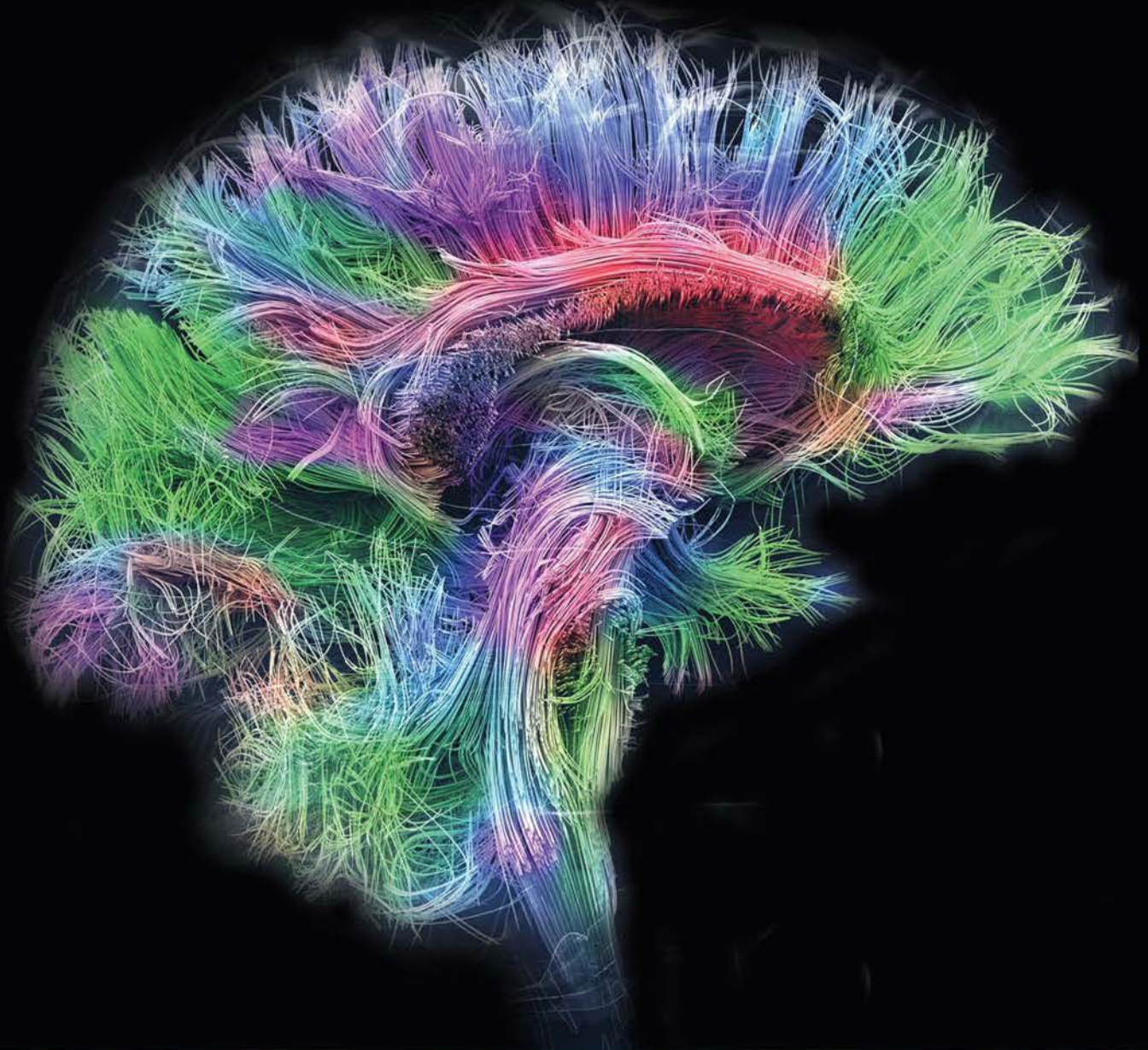
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# Neuroanatomy

## *Text and Atlas*

Fifth Edition

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*For Carol, once more and forever*

# BOX FEATURES

**Box 1–1** Development of the Basic Plan of the Brain and Spinal Cord 10

**Box 1–2** C-shaped Development of the Cerebral Hemisphere 20

**Box 2–1** Anatomical Techniques for Studying the Regional and Microscopic Anatomy of the Human Central Nervous System 34

**Box 2–2** MRI Visualizes the Structure and Function of the Living Human Brain 36

**Box 3–1** Radiological Imaging of Cerebral Vasculature 64

**Box 5–1** The Patterns of Somatic Sensory Impairments After Spinal Cord Injury 108

**Box 6–1** Cranial Nerve and Nuclei Historical Nomenclature 125

**Box 7–1** Lesion of Different Higher-Order Visual Areas Produce Remarkably Specific Perceptual Impairments 161

**Box 9–1** Adult Neurogenesis in the Olfactory Bulb 201

**Box 10–1** Lesions of the Cortical Pathways in the Brain and Spinal Cord Produce Weakness and Paralysis and Increased Spinal Reflexes 222

**Box 11–1** Cortical Control of Swallowing and Dysphagia After Stroke 250

**Box 13–1** Inhibitory Circuitry of the Cerebellum 293

**Box 14–1** Knowledge of the Intrinsic Circuitry of the Basal Ganglia Helps to Explain Hypokinetic and Hyperkinetic Motor Signs 311

**Box 14–2** The Striatum Has a Compartmental Organization 320

**Box 15–1** Lesions in Diverse Locations Can Produce Horner Syndrome 351

**Box 16–1** Circuits of the Hippocampal Formation and Entorhinal Cortex Are Important for Memory 365

# CONTENTS

Preface	xi	Neurons of the Raphe Nuclei Use Serotonin as Their Neurotransmitter	33
Acknowledgments	xiii	<b>Guidelines for Studying the Regional Anatomy and Interconnections of the Central Nervous System</b>	<b>33</b>
Guide to Using This Book	xv	<b>The Spinal Cord Has a Central Cellular Region Surrounded by a Region That Contains Myelinated Axons</b>	<b>33</b>
<b>SECTION I   THE CENTRAL NERVOUS SYSTEM</b>		The Direction of Information Flow Has Its Own Set of Terms	38
<b>1. Organization of the Central Nervous System</b>	<b>3</b>	Surface Features of the Brain Stem Mark Key Internal Structures	38
<b>Neurons and Glia Are the Two Principal Cellular Constituents of the Nervous System</b>	<b>5</b>	The Organization of the Medulla Varies From Caudal to Rostral	39
All Neurons Have a Common Morphological Plan	6	The Pontine Nuclei Surround the Axons of the Corticospinal Tract in the Base of the Pons	40
Neurons Communicate With Each Other at Synapses	7	The Dorsal Surface of the Midbrain Contains the Colliculi	40
Glial Cells Provide Structural Support for Neurons and Additionally Serve a Broad Set of Diverse Functions	7	<b>The Thalamus Transmits Information From Subcortical Structures to the Cerebral Cortex</b>	<b>41</b>
<b>The Nervous System Consists of Separate Peripheral and Central Components</b>	<b>9</b>	<b>The Internal Capsule Contains Ascending and Descending Axons</b>	<b>43</b>
<b>The Spinal Cord Displays the Simplest Organization of All Seven Major Divisions</b>	<b>11</b>	<b>Cerebral Cortex Neurons Are Organized Into Layers</b>	<b>45</b>
<b>The Brain Stem and Cerebellum Regulate Body Functions and Movements</b>	<b>12</b>	The Cerebral Cortex Has an Input-Output Organization	45
<b>The Diencephalon Consists of the Thalamus and Hypothalamus</b>	<b>14</b>	The Cytoarchitectonic Map of the Cerebral Cortex Is the Basis for a Map of Cortical Function	45
<b>The Cerebral Hemispheres Have the Most Complex Shape of All Central Nervous System Divisions</b>	<b>14</b>	<b>3. Vasculature of the Central Nervous System and the Cerebrospinal Fluid</b>	<b>53</b>
The Subcortical Components of the Cerebral Hemispheres Mediate Diverse Motor, Cognitive, and Emotional Functions	14	<b>Neural Tissue Depends on Continuous Arterial Blood Supply</b>	<b>55</b>
The Four Lobes of the Cerebral Cortex Each Have Distinct Functions	15	<b>The Vertebral and Carotid Arteries Supply Blood to the Central Nervous System</b>	<b>55</b>
<b>Cavities Within the Central Nervous System Contain Cerebrospinal Fluid</b>	<b>19</b>	<b>The Spinal and Radicular Arteries Supply Blood to the Spinal Cord</b>	<b>55</b>
<b>The Central Nervous System Is Covered by Three Meningeal Layers</b>	<b>19</b>	<b>The Vertebral and Basilar Arteries Supply Blood to the Brain Stem</b>	<b>57</b>
<b>An Introduction to Neuroanatomical Terms</b>	<b>21</b>	<b>The Internal Carotid Artery Has Four Principal Portions</b>	<b>60</b>
<b>2. Structural and Functional Organization of the Central Nervous System</b>	<b>27</b>	<b>The Anterior and Posterior Circulations Supply the Diencephalon and Cerebral Hemispheres</b>	<b>61</b>
<b>The Dorsal Column–Medial Lemniscal System and Corticospinal Tract Have a Component at Each Level of the Neuraxis</b>	<b>30</b>	Collateral Circulation Can Rescue Brain Regions Deprived of Blood	61
<b>The Modulatory Systems of the Brain Have Diffuse Connections and Use Different Neurotransmitters</b>	<b>31</b>	Deep Branches of the Anterior and Posterior Circulations Supply Subcortical Structures	62
Neurons in the Basal Forebrain and Diencephalon Contain Acetylcholine	32	Different Functional Areas of the Cerebral Cortex Are Supplied by Different Cerebral Arteries	62
The Substantia Nigra and Ventral Tegmental Area Contain Dopaminergic Neurons	33	<b>Cerebral Veins Drain Into the Dural Sinuses</b>	<b>64</b>
Neurons in the Locus Ceruleus Give Rise to a Noradrenergic Projection	33	<b>The Blood-Brain Barrier Isolates the Chemical Environment of the Central Nervous System From That of the Rest of the Body</b>	<b>67</b>

<b>CSF Serves Many Diverse Functions</b>	<b>69</b>
Most of the CSF Is Produced by the Choroid Plexus	71
CSF Circulates Throughout the Ventricles and Subarachnoid Space	71
CSF Is Drawn From the Lumbar Cistern	71
The Dural Sinuses Provide the Return Path for CSF	73

## SECTION II | **SENSORY SYSTEMS**

### **4. Somatic Sensation: Spinal Mechanosensory Systems** **79**

<b>Somatic Sensations</b>	<b>81</b>
<b>Functional Anatomy of the Spinal Mechanosensory System</b>	<b>82</b>
Mechanical Sensations Are Mediated by the Dorsal Column–Medial Lemniscal System	82
<b>Regional Anatomy of the Spinal Mechanosensory System</b>	<b>82</b>
The Peripheral Axon Terminals of Dorsal Root Ganglion Neurons Contain the Somatic Sensory Receptors	82
Dermatomes Have a Segmental Organization	83
The Spinal Cord Gray Matter Has a Dorsoroventral Sensory–Motor Organization	89
Mechanoreceptor Axons Terminate in Deeper Portions of the Spinal Gray Matter and in the Medulla	89
The Ascending Branches of Mechanoreceptive Sensory Fibers Travel in Dorsal Columns	90
The Dorsal Column Nuclei Are Somatotopically Organized	90
The Decussation of the Dorsal Column–Medial Lemniscal System Is in the Caudal Medulla	90
Mechanosensory Information Is Processed in the Ventral Posterior Nucleus	90
The Primary Somatic Sensory Cortex Has a Somatotopic Organization	93
The Primary Somatic Sensory Cortex Has a Columnar Organization	94
Higher-Order Somatic Sensory Cortical Areas Are Located in the Parietal Lobe, Parietal Operculum, and Insular Cortex	95

### **5. Somatic Sensation: Spinal Systems for Pain, Temperature, and Itch** **99**

<b>Functional Anatomy of the Spinal Protective Systems</b>	<b>101</b>
Pain, Temperature, and Itch Are Mediated by the Anterolateral System	101
Visceral Pain Is Mediated by Dorsal Horn Neurons Whose Axons Ascend in the Dorsal Columns	101
<b>Regional Anatomy of the Spinal Protective Systems</b>	<b>105</b>
Small-Diameter Sensory Fibers Mediate Pain, Temperature, and Itch	105
Small-Diameter Sensory Fibers Terminate Primarily in the Superficial Laminae of the Dorsal Horn	105
Anterolateral System Projection Neurons Are Located in the Dorsal Horn and Decussate in the Ventral Commissure	106
Vascular Lesions of the Medulla Differentially Affect Somatic Sensory Function	109
Descending Pain Suppression Pathways Originate From the Brain Stem	110
<b>Several Nuclei in the Thalamus Process Pain, Temperature, and Itch</b>	<b>111</b>
Limbic and Insular Areas Contain the Cortical Representations of Pain, Itch, and Temperature Sensations	113

### **6. Somatic Sensation: Trigeminal and Viscerosensory Systems** **119**

<b>Cranial Nerves and Nuclei</b>	<b>121</b>
Important Differences Exist Between the Sensory and Motor Innervation of Cranial Structures and Those of the Limbs and Trunk	124
There Are Seven Functional Categories of Cranial Nerves	125

Cranial Nerve Nuclei are Organized into Distinctive Columns	126
<b>Functional Anatomy of the Trigeminal and Viscerosensory Systems</b>	<b>127</b>
Separate Trigeminal Pathways Mediate Touch and Pain and Temperature Senses	127
The Viscerosensory System Originates From the Caudal Solitary Nucleus	130

### **Regional Anatomy of the Trigeminal and Viscerosensory Systems** **131**

Separate Sensory Roots Innervate Different Parts of the Face and Mucous Membranes of the Head	131
The Three Trigeminal Nuclei Are Present at All Levels of the Brain Stem	133
The Caudal Solitary and Parabrachial Nuclei Are Key Brain Stem Viscerosensory Integrative Centers	137
Somatic and Visceral Sensation Are Processed by Separate Thalamic Nuclei	137

### **7. The Visual System** **145**

#### **Functional Anatomy of the Visual System** **147**

Anatomically Separate Visual Pathways Mediate Perception and Ocular Reflex Function	147
The Pathway to the Primary Visual Cortex Is Important for Perception of the Form, Color, Location, and Motion of Visual Stimuli	147
The Pathway to the Midbrain Is Important in Voluntary and Reflexive Control of the Eyes	147

#### **Regional Anatomy of the Visual System** **149**

The Visual Field of Each Eye Partially Overlaps	149
Optical Properties of the Eye Transform Visual Stimuli	149
The Retina Contains Three Major Cell Layers	149
Each Optic Nerve Contains All of the Axons of Ganglion Cells in the Ipsilateral Retina	151
The Superior Colliculus Is Important in Ocular Motor Control and Spatial Orientation	153
The Lateral Geniculate Nucleus Transmits Retinotopically Organized Information to the Primary Visual Cortex	154
The Magnocellular, Parvocellular, and Koniocellular Systems Have Differential Laminal Projections in the Primary Visual Cortex	155
The Primary Visual Cortex Has a Laminar and Columnar Organization	156
Higher-Order Visual Cortical Areas Analyze Distinct Aspects of Visual Stimuli	158
Object Recognition Is Transmitted by the Ventral Stream and Spatial Localization and Action, by the Dorsal Stream	160
The Visual Field Changes in Characteristic Ways After Damage to the Visual System	160

### **8. The Auditory System** **167**

#### **Functional Anatomy of the Auditory System** **169**

Parallel Ascending Auditory Pathways Are Involved in Different Aspects of Hearing	169
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#### **Regional Anatomy of the Auditory System** **171**

The Auditory Sensory Organs Are Located Within the Membranous Labyrinth	171
The Cochlear Nuclei Are the First Central Nervous System Relays for Auditory Information	173
The Superior Olivary Complex Processes Stimuli From Both Ears for Horizontal Sound Localization	173
The Olivocochlear System Regulates Auditory Sensitivity in the Periphery	173
Auditory Brain Stem Axons Ascend in the Lateral Lemniscus	175
The Inferior Colliculus Is Located in the Midbrain Tectum	175
The Medial Geniculate Nucleus Is the Thalamic Auditory Relay Nucleus	176
The Primary Auditory Cortex Comprises Several Tonotopically Organized Representations Within Heschl's Gyri	177
Caudal Secondary and Higher-Order Auditory Areas Give Rise to Projections for Distinguishing the Location of Sounds	178

Rostral Secondary and Higher-Order Auditory Areas Give Rise to Projections for Processing the Linguistic Characteristics of Sounds	179
Damage to Frontotemporal Regions in the Left Hemisphere Produces Aphasias	179

## 9. Chemical Senses: Taste and Smell 185

<b>The Gustatory System: Taste</b>	<b>187</b>
The Ascending Gustatory Pathway Projects to the Ipsilateral Insular Cortex	187
<b>Regional Anatomy of the Gustatory System</b>	<b>188</b>
Branches of the Facial, Glossopharyngeal, and Vagus Nerves Innervate Different Parts of the Oral Cavity	188
The Solitary Nucleus Is the First Central Nervous System Relay for Taste	189
The Parvocellular Portion of the Ventral Posterior Medial Nucleus Relays Gustatory Information to the Insular Cortex and Operculum	190
<b>The Olfactory System: Smell</b>	<b>191</b>
The Olfactory Projection to the Cerebral Cortex Does Not Relay Through the Thalamus	191
<b>Regional Anatomy of the Olfactory System</b>	<b>194</b>
The Primary Olfactory Neurons Are Located in the Nasal Mucosa	194
The Olfactory Bulb Is the First Central Nervous System Relay for Olfactory Input	197
The Olfactory Bulb Projects to Structures on the Ventral Brain Surface Through the Olfactory Tract	197
The Primary Olfactory Cortex Receives a Direct Input From the Olfactory Bulb	197
Olfactory and Gustatory Information Interacts in the Insular and Orbitofrontal Cortex for Sensing Flavors	200

## SECTION III | MOTOR SYSTEMS

## 10. Descending Motor Pathways and the Motor Function of the Spinal Cord 209

<b>Functional Anatomy of the Motor Systems for Limb Control and Posture</b>	<b>211</b>
Diverse Central Nervous System Structures Comprise the Motor Systems	211
Many Cortical Regions Are Recruited Into Action During Visually Guided Movements	213
<b>Functional Anatomy of the Descending Motor Pathways</b>	<b>213</b>
Multiple Parallel Motor Control Pathways Originate From the Cortex and Brain Stem	213
Three Rules Govern the Logic of the Organization of the Descending Motor Pathways	215
<b>Two Laterally Descending Pathways Control Limb Muscles</b>	<b>215</b>
Four Medially Descending Pathways Control Axial and Girdle Muscles to Regulate Posture	218
<b>Regional Anatomy of the Motor Systems and the Descending Motor Pathways</b>	<b>220</b>
The Cortical Motor Areas Are Located in the Frontal Lobe	220
The Projection From Cortical Motor Regions Passes Through the Internal Capsule En Route to the Brain Stem and Spinal Cord	224
The Corticospinal Tract Courses in the Base of the Midbrain	225
The Pontine and Medullary Reticular Formation Gives Rise to the Reticulospinal Tracts	225
The Lateral Corticospinal Tract Decussates in the Caudal Medulla	227
The Intermediate Zone and Ventral Horn of the Spinal Cord Receive Input From the Descending Pathways	228

## 11. Cranial Nerve Motor Nuclei and Brain Stem Motor Functions 237

<b>Organization of Cranial Motor Nuclei</b>	<b>239</b>
There Are Three Columns of Cranial Nerve Motor Nuclei	239
Neurons in the Somatic Skeletal Motor Column Innervate Tongue and Extraocular Muscles	239
The Branchiomeric Motor Column Innervates Skeletal Muscles That Develop From the Branchial Arches	239
The Autonomic Motor Column Contains Parasympathetic Preganglionic Neurons	241
<b>The Functional Organization of the Corticobulbar Tract</b>	<b>242</b>
The Cranial Motor Nuclei Are Controlled by the Cerebral Cortex and Diencephalon	242
Bilateral Corticobulbar Tract Projections Innervate the Hypoglossal Nucleus, Trigeminal Nucleus, and Nucleus Ambiguus	243
Cortical Projections to the Facial Motor Nucleus Have a Complex Pattern	243
<b>Regional Anatomy of Cranial Motor Nuclei and Corticobulbar Tract</b>	<b>245</b>
Lesion of the Genu of the Internal Capsule Interrupts the Corticobulbar Tract	246
The Trigeminal Motor Nucleus Is Medial to the Main Trigeminal Sensory Nucleus	246
The Fibers of the Facial Nerve Have a Complex Trajectory Through the Pons	247
The Glossopharyngeal Nerve Enters and Exits From the Rostral Medulla	248
A Level Through the Mid-Medulla Reveals the Locations of Six Cranial Nerve Nuclei	249
The Spinal Accessory Nucleus Is Located at the Junction of the Spinal Cord and Medulla	252

## 12. The Vestibular System and Eye Movements 257

<b>Functional Anatomy of the Vestibular System</b>	<b>259</b>
An Ascending Pathway From the Vestibular Nuclei to the Thalamus Is Important for Perception, Orientation, and Posture	259
The Vestibular System Regulates Blood Pressure in Response to Changes in Body Posture and Gravity	260
The Vestibular Nuclei Have Functionally Distinct Descending Spinal Projections for Axial Muscle Control	262
<b>Functional Anatomy of Eye Movement Control</b>	<b>262</b>
The Extraocular Motor Neurons Are Located in Three Cranial Nerve Motor Nuclei	262
The Vestibuloocular Reflex Maintains Direction of Gaze During Head Movement	262
Voluntary Eye Movements Are Controlled by Neurons in the Frontal Lobe and the Parietal-Temporal-Occipital Association Cortex	262
<b>Regional Organization of the Vestibular and Eye Movement Control Systems</b>	<b>264</b>
Vestibular Sensory Organs Are Contained Within the Membranous Labyrinth	264
The Vestibular Nuclei Have Functionally Diverse Projections	266
The Extraocular Motor Nuclei Are Located Adjacent to the MLF in the Pons and Midbrain	267
Parasympathetic Neurons in the Midbrain Regulate Pupil Size	270
Eye Movement Control Involves the Integrated Functions of Many Brain Stem Structures	271
The Ventral Posterior Nucleus of the Thalamus Transmits Vestibular Information to the Parietal and Insular Cortical Areas	271
Multiple Areas of the Cerebral Cortex Function in Eye Movement Control	273
<b>13. The Cerebellum 277</b>	<b>277</b>
<b>Gross Anatomy of the Cerebellum</b>	<b>279</b>
<b>Functional Anatomy of the Cerebellum</b>	<b>279</b>
The Cerebellum Has a Basic Circuit	279

All Three Functional Divisions of the Cerebellum Display a Similar Input-Output Organization 279

Damage to the Cerebellum Produces Limb Motor Signs on the Same Side as the Lesion 287

**Regional Anatomy of the Cerebellum 289**

Spinal Cord and Medullary Sections Reveal Nuclei and Paths Transmitting Somatic Sensory Information to the Cerebellum 290

The Inferior Olivary Nucleus Is the Only Source of Climbing Fibers 291

The Vestibulocerebellum Receives Input From Primary and Secondary Vestibular Neurons 291

The Pontine Nuclei Provide the Major Input to the Cerebrocerebellum 291

The Intrinsic Circuitry of the Cerebellar Cortex Is the Same for the Different Functional Divisions 291

The Deep Cerebellar Nuclei Are a Major Source of Input to the Brain Stem and Cortical Motor Pathways 295

A Major Part of the Dentate Nucleus Is Important for Nonmotor Functions 295

The Corticopontine Projection Brings Information From Diverse Cortical Areas to the Cerebellum for Motor Control and Nonmotor Functions 295

**14. The Basal Ganglia 303**

**Organization and Development of the Basal Ganglia 305**

Separate Components of the Basal Ganglia Process Incoming Information and Mediate the Output 305

The Complex Shapes and Fractionation of Basal Ganglia Components Are Understood by How the Basal Ganglia Develop 305

**Functional Anatomy of the Basal Ganglia 308**

Direct and Indirect Pathways Form Common Circuits Throughout All Functional Divisions of the Basal Ganglia 308

Knowledge of Basal Ganglia Connections and Neurotransmitters Provides Insight Into Their Function in Health and Disease 310

Functionally Distinct Parallel Circuits Course Through the Basal Ganglia 314

Integration of Information Between the Basal Ganglia Loops Is Needed for Adaptive Behaviors 314

**Regional Anatomy of the Basal Ganglia 314**

The Anterior Limb of the Internal Capsule Separates the Head of the Caudate Nucleus From the Putamen 316

The Three Components of the Striatum Are Located at the Level of the Anterior Horn of the Lateral Ventricle 316

The External Segment of the Globus Pallidus and the Ventral Pallidum Are Separated by the Anterior Commissure 319

The Ansa Lenticularis and the Lenticular Fasciculus Are Output Tracts of the Internal Segment of the Globus Pallidus 319

Lesion of the Subthalamic Nucleus Produces Hemiballism 321

The Substantia Nigra Contains Two Anatomical Divisions 321

The Pedunculopontine Nucleus Is Part of a Parallel Path From the Basal Ganglia to Brain Stem Locomotor Control Centers 322

Stimulation-Based Treatments for Movement and Nonmovement Disorders Demand a Precise Knowledge of the Regional Anatomy of the Basal Ganglia 322

The Vascular Supply of the Basal Ganglia Is Provided by the Middle Cerebral Artery 323

**SECTION IV | INTEGRATIVE SYSTEMS**

**15. The Hypothalamus and Regulation of Bodily Functions 329**

**Gross Anatomy of the Hypothalamus 331**

**Functional Anatomy of the Hypothalamus 333**

Separate Parvocellular and Magnocellular Neurosecretory Systems Regulate Hormone Release From the Anterior and Posterior Lobes of the Pituitary 333

The Parasympathetic and Sympathetic Divisions of the Autonomic Nervous System Originate From Different Central Nervous System Locations 337

Hypothalamic Nuclei Coordinate Integrated Visceral Responses to Body and Environmental Stimuli 340

The Hypothalamus Coordinates Circadian Responses, Sleep, and Wakefulness 342

**Regional Anatomy of the Hypothalamus 344**

The Preoptic Area Influences Release of Reproductive Hormones From the Anterior Pituitary 344

Section Through the Median Eminence Reveals Parvocellular and Magnocellular Nuclei 344

The Posterior Hypothalamus Contains the Mammillary Bodies 346

Descending Autonomic Fibers Course in the Periaqueductal Gray Matter and in the Lateral Tegmentum 346

Nuclei in the Pons Are Important for Bladder Control 347

Dorsolateral Brain Stem Lesions Interrupt Descending Sympathetic Fibers 347

Preganglionic Neurons Are Located in the Lateral Intermediate Zone of the Spinal Cord 350

**16. The Limbic System and Cerebral Circuits for Reward, Emotions, and Memory 357**

**Anatomical and Functional Overview of Neural Systems for Reward, Emotions, and Memory 359**

The Limbic Association Cortex Is Located on the Medial Surface of the Frontal, Parietal, and Temporal Lobes 359

The Hippocampal Formation Plays a Role in Consolidating Explicit Memories 362

The Amygdala Contains Three Major Functional Divisions for Emotions and Their Behavioral Expression 366

The Mesolimbic Dopamine System and Ventral Striatum Are Important in Reward 368

Connections Exist Between Components of the Limbic System and the Three Effector Systems 368

All Major Neurotransmitter Regulatory Systems Have Projections to the Limbic System 370

**Regional Anatomy of Neural Systems for Emotions, Learning, and Memory, and Reward 371**

The Nucleus Accumbens and Olfactory Tubercle Comprise Part of the Basal Forebrain 371

Basal Forebrain Cholinergic Systems Have Diffuse Limbic and Neocortical Projections 371

The Cingulum Courses Beneath the Cingulate and Parahippocampal Gyri 374

The Three Nuclear Divisions of the Amygdala Are Revealed in Coronal Section 374

The Hippocampal Formation Is Located in the Floor of the Inferior Horn of the Lateral Ventricle 376

A Sagittal Cut Through the Mammillary Bodies Reveals the Fornix and Mammillothalamic Tract 378

Nuclei in the Brain Stem Link Telencephalic and Diencephalic Limbic Structures With the Autonomic Nervous System and the Spinal Cord 380

**SECTION V | ATLAS**

**Atlas I: Surface Topography of the Central Nervous System 387**

**Atlas II: Myelin-Stained Sections Through the Central Nervous System 403**

Answers to Clinical Cases 467

Answers to Study Questions 473

Glossary 479

Index 505

# PREFACE

Neuroanatomy plays a crucial role in the health science curriculum by preparing students to understand the anatomical basis of neurology and psychiatry. Imaging the human brain, in both the clinical and research setting, helps us to identify its basic structure and connections. And, when the brain becomes damaged by disease or trauma, imaging localizes the extent of the injury. Functional imaging helps to identify the parts of the brain that become active during our thoughts and actions, and reveals brain regions where drugs act to produce their neurological and psychiatric effects. Complementary experimental approaches in animals—such as mapping neural connections, localizing particular neuroactive chemicals within different brain regions, and determining the effects of lesioning or inactivating a brain region—provide the neuroscientist with the tools to study the biological substrates of normal and disordered behavior. To interpret this wealth of clinical and basic science information requires a high level of neuroanatomical competence.

Knowledge of human neuroanatomy is becoming increasingly more important for procedures to treat central nervous system diseases. Therapeutic electrophysiological interventions target specific brain regions, such as deep brain stimulation (DBS) of the basal ganglia for Parkinson disease. Interventional neuroradiology is a chosen approach for treating many vascular abnormalities, such as repair of arterial aneurysms. Surgery to resect a portion of the temporal lobe is the treatment of choice to reduce the incidence of seizures for many patients with epilepsy. Neurosurgeons routinely use high-resolution imaging tools to characterize the functions and even the connections of regions surrounding tumors, to resect the tumor safely and minimize risk of loss of speech or motor function. Mathematical modeling of brain tissue characteristics based on high-resolution MRI is used to guide placement of surface electrodes for transcranial magnetic and direct current electric stimulation. Each of these innovative approaches clearly requires that the clinical team have a sufficient knowledge of functional neuroanatomy—that is, to have knowledge of brain functions and in which structures these functions are localized—to design and carry out these tasks. And this demand for knowledge of brain structure, function, and connectivity will only be more important in the future as higher-resolution imaging and more effective interventional approaches are developed to repair the damaged brain.

Neuroanatomy helps to provide key insights into disease by providing a bridge between molecular and clinical neural science. We are learning the genetic and molecular bases for many neurological and psychiatric diseases, such as amyotrophic lateral sclerosis, Huntington disease, and schizophrenia. Localizing defective genes to particular brain regions, neural circuits, and even neuron and glial cell classes helps to further our understanding of how pathological changes in brain structure alter brain function. And this knowledge, in turn, will hopefully lead to breakthroughs in treatments and even cures.

An important goal of *Neuroanatomy: Text and Atlas* is to prepare the reader for interpreting the new wealth of human brain images—structural, functional, and connectivity—by developing an understanding of the anatomical localization of brain functions. To provide a workable focus, this book is largely restricted to the central nervous system. It takes a traditional approach to gaining neuroanatomical competence: Because the basic imaging picture is a two-dimensional slice through the brain (e.g., CT or MRI scan), the locations of structures and consideration of their functions are examined on two-dimensional myelin-stained sections through the human central nervous system.

All chapters have been revised for the fifth edition of *Neuroanatomy: Text and Atlas* to reflect advances in neural science since the last edition, with many new full color illustrations. Designed as a self-study guide and resource for information on the structure and function of the human central nervous system, this book can serve as both text and atlas for an introductory laboratory course in human neuroanatomy.

For over 30 years, both at Columbia University's College of Physicians and Surgeons and now at the City University of New York's Medical School, we use this book in conjunction with a series of neuroanatomy laboratory exercises during the neuroscience/neurology-psychiatry teaching block in the curriculum. Rather than presenting the material in a traditional lecture format, we have successfully taught neuroanatomy in a dynamic small group learning environment. Supplemented with use of brain models and specimens, neuroanatomy small group sessions complement neural science, neurology, and psychiatry lecture material and round-out medical, graduate, and allied health science students' learning experience.

The organization of *Neuroanatomy: Text and Atlas* continues to parallel that of *Principles of Neural Science*, edited by Eric R. Kandel, Steven A. Siegelbaum, Sarah Mack, and John Koester (McGraw Hill). Like *Principles of Neural Science*, *Neuroanatomy: Text and Atlas* is aimed at medical students, and graduate students in neuroscience, biology, and psychology programs. The content of many of the chapters is geared to dental students, such as a chapter focus on the trigeminal system,

as well as physical therapy and occupational therapy students by considering the motor systems in detail. *Neuroanatomy: Text and Atlas* is also being used by neurology and neurosurgery residency programs, as part of their didactic learning experiences and board certification review courses.

**John H. Martin**

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# GUIDE TO USING THIS BOOK

*Neuroanatomy: Text and Atlas* takes a combined regional and functional approach to teaching neuroanatomy: Knowledge of the spatial interrelations and connections between brain regions is developed in relation to the functions of the brain's various components. The book first introduces the major concepts of central nervous system organization. Subsequent chapters consider neural systems subserving particular sensory, motor, and integrative functions. At the end of the book is an atlas of surface anatomy of the brain and myelin-stained histological sections, and a glossary of key terms and structures.

Each chapter begins with a clinical case to illustrate the connections and function of the key material. There are key questions in the case that the reader can answer based primarily on the chapter readings, but also on prior chapter material. Chapters also end with a series of multiple choice review questions. Answers both to the case and review questions are at the back of the book. Material on central nervous system development is included in the relevant individual chapters.

## Overview of Chapters

The general structural organization of the mature central nervous system is surveyed in Chapter 1. This chapter also introduces neuroanatomical nomenclature and fundamental histological and imaging techniques for studying brain structure and function. The three-dimensional shapes of key deep structures are also considered in this chapter. The functional organization of the central nervous system is introduced in Chapter 2. This chapter considers how different neural circuits, spanning the entire central nervous system, serve particular functions. The circuits for touch perception and voluntary movement control are used as examples. The major neurotransmitter systems are also discussed.

Central nervous system vasculature and cerebrospinal fluid are the topics of Chapter 3. By considering vasculature early in the book, the reader can better understand why particular functions can become profoundly disturbed when brain regions are deprived of nourishment. These three chapters are intended to provide a synthesis of the basic concepts of the structure of the central nervous system and its functional architecture. A fundamental neuroanatomical vocabulary is also established in these chapters.

The remaining 13 chapters examine the major functional neural systems: sensory, motor, and integrative. These chapters reexamine the views of the surface and internal structures of the central nervous system presented in the introductory chapters, but now from the perspective of the different functional neural systems. As these latter chapters on functional brain architecture unfold, the reader gradually builds a neuroanatomical knowledge of the regional and functional organization of the spinal cord and brain, one system at a time.

These chapters on neural systems have a different organization from that of the introductory chapters: Each is divided into two parts, functional and regional neuroanatomy. The initial part, on functional neuroanatomy, considers how the brain regions that comprise the particular neural system work together to produce their intended functions. This part of the chapter presents an overall view of function in relation to structure before considering the detailed anatomical organization of the neural system. Together with descriptions of the functions of the various components, diagrams illustrate each system's anatomical organization, including key connections that help to show how the particular system accomplishes its tasks. Neural circuits that run through various divisions of the brain are depicted in a standardized format: Representations of myelin-stained sections through selected levels of the spinal cord and brain stem are presented with the neural circuit superimposed.

Regional neuroanatomy is emphasized in the latter part of the chapter. Here, structures are depicted on myelin-stained histological sections through the brain, as well as magnetic resonance images (MRIs). These sections reveal the locations of major pathways and neuronal integrative regions. Typically, this part examines a sequence of myelin-stained sections ordered according to the flow of information processing in the system. For example, coverage of regional anatomy of the auditory system begins with the ear, where sounds are received and initially processed, and ends with the cerebral cortex, where our perceptions are formulated. In keeping with the overall theme of the book, the relation between the structure and the function of discrete brain regions is emphasized.

Emphasis is placed on the close relationship between neuroanatomy and neuroradiology especially through use of MRI scans. These scans are intended to facilitate the transition from learning the actual structure of the brain, as revealed by

histological sections, to that which is depicted on radiological images. This is important in learning to “read” the scans, an important clinical skill. MRI scans are presented either using the radiological convention of showing the ventral surface of the brain up or, when the focus is learning detailed regional anatomy, showing the ventral surface down together with corresponding myelin-stained sections. It should be recognized that there is no substitute for actual stained brain sections for developing an understanding of regional anatomy and localization of function. This is because current MRI resolution is not sufficient to reveal the breadth of brain and spinal cord structures whose functions need to be considered.

### Atlas of the Central Nervous System

This book’s atlas, in two parts, offers a complete reference of anatomical structure. The first part presents key views of the surface anatomy of the central nervous system. This collection of drawings is based on actual specimens but emphasizes common features. Thus, no single brain has precisely the form illustrated in the atlas. The second part of the atlas presents a complete set of photographs of myelin-stained sections through the central nervous system in three anatomical planes.

With few exceptions, the same surface views and histological sections used in the atlas are also present in the chapters. In this way, the reader does not have to cope with anatomical variability and is thus better able to develop a thorough understanding of a limited, and sufficiently complete, set of materials. Moreover, brain views and histological sections shown in the chapters have identified only the key structures and those important for the topics discussed. In the atlas, all illustrations are comprehensively labeled as a reference. The atlas also serves as a useful guide during a neuroanatomy laboratory.

### Didactic Boxes

Selected topics that complement material covered in the chapters are presented in boxes. In many of the boxes, a new perspective on neuroanatomy is presented, one that has emerged only recently from research. The neuroscience community is enthusiastic that many of these new perspectives may help explain changes in brain function that occur following brain trauma or may be used to repair the damaged nervous system.

### Clinical Cases

Each chapter begins with a clinical case, chosen to highlight a fascinating clinical feature of the neural system discussed in the chapter. Whereas some of these cases are rare and not apt to be seen in routine medical practice, they show how perception, motor behavior, or personality and emotions can change after a stroke or tumor damages the brain, or how brain structure and function change after a particular gene mutation. The case description is followed by an explanation of what structures and neural systems are damaged that produce the neurological signs. Questions are posed that can be answered on the basis of reading the case explanations and the chapter text. Detailed answers are provided at the end of the book.

### Study Questions

Each chapter ends with a set of study questions. Answers are provided at the end of the book. A brief explanation of the more integrative and difficult questions also is provided.

### Glossary

The glossary contains a listing of key terms and structures. Typically, these terms are printed in boldface within the chapters. Key terms are defined briefly in the context of their usage in the chapters. Key structures are identified by location and function.

### Additional Study Aids

This book offers three features that can be used as aids in learning neuroanatomy initially, as well as in reviewing for examinations, including professional competency exams:

- Summaries at the end of each chapter, which present concise descriptions of key structures in relation to their functions.
- A glossary of key terms.
- The atlas of key brain views and myelin-stained histological sections, which juxtapose unlabeled and labeled views. The unlabeled image can also be used for self-testing, such as for structure identification.

These study aids are designed to help the reader assimilate efficiently and quickly the extraordinary amount of detail required to develop a thorough knowledge of human neuroanatomy.

# The Central Nervous System



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# Organization of the Central Nervous System

# 1

## CLINICAL CASE | 79-Year-Old Man With Memory Impairment

A 79-year-old man has become forgetful, often misplacing items at home, and sometimes is confused when paying for his groceries. His family reports that his forgetfulness seems to be getting worse. On neurological examination, he reports the correct date and knows where he is and why he is there; he has normal speech. However, he is unable to recall three unrelated words 5 minutes after correctly repeating them. When asked to perform simple addition and subtraction, he is slow and has difficulty. His mental status was further evaluated by neuropsychological testing, which revealed additional cognitive impairments.

Magnetic resonance images (MRIs) of the patient and a healthy control are presented (Figure 1–1A 1–4, B1–4). In these images, which were obtained using a particular MRI protocol termed T1 weighting, white and gray matter of the brain appear as different shades of gray and cerebrospinal fluid, black. Cranial fatty substances (eg, in skin and the bony orbits) are white. Note how the ventricles, which are fluid-filled cavities, are thin in the healthy brain (right column), but dilated in the brain of the patient (left column). Note also how the gray and white matter are both thick in the healthy brain and thinner in the patient's brain. The hippocampal formation (Figures 1–1A4, B4, 1–10A; see Chapter 16) also is atrophic in the patient's brain. The generalized cortical atrophy and ventricular enlargement are also apparent on the other MRIs.

The patient died several years later after developing severe dementia. At autopsy, his brain was found to show clear evidence of degeneration compared with the brain from a healthy person (A5, B5). The gyri of the cerebral cortex are narrow, and the sulci are widened. By contrast, the external characteristics of the brain stem and cerebellum were unremarkable.

You should try to answer the following questions based on your reading of the chapter and inspection of the images. Note that the description of key neurological signs that follow the questions also will provide the answers.

1. Why is the ventricular system affected, even though it is a non-neuronal structure?
2. Are some brain areas more severely affected than others in the patient?

## CHAPTER CONTENTS

### Neurons and Glia Are the Two Principal Cellular Constituents of the Nervous System

- All Neurons Have a Common Morphological Plan
- Neurons Communicate With Each Other at Synapses
- Glial Cells Provide Structural Support for Neurons and Additionally Serve a Broad Set of Diverse Functions

### The Nervous System Consists of Separate Peripheral and Central Components

#### The Spinal Cord Displays the Simplest Organization of All Seven Major Divisions

#### The Brain Stem and Cerebellum Regulate Body Functions and Movements

#### The Diencephalon Consists of the Thalamus and Hypothalamus

#### The Cerebral Hemispheres Have the Most Complex Shape of All Central Nervous System Divisions

- The Subcortical Components of the Cerebral Hemispheres Mediate Diverse Motor, Cognitive, and Emotional Functions
- The Four Lobes of the Cerebral Cortex Each Have Distinct Functions

### Cavities Within the Central Nervous System Contain Cerebrospinal Fluid

#### The Central Nervous System Is Covered by Three Meningeal Layers

#### An Introduction to Neuroanatomical Terms

#### Box 1–1. Development of the Basic Plan of the Brain and Spinal Cord

#### Box 1–2. C-shaped Development of the Cerebral Hemisphere

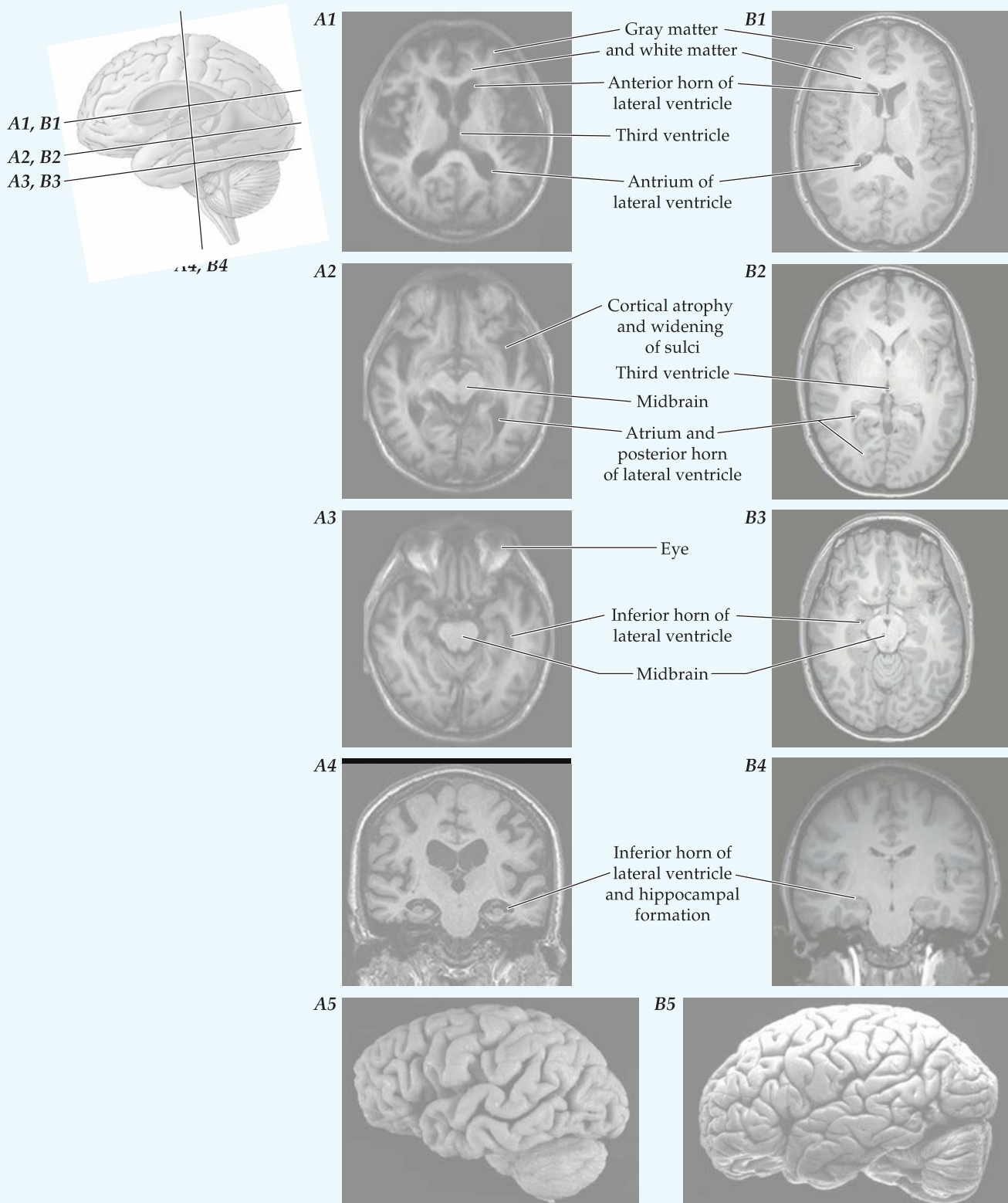
#### Summary

#### Selected Readings

#### Additional References

3. Among the various brain regions affected by the neuropathological process, which is most closely associated with the patient's memory impairment?
4. Autopsy revealed that the density of acetylcholine-containing neurons in a part of the forebrain was severely reduced in the patient. What impact might this have on the function of cortical neurons?
5. At autopsy it was discovered that the patient had large accumulations of amyloid plaques, which contain beta amyloid protein, as well as neurofibrillary tangles, which consist of an abnormal form of the microtubule-associated protein tau. What is the significance of these neuropathological findings?

—Continued next page



**FIGURE 1-1.** MRIs (transverse plane, 1-3; coronal plane, 4) from a person with Alzheimer disease (A) and a healthy person (B). The brain views (5) show generalized atrophy in Alzheimer disease. The MRIs (1-4) show cortical atrophy and ventricular enlargement. The MRIs are T1 images; brain tissues are shades of gray and cerebrospinal fluid, black. (A1, A2, A3, Images reproduced with permission from Dr. Frank Galliard, Radiopaedia.com. A4, Image courtesy of The Dementia Research Center, UCL Institute of Neurology. A5, Image courtesy of Dr. Mony J de Leon [NYU School of Medicine], Dr. Jerzy Wegiel [Institute for Basic Research], and Dr. Thomas Wisniewski [NYU School of Medicine]; NIH Alzheimer's Disease Center P30 AG08051.)

## Conclusion

The patient had Alzheimer disease, which is a neurodegenerative disease. The disease produced profound impairments of cognition, including memory disturbances, and widespread degeneration of the cerebral cortex.

## Key neurological signs and corresponding damaged brain structures

### Brain of person with Alzheimer disease and healthy brain

No description is necessary; the amount and extent of cortical atrophy is obvious in the brain of the person who had Alzheimer disease (part A5). Cortical atrophy is accompanied by atrophy in subcortical structures as well. Because the volume of the skull is fixed, as brain tissues decrease in volume, there is a corresponding increase in ventricular volume. Thus, ventricular enlargement is a consequence of loss of neural tissue.

### MRIs

Both the generalized cortical atrophy and ventricular enlargement can be seen on MRIs of the brain. A superior-to-inferior sequence of three images in the transverse plan (see insets) is shown. The MRI in part 1 slices through the anterior horn and atrium of the lateral ventricles, where enlargement is

enormous. Because of the extensive cortical atrophy, the cortical sulci are wider and filled with more cerebrospinal fluid. Note the region around lateral sulcus and insular cortex (Figure 1–1A1, where the mixture of a greater amount of cerebrospinal fluid and thinned cortex produces a large dark region. The inset in Figure 1–11A illustrates the insular cortex. The hippocampal formation is key to consolidation of short-term to long-term memory (see Chapter 16). Its reduction in Alzheimer disease, together with degeneration of temporal lobe cortex, leaves a gaping hole in the temporal lobe. Hippocampal degeneration can explain why the patient has poor memory. Although not visible on these images, a small nucleus on the inferior brain surface, the basal nucleus, is severely affected early in Alzheimer disease. This nucleus contains neurons that use the excitatory neurotransmitter acetylcholine. These neurons project widely throughout the cortex, and with their loss, many cortical neurons are deprived of excitatory input. This, together with the gross degeneration, helps to explain the cognitive impairments in the patient. These images also reveal that the brain stem is not grossly affected. The sizes of the midbrain (parts A2–A3 and B2–B3) and pons (parts A5 and B5) appear normal.

### Reference

Brust JCM. *The Practice of Neural Science*. New York, NY: McGraw-Hill; 2000.

The human nervous system carries out an enormous number of functions by means of many subdivisions. Indeed, the brain's complexity has traditionally made the study of neuroanatomy a demanding task. This task can be greatly simplified by approaching the study of the nervous system from the dual perspectives of its regional and functional anatomy. **Regional neuroanatomy** examines the spatial relations between brain structures within a portion of the nervous system. Regional neuroanatomy defines the major brain divisions as well as local, neighborhood relationships within the divisions. In contrast, **functional neuroanatomy** examines those parts of the nervous system that work together to accomplish a particular task, for example, visual perception. Functional systems are formed by specific neural connections within and between regions of the nervous system; connections that form complex neural circuits. A goal of functional neuroanatomy is to develop an understanding of the neural circuitry underlying behavior. By knowing regional anatomy together with the functions of particular brain structures, the clinician can determine the location of nervous system damage in a patient who has a particular neurological impairment and, in many cases, a psychiatric impairment. Combined knowledge of what structures do and where they are located is essential for a complete understanding of nervous system organization. The term *neuroanatomy* is

therefore misleading because it implies that knowledge of structure is sufficient to master this discipline. Indeed, in the study of neuroanatomy, structure and function are tightly interwoven—so much so that they should not be separated. The interrelationships between structure and function underlie **functional localization**, a key principle of nervous system organization.

This chapter examines the organization of the nervous system and the means to study it by developing the vocabulary to describe its regional anatomy. First, the cellular constituents of the nervous system are described briefly. Then the chapter focuses on the major regions of the nervous system and the functions of these regions. This background gives the reader insight into functional localization.

## Neurons and Glia Are the Two Principal Cellular Constituents of the Nervous System

The nerve cell, or **neuron**, is the functional cellular unit of the nervous system. Neuroscientists strive to understand the myriad functions of the nervous system partly in terms of the interconnections between neurons. The other major cellular constituent of the nervous system is the neuroglial cell, or **glia**. Glia, once thought only to provide structural and metabolic support for neurons, are now recognized also to be important

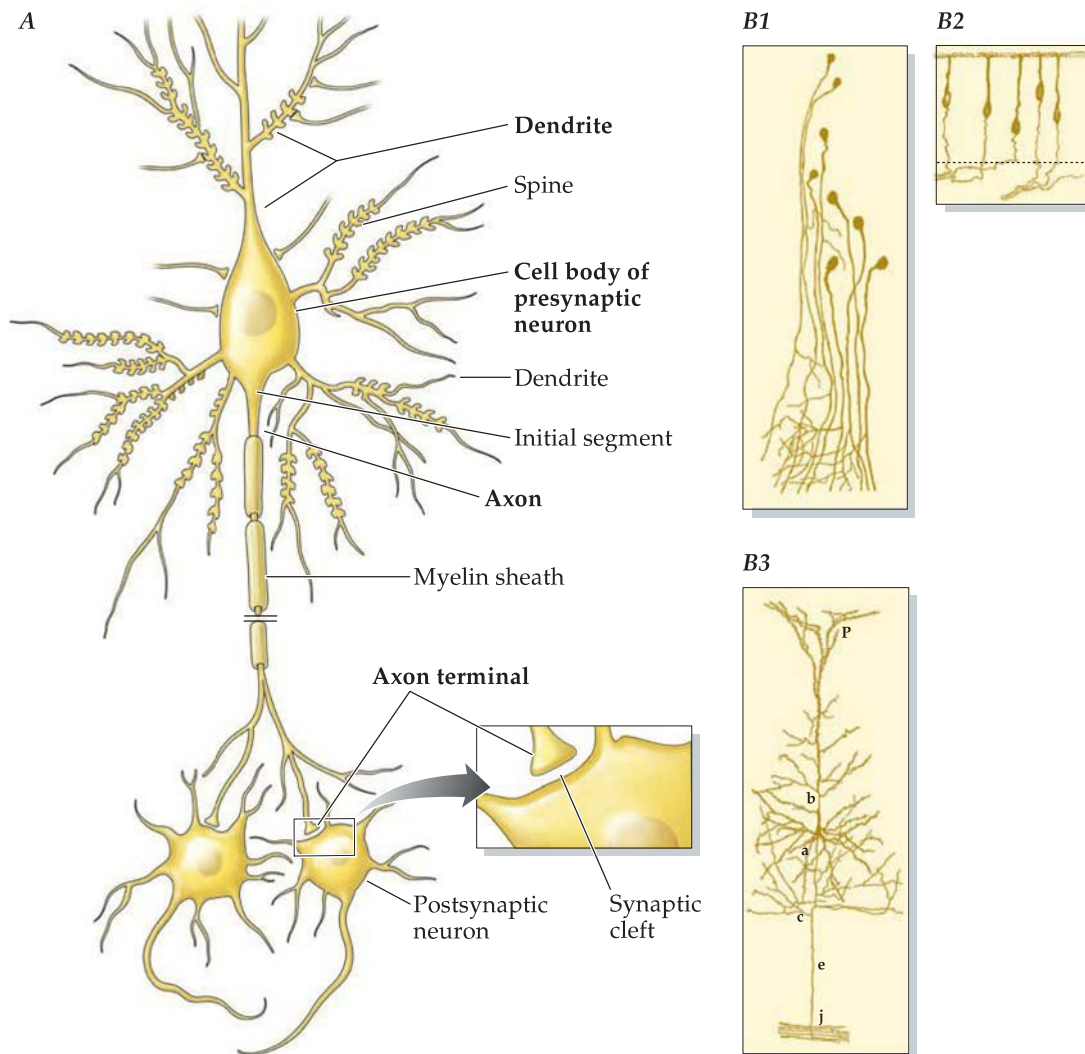
players with neurons in diverse brain functions, such as neural circuit development, learning, and the nervous system's response to injury.

### All Neurons Have a Common Morphological Plan

It is estimated that there are about 100 billion neurons in the adult human brain. Although neurons come in different shapes and sizes, each has four morphologically specialized regions with particular functions: dendrites, cell body, axon, and axon terminals (Figure 1–2A). **Dendrites** receive information from other neurons. The **cell body** contains the nucleus and cellular organelles critical for the neuron's survival and function. The cell body also receives information from other neurons and serves important integrative functions. The **axon** conducts information, which is encoded in the form of action potentials, to the **axon terminal**. Connections between two neurons in a neural circuit are made by the axon terminals of one and the dendrites and cell body of the other, at the synapse (discussed below).

Despite a wide range of morphology, we can distinguish three classes of neuron based on the configuration of their dendrites and axons: unipolar, bipolar, and multipolar (Figure 1–2B). These neurons were drawn by the distinguished Spanish neuroanatomist and Nobel laureate Santiago Ramón y Cajal at the beginning of the twentieth century. **Unipolar neurons** are the simplest in shape (Figure 1–2B1). They have no dendrites; the cell body of unipolar neurons receives and integrates incoming information. A single axon, which originates from the cell body, gives rise to multiple processes at the terminal. In the human nervous system, unipolar neurons are the least common. They control exocrine gland secretions and smooth muscle contractility.

**Bipolar neurons** have two processes that arise from opposite poles of the cell body (Figure 1–2B2). The flow of information in bipolar neurons is from one of the processes, which function like a dendrite, across the cell body to the other process, which functions like an axon. A bipolar neuron subtype is a



**FIGURE 1–2. Neurons are the functional cellular unit of the nervous system.** **A.** A schematic nerve cell is shown, illustrating the dendrites, cell body, and axon. Dendritic spines are located on the dendrites. These are sites of excitatory synapses. Inhibitory synapses are located on the shaft of the dendrites, the cell body, and the initial segment. The axon can be seen to emerge from the cell body. The presynaptic terminals of the neuron are shown synapsing on the cell bodies of the postsynaptic neurons. The inset shows the spatial relations of three components of the synapse: the presynaptic axon terminal, the synaptic cleft, and the postsynaptic neuron. **B.** Selected examples of three neuron classes: (**B1**) unipolar, (**B2**) bipolar, and (**B3**) multipolar. (**A**, Adapted from Kandel ER, Schwartz JH, Jessell TM, eds. *Principles of Neural Science*. 4th ed. New York, NY: McGraw-Hill, 2000. **B**, Reproduced with permission from Cajal SR. *Histologie du système nerveux de l'homme et des vertébrés*. 2 vols. Maloigne, 1909–1911.)

pseudounipolar neuron (see Figure 6–3 top). During development the two processes of the embryonic bipolar neuron fuse into a single process in the pseudounipolar neuron, which bifurcates a short distance from the cell body. Many sensory neurons, such as those that transmit information about odors or touch to the brain, are bipolar and pseudounipolar neurons.

**Multipolar neurons** feature a complex array of dendrites on the cell body and a single axon that branches extensively (Figure 1–2B3). Most of the neurons in the brain and spinal cord are multipolar. Multipolar neurons that have long axons, with axon terminals located in distant sites, are termed **projection neurons**. Projection neurons mediate communication between regions of the nervous system and between the nervous system and peripheral targets, such as striated muscle cells. The neuron in Figure 1–2B3 is a particularly complex projection neuron. The terminals of this neuron are not shown because they are located far from the cell body. For this type of neuron in the human, the axon may be up to 1 m long, about 50,000 times the width of the cell body. Other multipolar neurons, commonly called **interneurons**, have short axons that remain in the same region of the nervous system in which the cell body is located. Interneurons help to process neuronal information within a local brain region.

### Neurons Communicate With Each Other at Synapses

Information flow along a neuron is polarized. The dendrites and cell body receive and integrate incoming information, which is transmitted along the axon to the terminals. Communication of information from one neuron to another also is polarized and occurs at specialized sites of contact called **synapses**. The neuron that sends information is the **presynaptic neuron** and the one that receives the information is the **postsynaptic neuron**. The information carried by the presynaptic neuron is most typically transduced at the synapse into a chemical signal that is received by specialized membrane receptors on the dendrites and cell body of the postsynaptic neuron.

The synapse consists of three distinct elements: (1) the **presynaptic terminal**, the axon terminal of the presynaptic neuron, (2) the **synaptic cleft**, the narrow intercellular space between the neurons, and (3) the **receptive membrane** of the postsynaptic neuron. Synapses are present on dendrites, the cell body, the **initial segment** of the axon, or the portion of the axon closest to the cell body, and the presynaptic axon terminal. Synapses located on different sites can serve different functions.

To send a message to its postsynaptic neurons, a presynaptic neuron releases **neurotransmitter**, packaged into vesicles, into the synaptic cleft. Neurotransmitters are small molecular weight compounds; among these are amino acids (eg, glutamate, glycine, and  $\gamma$ -aminobutyric acid [GABA]), acetylcholine, and monoaminergic compounds such as norepinephrine and serotonin. Larger molecules, such as peptides (eg, enkephalin and substance P), also can function as neurotransmitters. After release into the synaptic cleft, the neurotransmitter molecules diffuse across the cleft and bind to receptors on the postsynaptic membrane. Neurotransmitters change the permeability of the neuronal membrane to particular ions. A neurotransmitter can either excite the postsynaptic neuron by depolarizing it or inhibit the neuron by hyperpolarizing it. For example, excitation can be produced by a neurotransmitter that increases the

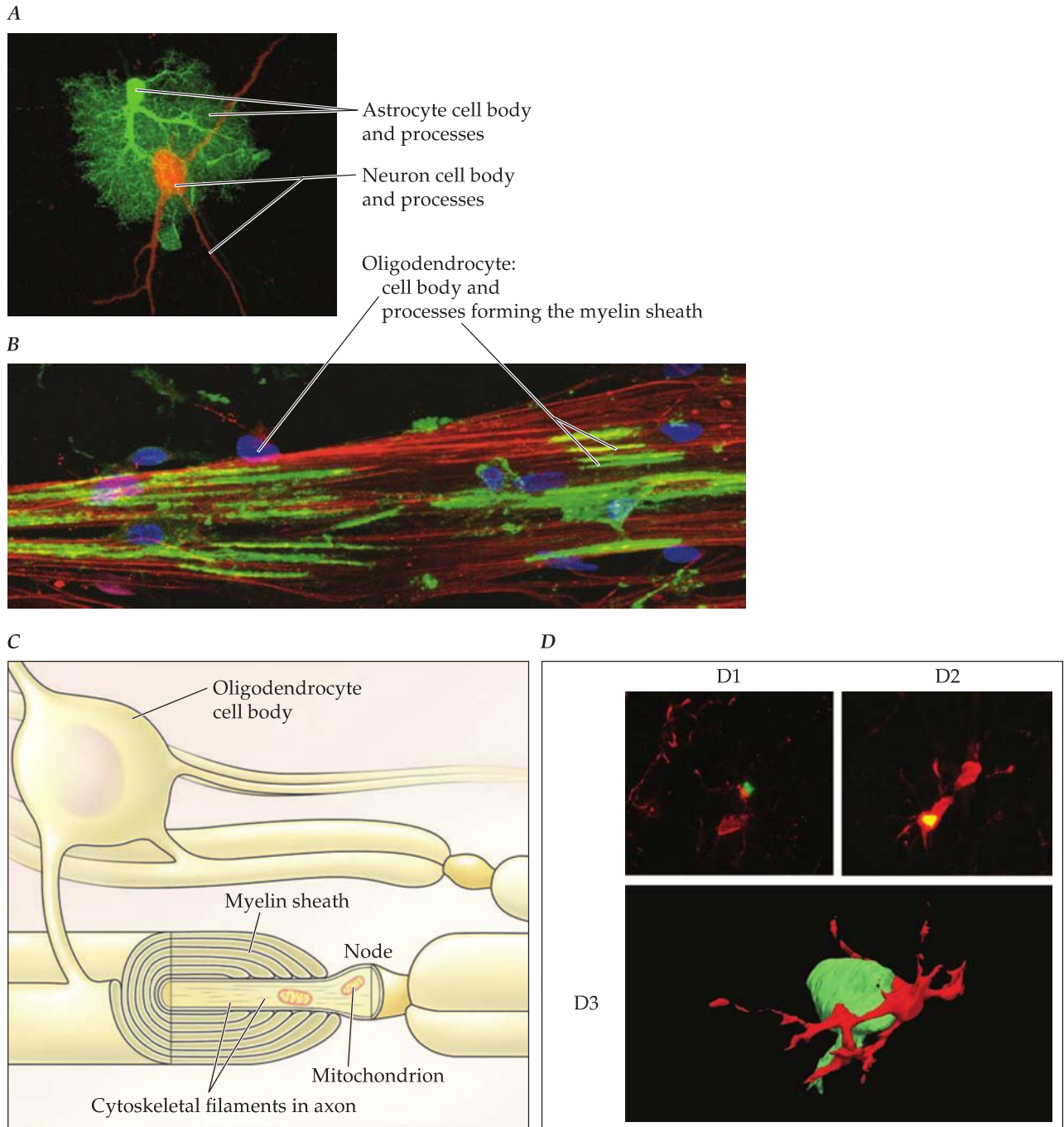
flow of sodium ions across the membrane and into a neuron (ie, depolarization), and inhibition can be produced by a neurotransmitter that increases the flow of chloride ions into a neuron (ie, hyperpolarization). Glutamate and acetylcholine typically excite neurons, whereas GABA and glycine typically inhibit neurons.

Many neurotransmitters, like dopamine and serotonin, have more varied actions, exciting some neurons and inhibiting others. Their action depends on a myriad of factors, such as the particular membrane receptor subtype that the neurotransmitter engages and whether the binding of the neurotransmitter to the receptor leads directly to the change in ion permeability or if the change is mediated by the actions on second messengers and other intracellular signaling pathways (eg, G protein-coupled receptors). For example, the dopamine receptor subtype 1 is depolarizing, whereas the type 2 receptor is hyperpolarizing; both act through G protein-coupled mechanisms. A neurotransmitter can even have opposing actions on the same neuron depending on the composition of receptor subtypes on the neuron's membrane. Action through second messengers and other intracellular signaling pathways can have short-term effects, such as changing membrane ion permeability, or long-term effects, such as changing gene expression. Many small molecules that produce strong effects on neurons are not packaged into vesicles; they are thought to act through diffusion. These compounds, for example, nitric oxide, are produced in the postsynaptic neuron and are thought to act as retrograde messengers that serve important regulatory functions on pre- and postsynaptic neurons, including maintaining and modulating the strength of synaptic connections. These actions are important for learning and memory.

Although chemical synaptic transmission is the most common way of sending messages from one neuron to another, purely electrical communication can occur between neurons. At such **electrical synapses**, there is direct cytoplasmic continuity between the presynaptic and postsynaptic neurons, through gap junctions.

### Glial Cells Provide Structural Support for Neurons and Additionally Serve a Broad Set of Diverse Functions

Glial cells comprise the other major cellular constituent of the nervous system; they outnumber neurons by about 10 to 1. Given this high ratio, the functions of glial cells must be complex and diverse. There are two major classes of glia: macroglia and microglia. **Macroglia**, of which there are four separate types—oligodendrocytes, Schwann cells, astrocytes, and ependymal cells—have a variety of support and nutritive functions. **Schwann cells** and **oligodendrocytes** form the **myelin sheath** around peripheral and central axons, respectively (Figures 1–2A and 1–3). The myelin sheath increases the velocity of action potential conduction. It is whitish in appearance because it is rich in a fatty substance called **myelin**, which is composed of many different kinds of myelin proteins. Schwann cells also play important roles in organizing the formation of the connective tissue sheaths surrounding peripheral nerves during development and in axon regeneration following damage in maturity. **Astrocytes** have important structural and metabolic functions. For example, in the developing nervous system, astrocytes act as scaffolds for growing axons and guides



**FIGURE 1-3. Astrocytes and oligodendrocytes are the most ubiquitous types of glial cells in the central nervous system.** Parts **A** and **B** are histological sections showing examples of these cell types. **A**. An astrocyte (green) is shown enveloping a neuronal cell body (red). **B**. Oligodendrocytes are shown forming the myelin sheaths surrounding axons. A blue stain (DAPI) marks nuclei in the cell bodies. The processes (green) are stained for an important component of the myelin sheath, myelin basic protein (MBP). **C**. Schematic drawing of an oligodendrocyte and the myelin sheath that it forms around an axon. Note the multiple wrappings of the oligodendrocyte process around the axon. The node of Ranvier is not covered by the oligodendrocyte process, forming a gap between the axon membrane and the extracellular space. Cytoskeletal filaments are present in the axon and mitochondria are in the region of the node of Ranvier. **D**. Microglial cells. Microglia phagocytose proteins as well as cells in the CNS that express receptors on their membranes that enable targeting by microglia. In an animal model of Alzheimer disease, a micrograph shows a microglial process (red) that is contacting a beta amyloid plaque (green; **D1**). Subsequent to engulfment, the plaque within the microglial cell is degraded and digested (**D2**, yellow). In a model of neuronal degeneration (**D3**), this 3D reconstruction, from a series of micrographs, shows a microglial cell (red) contacting a neuron (green) in the spinal cord. (**A**, Image courtesy of Ellisman M, Bushong E, Univ. California, San Diego. Allen NJ, Barres BA. Neuroscience glia: more than just brain glue. *Nature*. 2009;457 [7230]:675-677. **B**, Reproduced with permission from Lee PR, Fields RD. Regulation of myelin genes implicated in psychiatric disorders by functional activity in axons. *Front Neuroanat*. 2009;3:4. **C**, Adapted from Kandel ER, Schwartz JS, Jessell TM, eds. *Principles of Neural Science*. 4th ed. New York, NY: McGraw-Hill; 2000.) **D1**, **D2**, Courtesy of Jasmine L. Pathan and Dr. Gwenn A. Garden (Department of Neurology, School of Medicine, University of Washington, Seattle, WA); **D3**, Jiang Y, Sarkar A, Amer A, Martin J. Transneuronal down-regulation of the premotor cholinergic system after corticospinal tract loss. *J Neurosci* (2018) 38(39): 8329-8344. PMID: 30049887).

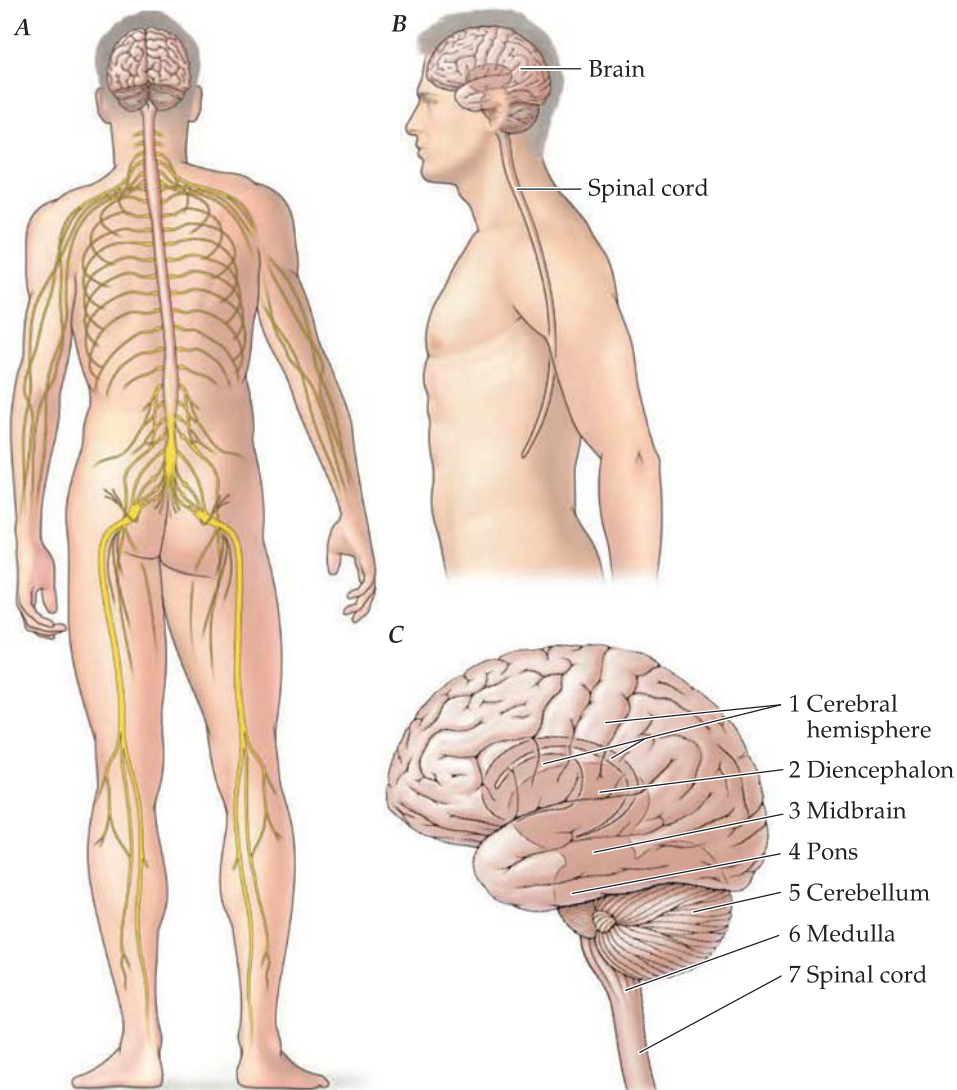
for migrating immature neurons. Many synapses are associated with astrocyte processes that may monitor synaptic actions and provide chemical feedback. Astrocytes also contribute to the blood-brain barrier, which protects the vulnerable environment of the brain from invasion of chemicals from the periphery, which can influence neuronal firing. The last class of macroglia, **ependymal cells**, line fluid-filled cavities in the central nervous system (see below). They play an important role in regulating the flow of chemicals from these cavities into the brain. Macroglia figure importantly in disease and nervous system trauma. For example, in multiple sclerosis, damage to oligodendrocytes results in the loss of the myelin sheath of axons in particular brain regions. This, in turn, leads to impairments in neural connections and functions. Astrocytes react to inflammation after injury and neurodegenerative processes.

**Microglia** subserve a phagocytic or scavenger role, responding to nervous system infection or damage. They are rapidly mobilized—they become activated (Figure 1–3D)—in response to different pathophysiological conditions and trauma.

Activated microglia can destroy invading microorganisms, remove debris, and promote tissue repair. Interestingly, they also mediate changes in neuronal properties after nervous system damage; sometimes maladaptive changes, so they may also hinder recovery after injury. For example, neurons often become hyperexcitable after nervous system damage, and microglia can be involved in this process. Microglia also play a key role in the modification of connections between neurons, especially in the elimination of unnecessary presynaptic connections during development.

## The Nervous System Consists of Separate Peripheral and Central Components

Neurons and glial cells of the nervous system are organized into two anatomically separate but functionally interdependent parts: the **peripheral** and the **central nervous systems** (Figure 1–4A). The peripheral nervous system is subdivided into **somatic**, **autonomic**, and **enteric** divisions. The somatic



**FIGURE 1–4.** A. Location of the central and peripheral nervous system in the body. Major peripheral nerves are shown in yellow. B. The brain and spinal cord, viewed laterally. C. There are seven major divisions of the central nervous system: (1) cerebral hemispheres, (2) diencephalon, (3) midbrain, (4) pons, (5) cerebellum, (6) medulla, and (7) spinal cord. The midbrain, pons, and medulla comprise the brain stem.

division contains the sensory neurons that innervate the skin, muscles, and joints. These neurons detect and, in turn, inform the central nervous system of stimuli. This division also contains the axons of motor neurons that innervate skeletal muscle, although the cell bodies of motor neurons lie within the central nervous system. These axons transmit signals to muscle to regulate the force of muscle contraction. The autonomic division contains the neurons that innervate glands and the smooth muscle of the viscera and blood vessels (see Chapter 15). This division, with its separate **sympathetic and parasympathetic** subdivisions, regulates body functions based, in part, on information about the body's internal state. The **enteric nervous system** contains neurons that innervate the gastrointestinal system. It functions independent of, as well as in concert with, the autonomic nervous system.

The central nervous system consists of the **spinal cord and brain** (Figure 1–4B), and the brain is further subdivided into the medulla, pons, cerebellum, midbrain, diencephalon, and

cerebral hemispheres (Figure 1–4C). Within each of the seven central nervous system divisions resides a component of the **ventricular system**, a labyrinth of fluid-filled cavities that serve various supportive functions (see Figure 1–13). Box 1–1 shows how all of the divisions of the central nervous system and the components of the ventricular system are present from very early in development, from about the first month after conception.

Neuronal cell bodies and axons are not distributed uniformly within the nervous system. In the peripheral nervous system, cell bodies collect in peripheral **ganglia** and axons are contained in **peripheral nerves**. In the central nervous system, neuronal cell bodies and dendrites are located in **cortical** areas, which are flattened sheets of cells (or laminae) located primarily on the surface of the cerebral hemispheres, and in **nuclei**, which are clusters of neurons located beneath the surface of all of the central nervous system divisions. Nuclei come in various sizes and shapes; they are commonly oval and columnar but sometimes occur in complex three-dimensional configurations (see Figure 1–10).

## BOX 1–1

### Development of the Basic Plan of the Brain and Spinal Cord

The central nervous system develops from a specialized portion of the embryonic ectoderm, the neural plate. Originally a flattened sheet of cells, the neural plate forms a tube-like structure—termed the neural tube—as the neurons and glial cells proliferate. The walls of the neural tube form the neuronal structure of the central nervous system. The cavity in the neural tube forms the ventricular system.

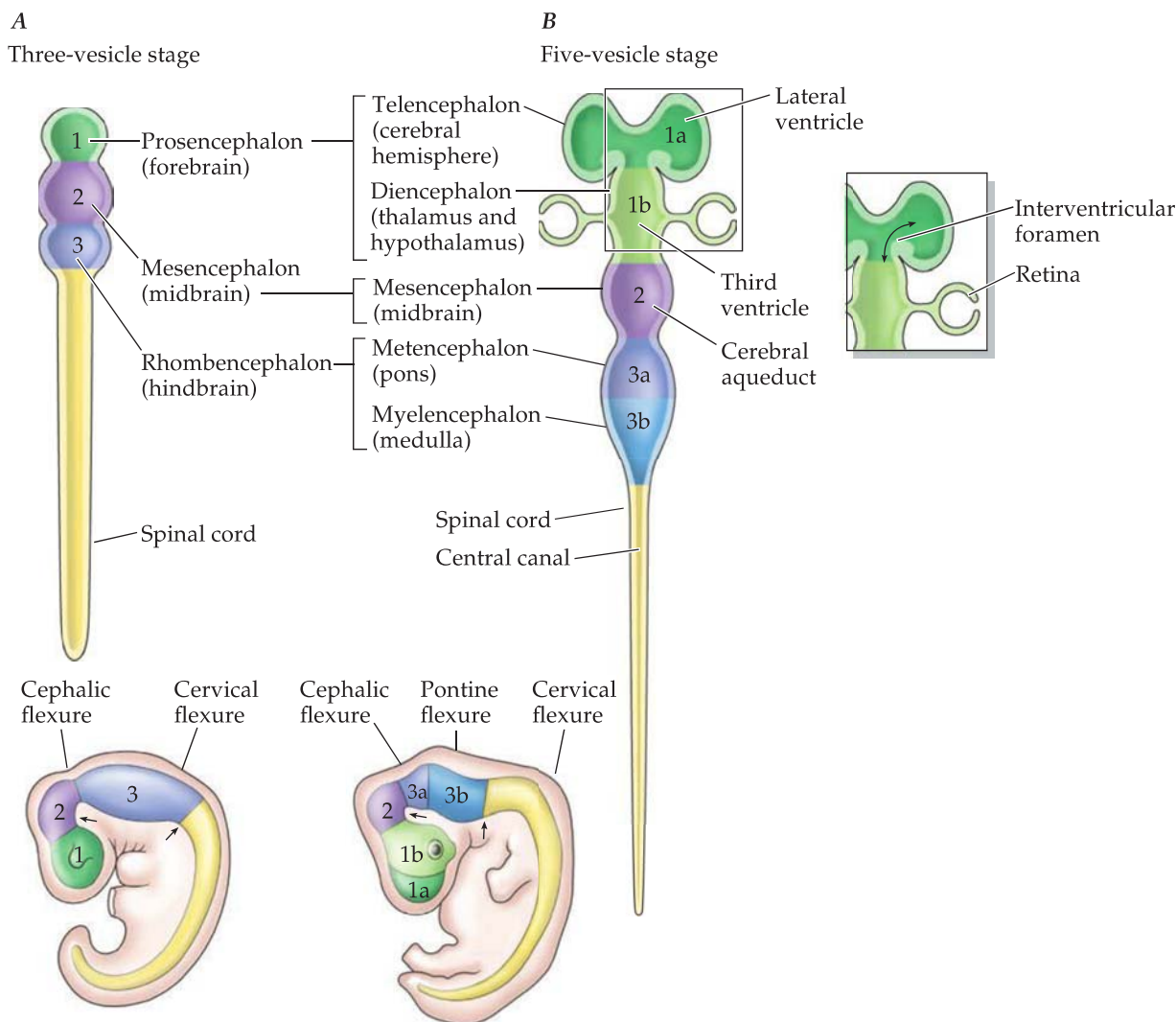
Very early in development the rostral portion of the neural tube forms the three hollow swellings, or vesicles, corresponding to where there is an enormous proliferation of developing neurons (Figure 1–5): (1) the **prosencephalon** or **forebrain**, (2) the **mesencephalon** or **midbrain**, and (3) the **rhombencephalon** or **hindbrain**. The caudal portion of the neural tube remains relatively undifferentiated and forms the **spinal cord**. Two secondary vesicles emerge from the prosencephalon later in development: the **telencephalon** (or cerebral hemisphere) and the **diencephalon** (or thalamus and hypothalamus). Whereas the mesencephalon remains undivided throughout further brain development, the rhombencephalon gives rise to the **metencephalon** (or pons and cerebellum) and the **myelencephalon** (or medulla). The five brain vesicles and primitive spinal cord, already identifiable by the fifth week of fetal development, give rise to the seven major divisions of the central nervous system (see Figure 1–4).

The complex configuration of the mature brain is determined in part by how the developing brain bends, or **flexes**. Flexures occur because proliferation of cells in the brain stem and cerebral hemispheres is enormous, and the space that the developing brain occupies in the cranium is constrained. At the three-vesicle stage, there are two prominent flexures: the **cervical flexure**, at the junction of the spinal cord and the caudal hindbrain (or future medulla), and the **cephalic flexure**, at the level of the midbrain (Figure 1–5, bottom). At the five-vesicle stage, a third flexure becomes prominent, the **pontine flexure**. By birth the cervical and pontine flexures have straightened out. The cephalic flexure, however, remains prominent and causes the longitudinal axis of the forebrain to

deviate from that of the midbrain, hindbrain, and spinal cord (see Figure 1–16B).

The large cavities within the cerebral vesicles develop into the ventricular system of the brain, and the caudal cavity becomes the central canal of the spinal cord (Figure 1–5). The ventricular system contains **cerebrospinal fluid**, which is produced mainly by the **choroid plexus** (see Chapter 3). As the brain vesicles develop, the cavity within the cerebral hemispheres divides into the two **lateral ventricles** (formerly termed the first and second ventricles) and the **third ventricle** (Figure 1–5B). The lateral ventricles, which develop as outpouchings from the rostral portion of the third ventricle, are each interconnected with the third ventricle by an **inter-ventricular foramen** (of Monro) (Figure 1–5, inset). The **fourth ventricle**, the most caudal ventricle, develops from the cavity within the hindbrain. It is connected to the third ventricle by the **cerebral aqueduct** (of Sylvius) and merges caudally with the **central canal** (of the caudal medulla and spinal cord).

Cerebrospinal fluid normally exits from the ventricular system into the space overlying the central nervous system's surface through foramina in the fourth ventricle (discussed in Chapter 3). (The central canal does not have such an aperture for the outflow of cerebrospinal fluid.) Pathological processes can prevent flow of cerebrospinal fluid from the ventricular system. For example, later in development the cerebral aqueduct becomes narrowed because of cell proliferation in the midbrain. Its narrow diameter makes it vulnerable to the constricting effects of congenital abnormalities, tumors, or swelling from trauma. Occlusion can occur; however, cerebrospinal fluid continues to be produced despite occlusion. If occlusion occurs before the bones of the skull are fused (ie, in embryonic development or in infancy), ventricular volume will increase, the brain will enlarge rostral to the occlusion, and head size will increase. This condition is called **hydrocephalus**. If occlusion occurs after the bones of the skull are fused, ventricular size cannot increase without increasing intracranial pressure. This is a life-threatening condition.



**FIGURE 1-5.** Schematic illustration of the three- and five-vesicle stages of the neural tube during early central nervous system development. The top portion of the figure shows dorsal views of the neural tube drawn without flexures. The bottom portion of the figure presents lateral views. **A.** Three-vesicle stage. **B.** Five-vesicle stage. Note that the lineage of each vesicle at the five-vesicle stage is indicated by the shading. The two secondary vesicles from the forebrain have different green shades, and the two vesicles that derived from the hindbrain have different blue shades. The inset shows the location of the interventricular foramen on one side in the five-vesicle stage. (Adapted from Kandel ER, Schwartz JH, Jessell TM, eds. *Principles of Neural Science*. 3rd ed. New York, NY: McGraw-Hill; 1991.)

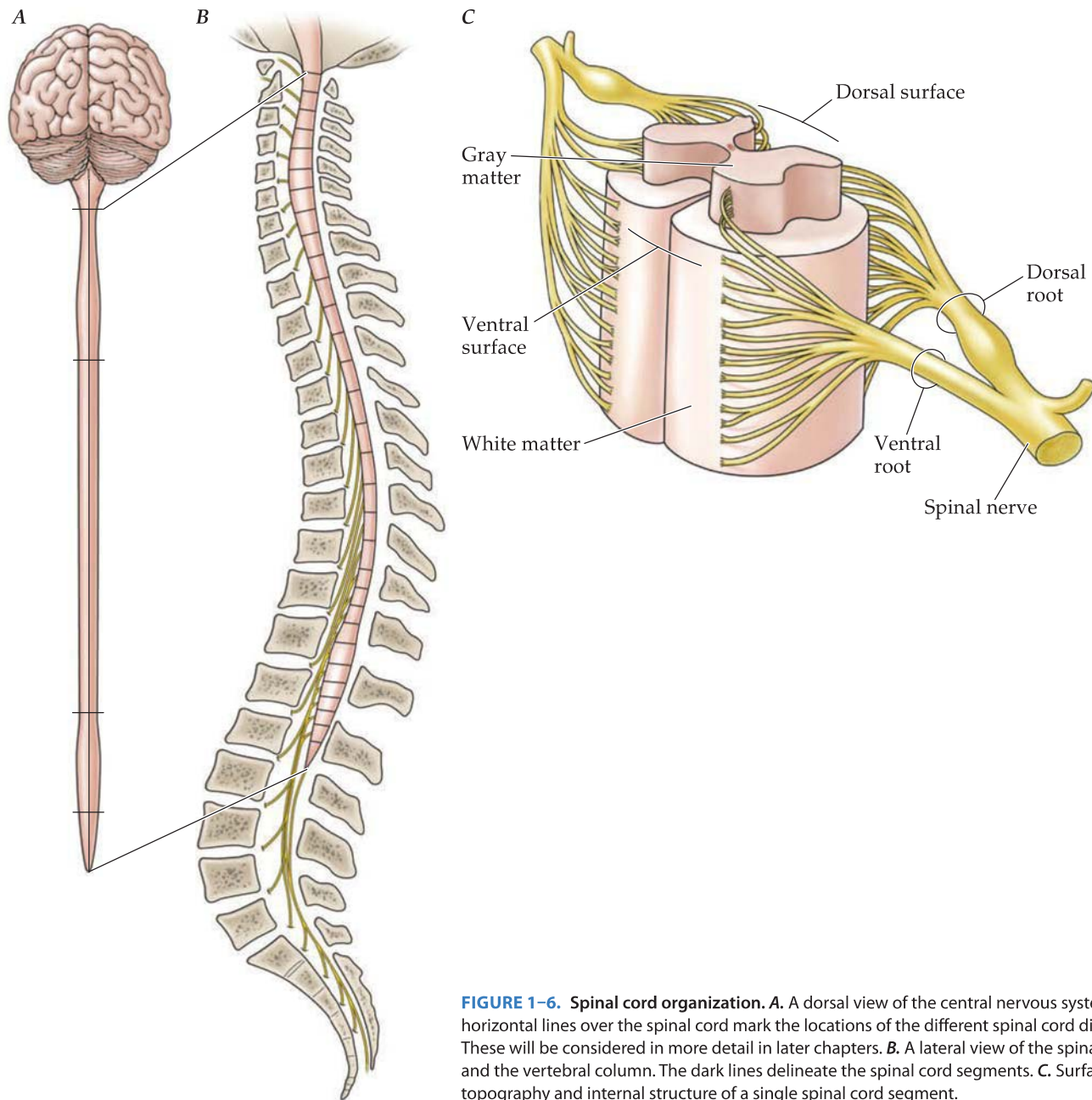
Regions of the central nervous system that contain axons have an unwieldy number of names, the most common of which is **tract**. In fresh tissue, nuclei and cortical areas appear grayish and tracts appear whitish, hence the familiar terms **gray matter** and **white matter**. The whitish appearance of tracts is caused by the presence of the myelin sheath surrounding the axons (see Figure 1-3). The gray and white matter can be distinguished in fixed tissue using anatomical methods and in the living brain using radiological methods (see Chapter 2, Boxes 2-1 and 2-2).

## The Spinal Cord Displays the Simplest Organization of All Seven Major Divisions

The spinal cord participates in processing sensory information from the limbs, trunk, and many internal organs; in controlling body movements directly; and in regulating many visceral functions (Figure 1-6). It also provides a conduit for the transmission of both sensory information in the white matter axon

tracts that ascend to the brain and motor information in the descending tracts.

The spinal cord consists of modules, termed segments, in which every segment has a similar basic structure (Figure 1-6C). Each spinal cord segment contains a pair of nerve roots (and associated rootlets) called the **dorsal** and **ventral roots**. (The terms *dorsal* and *ventral* describe the spatial relations of structures; these and other anatomical terms are explained later in this chapter.) Dorsal roots contain only sensory axons, which transmit sensory information into the spinal cord. By contrast, ventral roots contain motor axons, which transmit motor commands to muscle and other body organs. Dorsal and ventral roots exemplify the separation of function in the nervous system, a principle that is examined further in subsequent chapters. These sensory and motor axons, which are part of the peripheral nervous system, become intermingled in the **spinal nerves** enroute to their peripheral targets (Figure 1-6C).



**FIGURE 1-6. Spinal cord organization.** *A.* A dorsal view of the central nervous system. The horizontal lines over the spinal cord mark the locations of the different spinal cord divisions. These will be considered in more detail in later chapters. *B.* A lateral view of the spinal cord and the vertebral column. The dark lines delineate the spinal cord segments. *C.* Surface topography and internal structure of a single spinal cord segment.

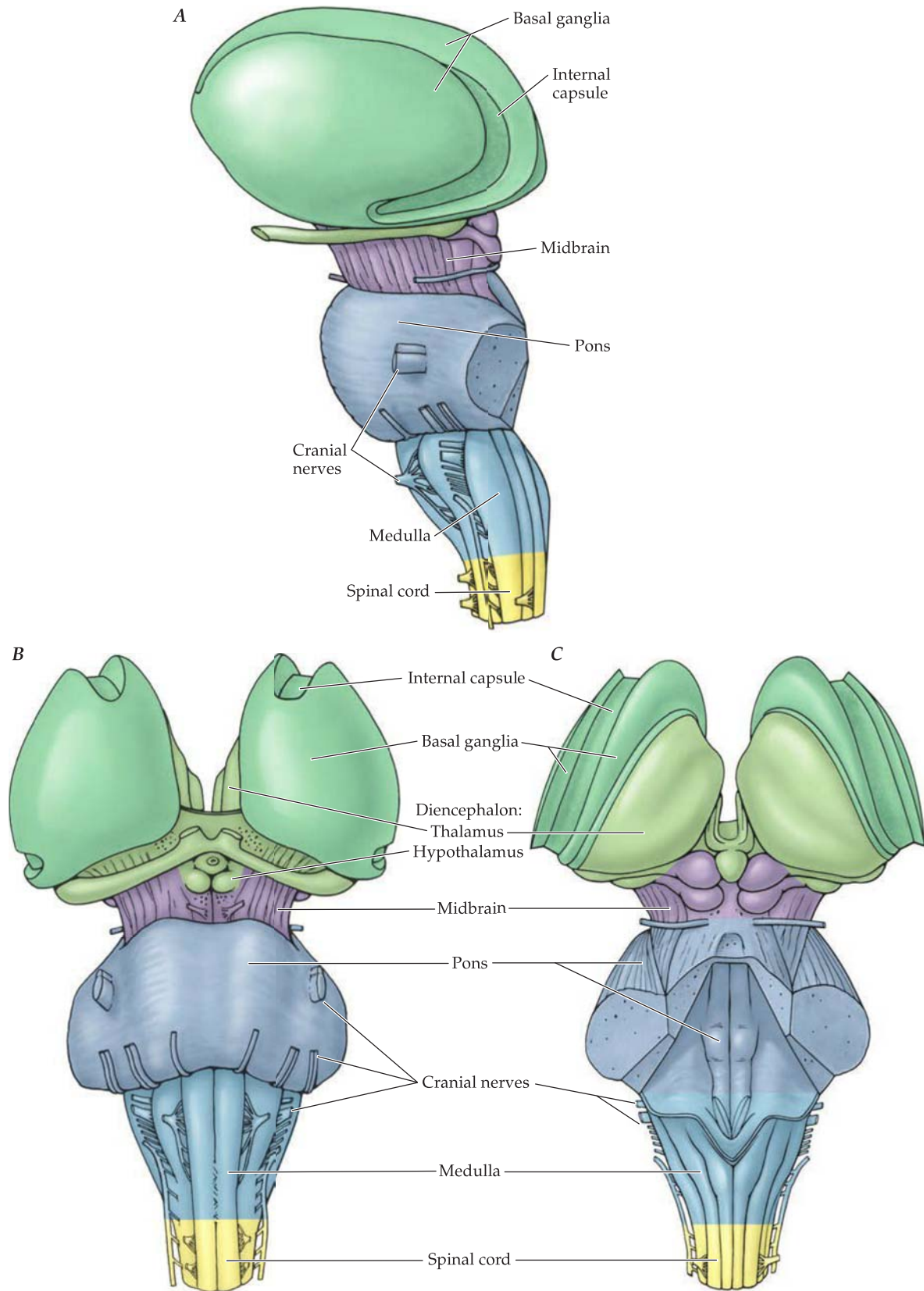
## The Brain Stem and Cerebellum Regulate Body Functions and Movements

The next three divisions—medulla, pons, and midbrain—comprise the **brain stem** (Figure 1-7). The brain stem has three general functions. First, it receives sensory information from cranial structures and controls the muscles of the head. These functions are similar to those of the spinal cord. **Cranial nerves**, the sensory and motor nerve roots that enter and exit the brain stem, are parts of the peripheral nervous system and are analogous to the spinal nerves (Figure 1-7). Second, similar to the spinal cord, the brain stem is a conduit for information flow because ascending sensory and descending motor tracts travel through it. Finally, nuclei in the brain stem integrate diverse information from a variety of sources for arousal,

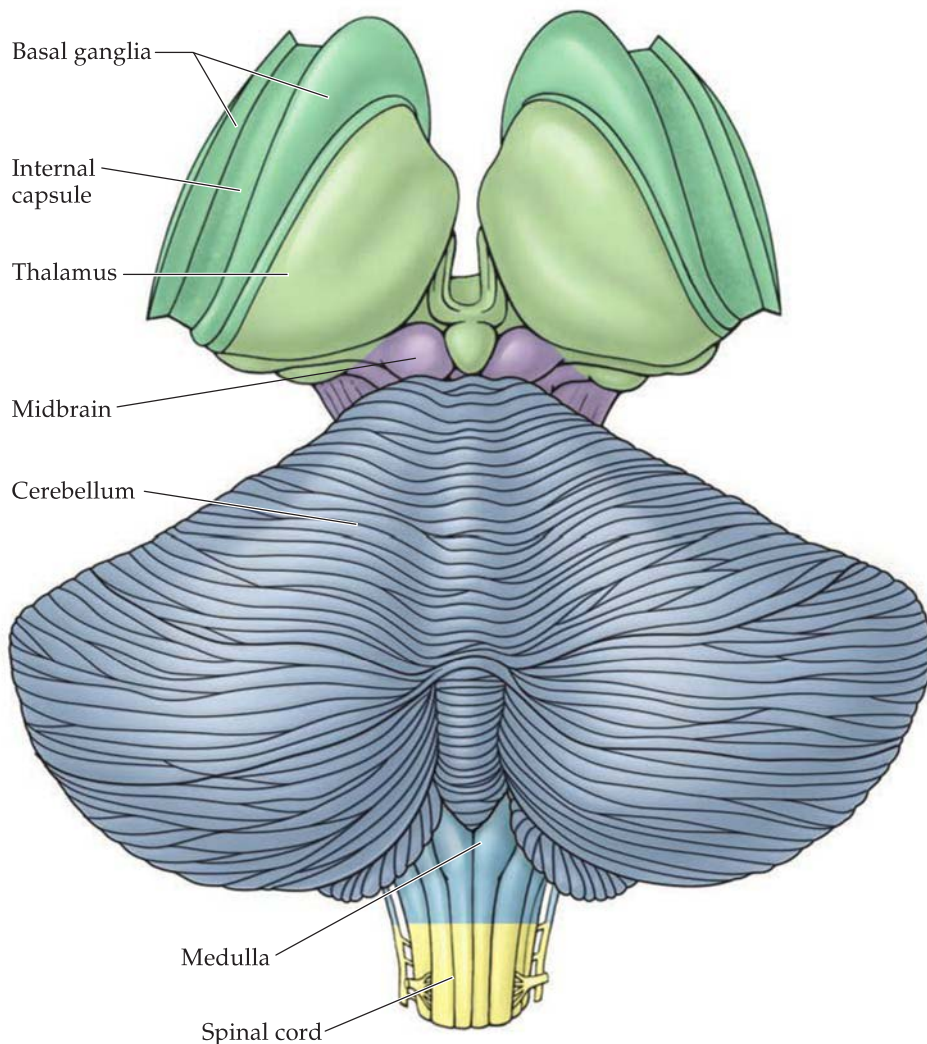
behavioral responses to the environment, and other higher brain functions.

In addition to these three general functions, the various divisions of the brain stem each subservise specific sensory and motor functions. For example, portions of the **medulla** participate in essential blood pressure and respiratory regulatory mechanisms. Indeed, damage to these parts of the brain is almost always life threatening. Parts of the **pons** and **midbrain** play a key role in the control of eye movement.

The principal functions of the **cerebellum** are to regulate eye and limb movements and to maintain posture and balance (Figure 1-8). Limb movements become poorly coordinated when the cerebellum is damaged. In addition, parts of the cerebellum play a role in higher brain functions, including language, cognition, and emotion (Chapter 13).



**FIGURE 1-7.** Lateral (A), ventral (B), and dorsal (C) surfaces of the brain stem, diencephalon, and basal ganglia. The different divisions of the brain are shaded in different colors.



**FIGURE 1-8.** Dorsal view of the cerebellum, together with the brain stem, thalamus, and basal ganglia.

## The Diencephalon Consists of the Thalamus and Hypothalamus

The two principal parts of the **diencephalon** participate in diverse sensory, motor, and integrative functions. One component, the **thalamus** (Figure 1-9), is a key structure for transmitting information to the cerebral hemispheres. The thalamus is composed of numerous nuclei. Neurons in separate thalamic nuclei transmit information to different cortical areas. In the brains of most people, a small portion of the thalamus in each half adheres at the midline, the **thalamic adhesion**. The other component of the diencephalon, the **hypothalamus** (Figure 1-9A; see also Figure 1-12A), controls endocrine hormone release from the pituitary gland and the overall functions of the autonomic nervous system.

## The Cerebral Hemispheres Have the Most Complex Shape of All Central Nervous System Divisions

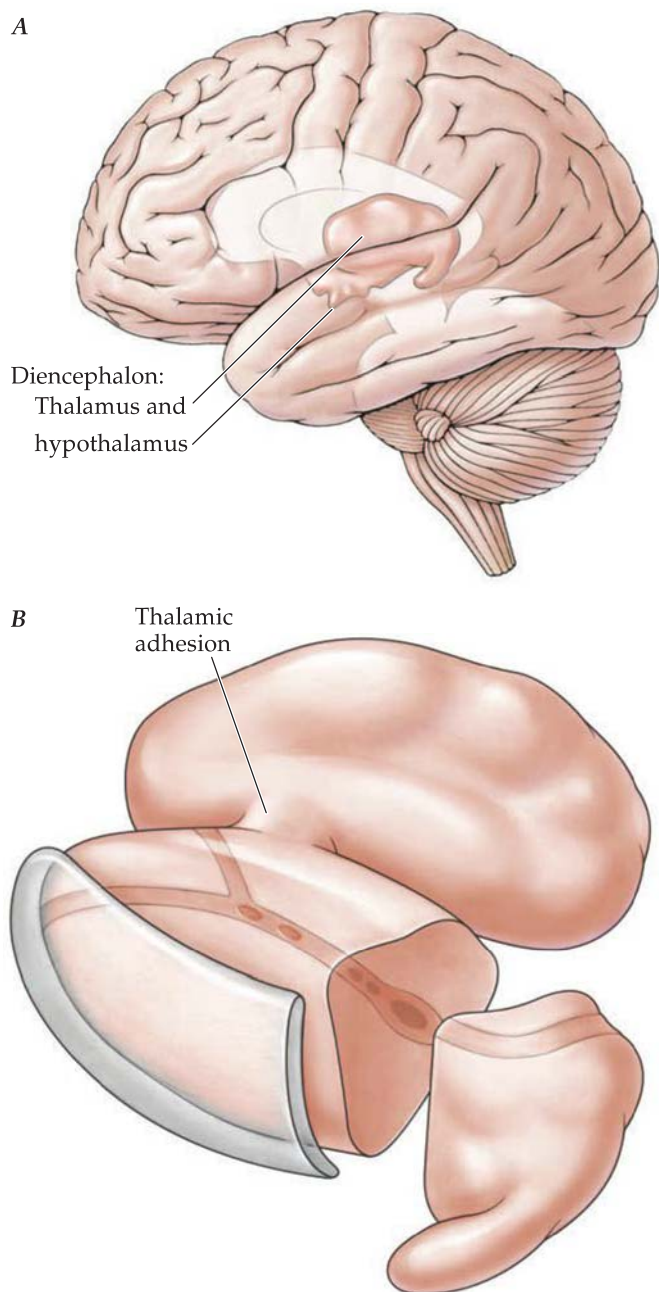
The **cerebral hemispheres** are the most highly developed portions of the human central nervous system. Each hemisphere is a distinct half, and each has four major components:

cerebral cortex, hippocampal formation, amygdala, and basal ganglia. Together, these structures mediate the most sophisticated of human behaviors, and they do so through complex anatomical connections.

### The Subcortical Components of the Cerebral Hemispheres Mediate Diverse Motor, Cognitive, and Emotional Functions

The **hippocampal formation** is important in learning and memory, whereas the **amygdala** not only participates in emotions but also helps to coordinate the body's response to stressful and threatening situations, such as preparing to fight (Figure 1-10A). These two structures are part of the **limbic system** (see Chapter 16), which includes other parts of the cerebral hemispheres, diencephalon, and midbrain. Because parts of the limbic system play a key role in mood, it is not surprising that psychiatric disorders are often associated with limbic system dysfunction.

The **basal ganglia** are another deeply located collection of neurons. The portion of the basal ganglia that has the most complex shape is called the **striatum** (Figure 1-10B). The importance of the basal ganglia in the control of movement is clearly revealed when they become damaged, as in Parkinson disease. Tremor and a slowing of movement are some of the overt signs



**FIGURE 1-9.** A. Lateral surface of the cerebral hemispheres and brain stem, illustrating the location of the thalamus and hypothalamus. B. Three-dimensional structure of the thalamus. The separate structure lateral to the main portion of the thalamus is the thalamic reticular nucleus, which forms a lamina over the lateral sides of the thalamus.

of this disease. The basal ganglia also participate in cognition and emotions in concert with the cerebral cortex and are key brain structures involved in addiction.

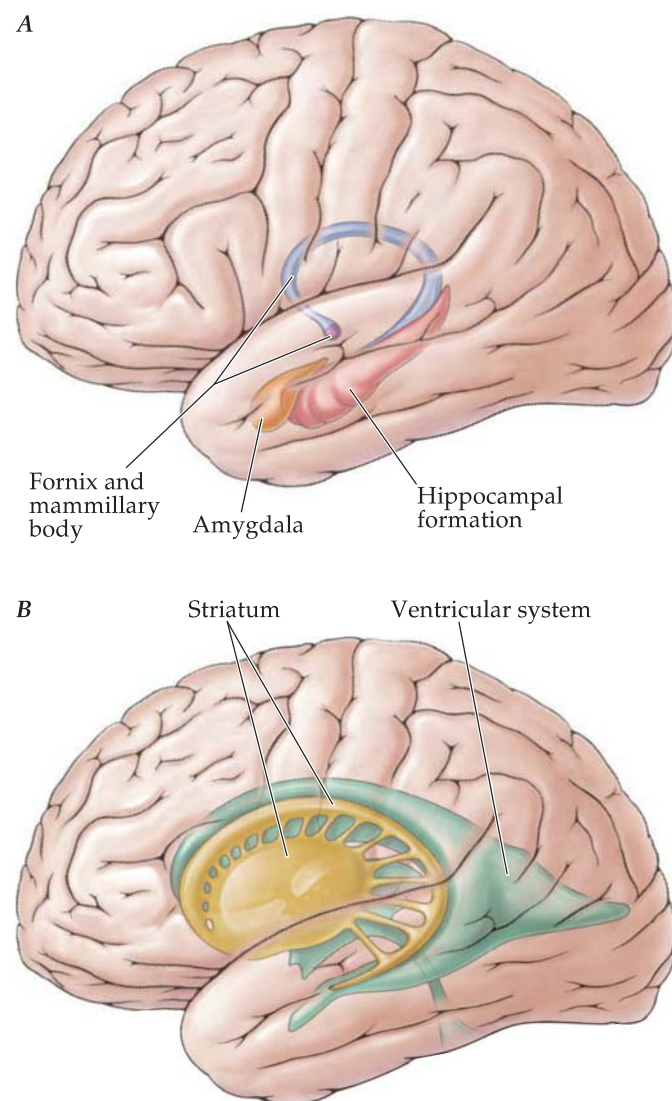
### The Four Lobes of the Cerebral Cortex Each Have Distinct Functions

The **cerebral cortex**, which is located on the surface of the brain, is highly convoluted (Figures 1-11 and 1-12). The human cerebral cortex is approximately 2500 cm<sup>2</sup>. Convolutions are an evolutionary adaptation to fit a greater surface area within the confined space of the cranial cavity. In fact, only one quarter to one third of the cerebral cortex is exposed on the surface. The elevated

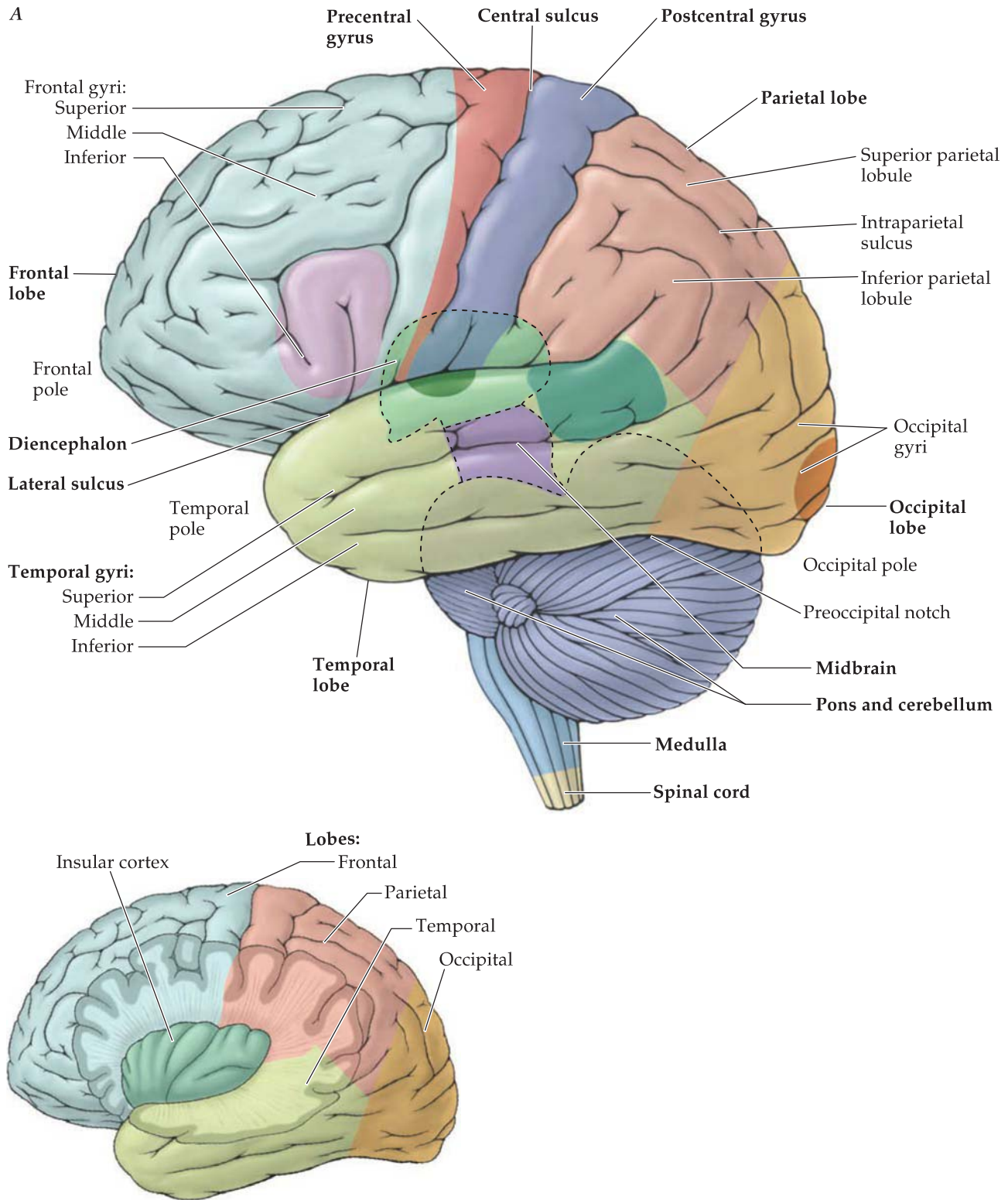
convolutions on the cortical surface, called **gyri**, are separated by grooves called **sulci** or **fissures** (which are particularly deep sulci). The cerebral hemispheres are separated from each other by the **sagittal** (or interhemispheric) **fissure** (Figure 1-12B).

The four **lobes** of the cerebral cortex are named after the cranial bones that overlie them: frontal, parietal, occipital, and temporal (Figure 1-11, inset). The functions of the different lobes are remarkably distinct, as are the functions of individual gyri within each lobe.

The **frontal lobe** serves diverse behavioral functions, from thoughts to action, cognition, and emotions. The **precentral gyrus** contains the **primary motor cortex**, which participates in controlling the mechanical actions of movement, such as the direction and speed of reaching. Many projection neurons in the primary motor cortex have an axon that terminates in the spinal cord. The superior, middle, and inferior frontal gyri form



**FIGURE 1-10.** Three-dimensional views of deep structures of the cerebral hemisphere. A. The hippocampal formation (red) and amygdala (orange). The fornix (blue) and mammillary body (purple) are structures that are anatomically and functionally related to the hippocampal formation. B. Striatum is a component of the basal ganglia with a complex three-dimensional shape. The ventricular system is also illustrated. Note the similarity in overall shapes of the striatum and the lateral ventricle.



**FIGURE 1-11. A. Lateral surface of cerebral hemisphere and brain stem and a portion of the spinal cord.** The different colored regions correspond to distinct functional cortical areas. The primary motor and somatic sensory areas are located in the pre- and postcentral gyri, respectively. The primary auditory cortex lies in the superior temporal gyrus adjacent to the sensory and motor areas. Broca's area comprises most of the inferior frontal gyrus, and Wernicke's area is in the posterior part of the superior temporal gyrus. Boldface labeling indicates key structures. The inset shows the four lobes of the cerebral cortex and the insular cortex in relation to the four lobes. **B. Medial surface.** The primary visual cortex is located in the banks of the calcarine fissure. A small portion extends onto the lateral surface. The divisions of the brain stem and the cerebellum are also shown in A and B.

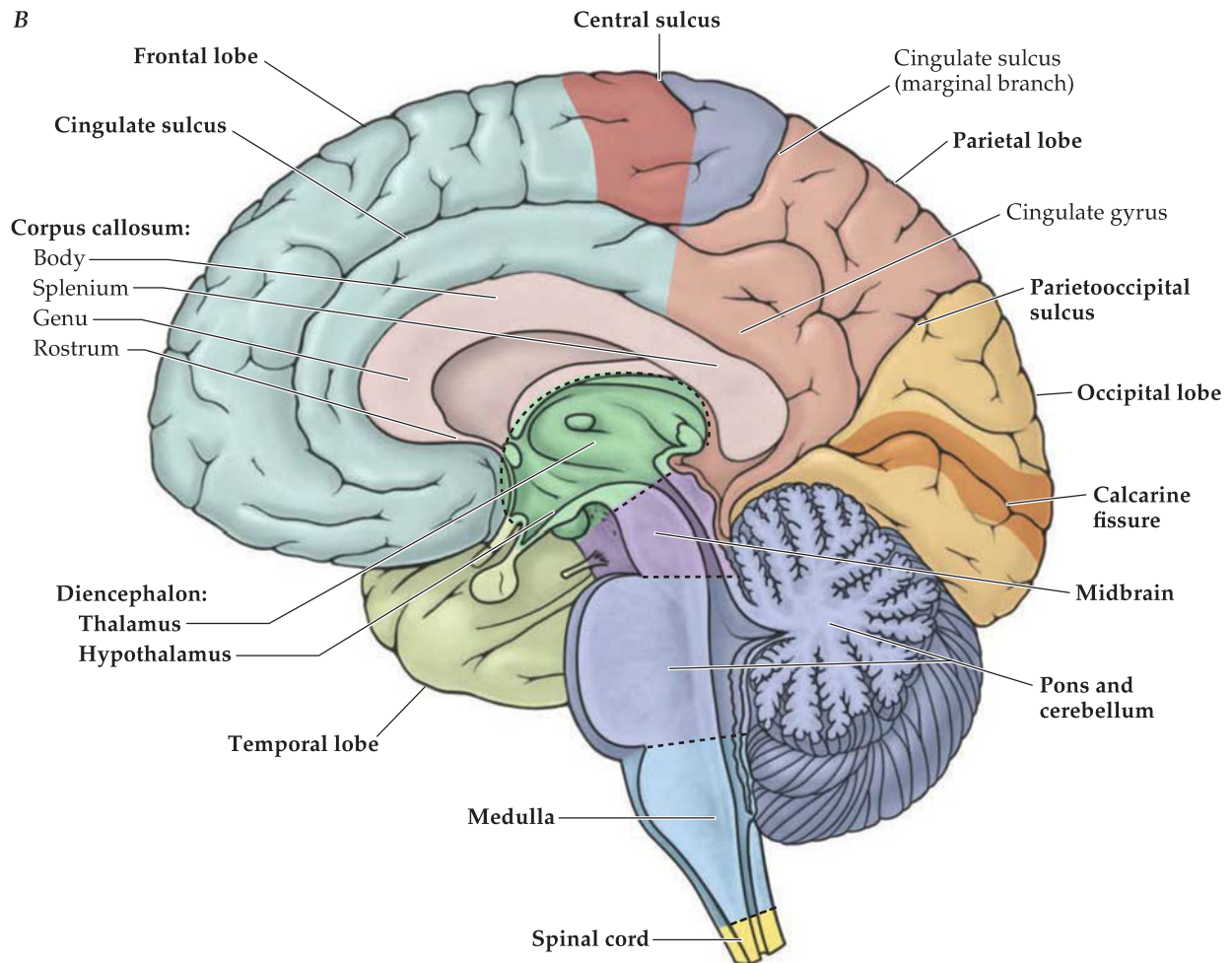


FIGURE 1-11. (Continued)

most of the remaining portion of the frontal lobe. The premotor areas, which are important in motor decision making and planning movements, are adjacent to the primary motor cortex in these gyri. The inferior frontal gyrus in the left hemisphere in most people contains Broca's area, which is essential for the articulation of speech. Much of the frontal lobe is **association cortex**. Association cortical areas in all lobes are involved in the complex processing of sensory and other information for higher brain functions, including emotions, organizing behavior, thoughts, language, and memories. The **frontal association cortex** consists of several distinct areas. The **prefrontal association cortex** is important in thought, cognition, and emotions. The **cingulate gyrus** (Figure 1-11B), medial frontal lobe, and most of the **orbital gyri** (Figure 1-12A) are association areas important in emotions. Psychiatric disorders of thought, as in schizophrenia, and mood disorders, such as depression, are linked with abnormal functions of frontal association cortex. The **basal forebrain**, which is on the ventral surface of the frontal lobe (Figure 1-12A), is a primitive form of cortex, which contains neurons that use acetylcholine to regulate cortical excitability. These neurons are examined further in Chapter 2. Although the olfactory sensory organ, the **olfactory bulb**, is located on the ventral surface of the frontal lobe, its connections are predominantly with the temporal lobe (Figure 1-12A).

The **parietal lobe**, which is separated from the frontal lobe by the **central sulcus**, mediates our perceptions of touch, pain, and limb position. These functions are carried out by the **primary somatic sensory cortex**, which is located in the **postcentral gyrus**. Primary sensory areas are the initial cortical processing stages for sensory information. The remaining portion of the parietal lobe on the lateral brain surface consists of the superior and inferior parietal lobules, which are separated by the intraparietal sulcus. The **superior parietal lobule** contains higher-order somatic sensory areas, for further processing of somatic sensory information, and other sensory areas. Together these areas are essential for a complete self-image of the body, and they mediate behavioral interactions with the world around us. A lesion in this portion of the parietal lobe in the right hemisphere, the side of the human brain that is specialized for spatial awareness, can produce bizarre neurological signs that include neglecting a portion of the body on the side opposite the lesion. For example, a patient may not dress one side of her body or comb half of her hair. The **inferior parietal lobule** is an association area involved in integrating diverse sensory information for perception and language, mathematical reasoning, and visuospatial cognition.

The **occipital lobe** is separated from the parietal lobe on the medial brain surface by the **parietooccipital sulcus**

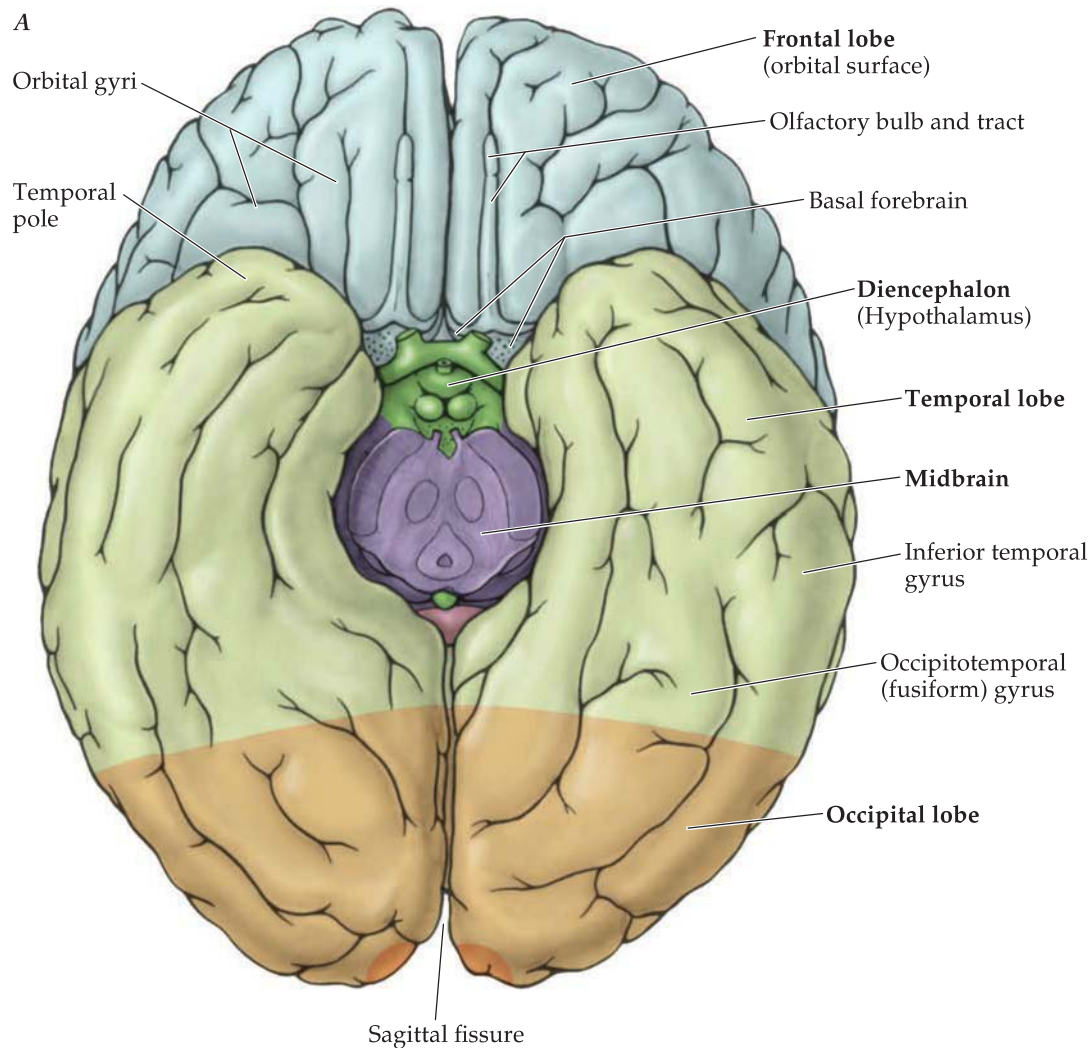
(Figure 1–11B). On the lateral and inferior surfaces, there are no distinct boundaries, only an imaginary line connecting the **preoccipital notch** (Figure 1–11A) with the parietooccipital sulcus. The occipital lobe is the most singular in function, subserving vision. The **primary visual cortex** is located in the walls and depths of the **calcarine fissure** on the medial brain surface (Figure 1–11B). Whereas the primary visual cortex is important in the initial stages of visual processing, the surrounding higher-order visual areas play a role in elaborating the sensory message that enables us to perceive the shape and color of objects. For example, on the ventral brain surface is a portion of the occipitotemporal gyrus in the occipital lobe (also termed the fusiform gyrus) that is important for recognizing faces (Figure 1–12A). Patients with a lesion of this area can confuse faces with inanimate objects.

The **temporal lobe**, separated from the frontal and parietal lobes by the **lateral sulcus** (or **Sylvian fissure**) (Figure 1–11A), mediates a variety of sensory functions and participates in memory and emotions. The **primary auditory cortex**, located on the **superior temporal gyrus**, works with surrounding areas on the superior temporal gyrus and within the lateral sulcus

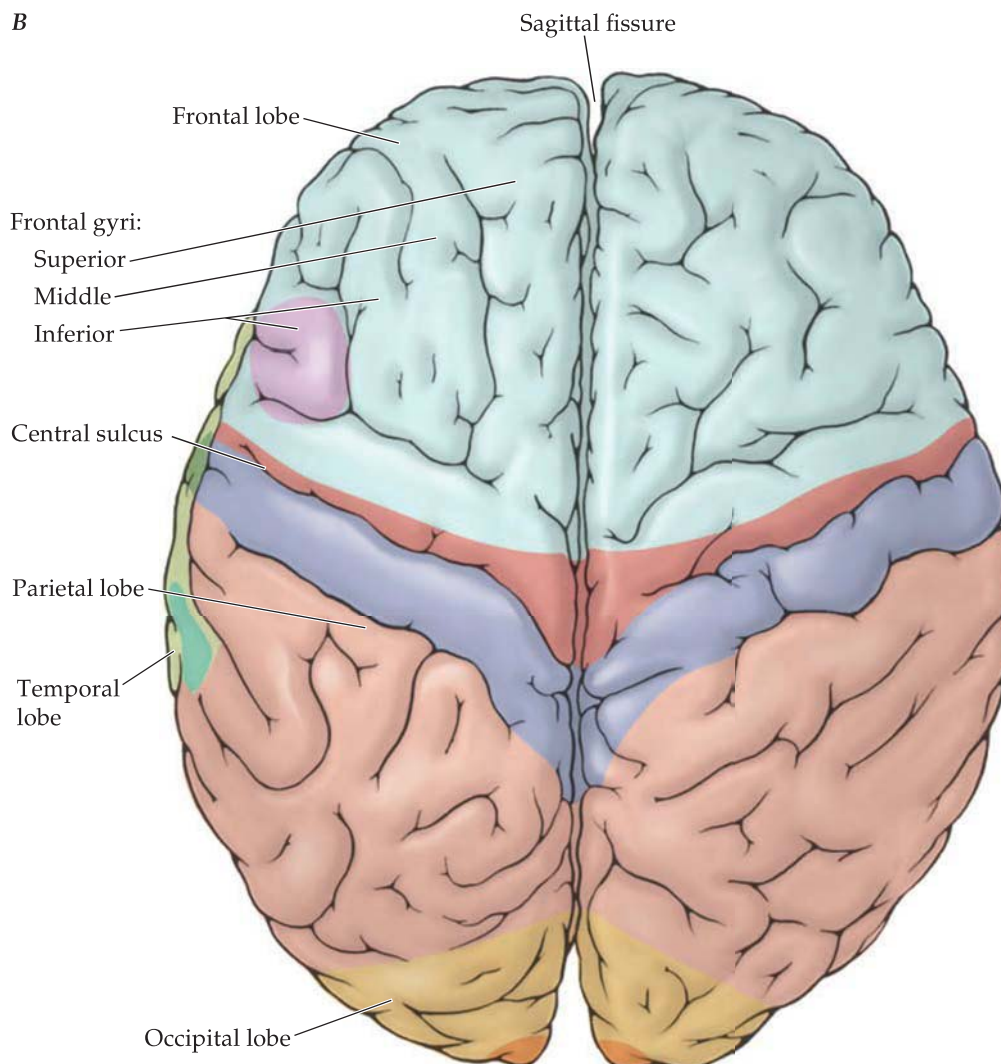
and the superior temporal sulcus for perception and localization of sounds (Figure 1–11A). The superior temporal gyrus on the left side is specialized for speech. Lesion of the posterior portion of this gyrus, which is the location of Wernicke's area, impairs the understanding of speech. The **middle temporal gyrus**, especially the portion close to the occipital lobe, is essential for perception of visual motion. The **inferior temporal gyrus** mediates the perception of visual form and color (Figures 1–11A and 1–12A). The cortex located at the **temporal pole** (Figure 1–12A), together with adjacent portions of the medial temporal lobe and inferior and medial frontal lobes, is important for emotions.

Deep within the lateral sulcus are portions of the frontal, parietal, and temporal lobes. This territory is termed the **insular cortex** (Figure 1–11, inset). It becomes buried late during prenatal development (see Figure 1–14). Portions of the insular cortex are important in taste, internal body senses, pain, and balance.

The **corpus callosum** contains axons that interconnect the cortex on the two sides of the brain (Figure 1–11B). Tracts containing axons that interconnect the two sides of the brain



**FIGURE 1–12.** *A.* Ventral surface of the cerebral hemisphere and diencephalon; the midbrain is cut in cross section. The primary visual cortex is shown at the occipital pole. *B.* Dorsal surface of the cerebral hemisphere. The primary motor and somatic sensory cortical areas are located anterior and posterior to the central sulcus. Broca's area is in the inferior frontal gyrus, and Wernicke's area is located in the posterior temporal lobe. The primary visual cortex is shown at the occipital pole.



**FIGURE 1-12.** (Continued)

are called **commissures**, and the corpus callosum is the largest of the brain's commissures. To integrate the functions of the two halves of the cerebral cortex, axons of the corpus callosum course through each of its four principal parts: rostrum, genu, body, and splenium (Figure 1-11B). Information between the occipital lobes travels through the splenium of the corpus callosum, whereas information from the other lobes travels through the rostrum, genu, and body.

### Cavities Within the Central Nervous System Contain Cerebrospinal Fluid

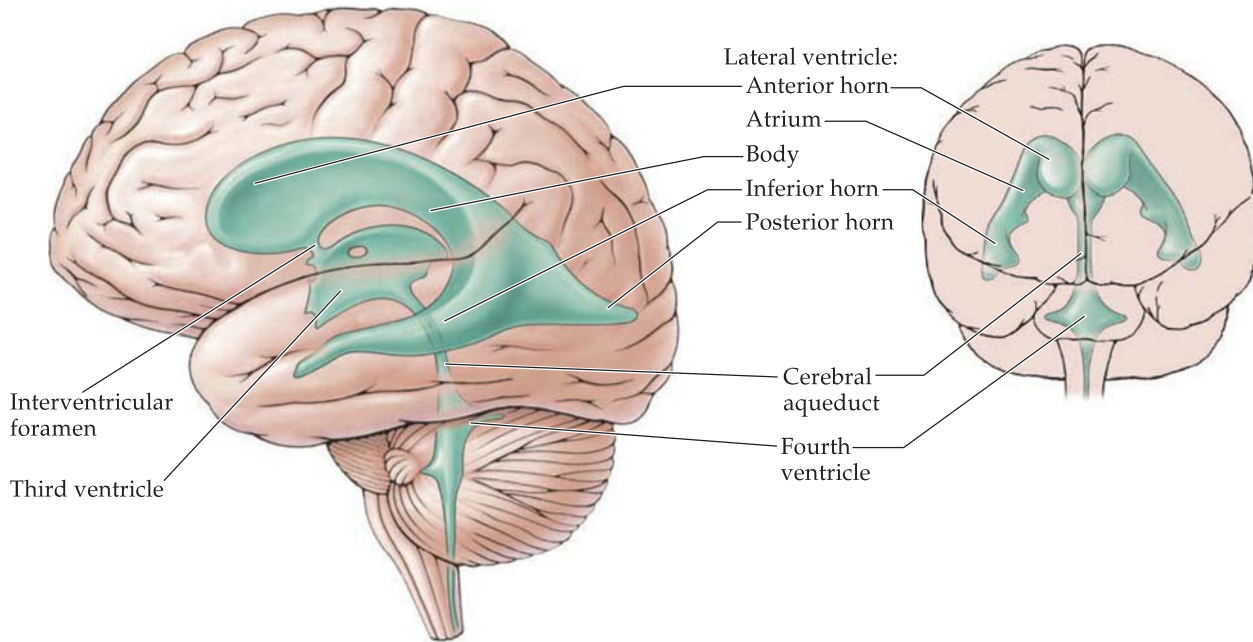
The central nervous system has a tubular organization. Within it are cavities, collectively termed the **ventricular system**, that contain **cerebrospinal fluid** (Figure 1-13). Cerebrospinal fluid is a watery fluid that cushions the central nervous system from physical shocks and is a medium for chemical communication. An intraventricular structure, the **choroid plexus**, secretes most of the cerebrospinal fluid. Cerebrospinal fluid production is considered in Chapter 3.

The ventricular system consists of ventricles, where cerebrospinal fluid accumulates, and narrow communication

channels. There are two **lateral ventricles**, each within one cerebral hemisphere, the **third ventricle**, between the two halves of the diencephalon, and the **fourth ventricle**, which is located between the brain stem and cerebellum. Development of the lateral ventricles is discussed in Box 1-2. The ventricles are interconnected by narrow channels: The **interventricular foramina** (of Monro) connect each of the lateral ventricles with the third ventricle, and the **cerebral aqueduct (of Sylvius)**, in the midbrain, connects the third and fourth ventricles. The ventricular system extends into the spinal cord as the **central canal**. Cerebrospinal fluid exits the ventricular system through several apertures in the fourth ventricle and bathes the surface of the entire central nervous system.

### The Central Nervous System Is Covered by Three Meningeal Layers

The **meninges** consist of the dura mater, the arachnoid mater, and the pia mater (see Figure 1-15). (The meninges are more commonly called the dura, arachnoid, and pia, without using the term *mater*.) The **dura mater** is the thickest and outermost of these membranes and serves a protective function. (*Dura mater*



**FIGURE 1-13. Ventricular system.** The lateral ventricles, third ventricle, cerebral aqueduct, and fourth ventricle are seen from the lateral brain surface (left) and the front (right). The lateral ventricle is divided into four main components: anterior (or frontal) horn, body, inferior (or temporal) horn, and posterior (or occipital) horn. The atrium of the lateral ventricle is the region of confluence of the body, inferior horn, and posterior horn. The interventricular foramen (of Monro) connects each lateral ventricle with the third ventricle. The cerebral aqueduct connects the third and fourth ventricles.

## BOX 1-2

### C-shaped Development of the Cerebral Hemisphere

The structure of the cerebral hemispheres is transformed markedly during development, in contrast to the spinal cord, brain stem, and diencephalon, which largely retain their longitudinal organization. This transformation is primarily the result of the enormous proliferation of cells of the **cerebral cortex**, the principal component of the cerebral hemispheres, and their subsequent cellular migration along predetermined axes. This leads to the distinctive shape of the cerebral cortex and many underlying structures.

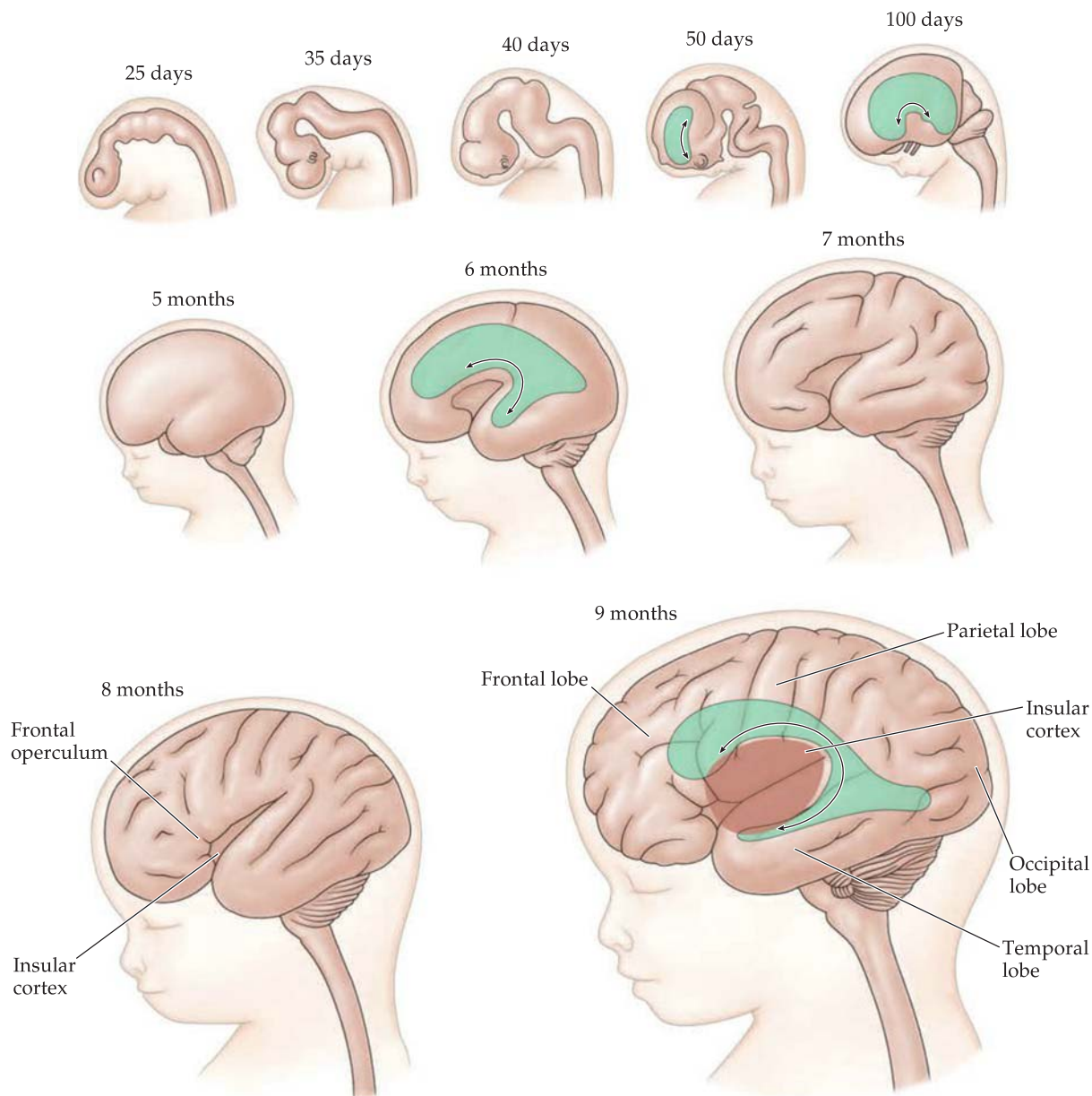
The surface area of the cerebral cortex increases enormously during development. First, the cortex is roughly spherical (Figure 1-14; 35 days). As the cortex develops, it encircles the diencephalon and takes on a **C-shape**. First, the surface area of the parietal lobe increases, followed by an increase in the frontal lobe. Next, the cortex expands posteriorly and inferiorly, forming the occipital and temporal lobes (Figure 1-14; 50–100 days). Because the cranial cavity does not increase in size in proportion to the increase in cortical surface area, this expansion is accompanied by tremendous infolding. Apart from the lateral sulcus, the cerebral cortex remains smooth, or lissencephalic, until the sixth or seventh month, when it develops gyri and sulci. About one third of the cerebral cortex is exposed, and the remainder is located within sulci. Interestingly, the hippocampal formation (see Figure 1-10A) is located on the medial brain surface very early in development. As it develops, it becomes infolded beneath the cortex of the temporal lobe.

Even before most of the gyri and sulci are present on the cortical surface, a lateral region becomes buried by the developing frontal, parietal, and temporal lobes. This region, the **insular cortex** (Figure 1-14; 7–9 months; also see Figure 1-11), is located deep within the lateral sulcus, one

of the earliest grooves to form on the lateral surface. In the mature brain, the insular cortex is revealed only when the banks of the lateral sulcus are partially separated or when the brain is sectioned (see Figure 8-8). The portions of the frontal, parietal, and temporal cortices that cover the insular cortex are termed the **opercula**. The frontal operculum of the dominant hemisphere (typically the left hemisphere in right-handed individuals) contains Broca's area, which is important in speech articulation (see Chapter 8). The parietal and temporal opercular regions and the insular cortex have important sensory functions.

As the cerebral cortex grows, it also forces many of the underlying subcortical structures to assume a C-shape: the lateral ventricle (Figure 1-10B), the striatum (Figure 1-10B), and the hippocampal formation and fornix (Figure 1-10A). The lateral ventricle is roughly spherical in shape at 1–2 months (Figure 1-14; 35 days) and is later transformed into a C-shape as the cortex develops (Figure 1-14; 100 days). By about 5 and 6 months, the lateral ventricle expands anteriorly to form the **anterior** (or frontal) **horn**, caudally to form the body and **posterior** (or occipital) **horn**, and inferiorly to form the **inferior** (or temporal) **horn** (Figure 1-14; noted on 9-month brain).

The **hippocampal formation** together with the **fornix**, where its output tracts travel, as well as the **striatum** also develop C-shapes (Figure 1-10), like that of the lateral ventricle. The hippocampal formation (Figure 1-10A) is critical for consolidating our short-term into long-term memories, and the striatum (Figure 1-10B) plays a key role in such diverse higher brain functions as cognition, limb and eye movement control, and emotions.



**FIGURE 1-14.** The development of the human brain is shown from the lateral surface in relation to the face and the general shape of the cranium. The lateral ventricle is colored green. The arrows drawn over the lateral ventricle show its emerging C-shape from an initial spherical shape (35 days). (Courtesy Tom Prentiss, illustrator.)

means “hard mother” in Latin.) Ancient surgeons knew that patients could survive even severe skull fractures if bone fragments had not penetrated the dura. Two important partitions arise from the dura and separate different components of the cerebral hemispheres and brain stem (see Figure 1-15B): (1) The **falx cerebri** separates the two cerebral hemispheres, and (2) the **tentorium cerebelli** separates the cerebellum from the cerebral hemispheres.

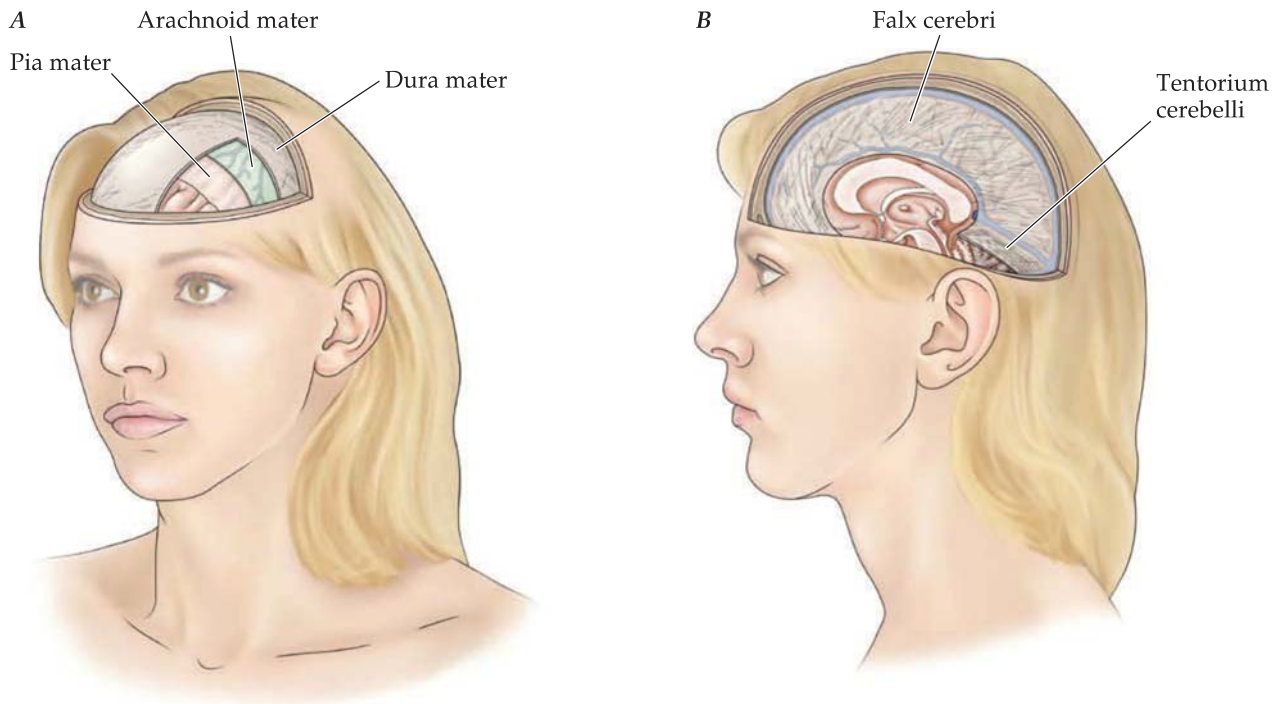
The **arachnoid mater** adjoins but is not tightly bound to the dura mater, thereby allowing a potential space, the **subdural space**, to exist between them. This space is important clinically. Because the dura mater contains blood vessels, breakage of one of its vessels due to head trauma can lead to subdural bleeding and to the formation of a blood clot (a **subdural hematoma**). In this condition the blood clot pushes the arachnoid mater

away from the dura mater, fills the subdural space, and compresses underlying neural tissue.

The innermost meningeal layer, the **pia mater**, is very delicate and adheres to the surface of the brain and spinal cord. (*Pia mater* means “tender mother” in Latin.) The space between the arachnoid mater and pia mater is the **subarachnoid space**. Filaments of arachnoid mater pass through the subarachnoid space and connect to the pia mater, giving this space the appearance of a spider’s web. (Hence the name *arachnoid*, which derives from the Greek word *arachne*, meaning “spider.”)

### An Introduction to Neuroanatomical Terms

The terminology of neuroanatomy is specialized for describing the brain’s complex three-dimensional organization. The central nervous system is organized along the **rostrocaudal** and



**FIGURE 1-15.** **A.** The meninges consist of the **dura mater**, **arachnoid mater**, and **pia mater**. **B.** The two major dural flaps are the **falx cerebri**, which incompletely separates the two cerebral hemispheres, and the **tentorium cerebelli**, which separates the cerebellum from the cerebral hemisphere. (A, B, Adapted with permission from Snell RS. *Clinical Neuroanatomy*. 7th ed. Lippincott Williams & Wilkins; 2010.)

**dorsoventral** axes of the body (Figure 1-16). These axes are most easily understood in animals with a central nervous system that is simpler than that of humans. In the rat, for example, the rostrocaudal axis runs approximately in a straight line from the nose to the tail (Figure 1-16A). This axis is the **longitudinal axis** of the nervous system and is often termed the **neuraxis** because the central nervous system has a predominant longitudinal organization. The dorsoventral axis, which is perpendicular to the rostrocaudal axis, runs from the back to the abdomen. The terms **posterior** and **anterior** are synonymous with dorsal and ventral, respectively.

The longitudinal axis of the human nervous system is not straight as it is in the rat (Figure 1-16B). During development the brain—and therefore its longitudinal axis—undergoes a prominent bend, or **flexure**, at the midbrain. Instead of describing structures located rostral to this flexure as dorsal or ventral, we typically use the terms **superior** and **inferior**. As described in Box 1-1, this axis bend reflects the persistence of the cephalic flexure (see Figure 1-5).

We define three principal planes relative to the longitudinal axis of the nervous system in which anatomical sections are made (Figure 1-17). **Horizontal** sections are cut parallel to the longitudinal axis, from one side to the other. **Transverse** sections are cut perpendicular to the longitudinal axis, between the dorsal and ventral surfaces. Transverse sections through the cerebral hemisphere are roughly parallel to the coronal suture of the skull and, as a consequence, are also termed **coronal** sections. **Sagittal** sections are cut parallel both to the longitudinal axis of the central nervous system and to the midline, between the dorsal and ventral surfaces. A **midsagittal** section divides the central nervous system into two symmetrical halves,

whereas a **parasagittal** section is cut off the midline. Radiological images are also obtained in these planes. This will be described in Chapter 2.

## Summary

### Cellular Organization of the Nervous System

The cellular constituents of the nervous system are *neurons* (Figure 1-2) and *glia* (Figure 1-3). Neurons have four specialized regions: (1) the *dendrites*, which receive information, (2) the *cell body*, which receives and integrates information, and (3) the *axon*, which transmits information from the cell body to (4) the *axon terminals*. There are three neuron classes: *unipolar*, *bipolar*, and *multipolar* (Figure 1-2B). Intercellular communication occurs at *synapses*, where *neurotransmitters* are released. The glia include four types of *macroglia*. *Oligodendrocytes* and *Schwann cells* form the myelin sheath in the central and peripheral nervous systems, respectively. *Astrocytes* serve as structural and metabolic support for neurons. *Ependymal cells* line the ventricular system. The glia also consist of the *microglia*, which are phagocytic.

### Regional Anatomy of the Nervous System

The nervous system contains two separate divisions: the *peripheral nervous system* and the *central nervous system* (Figure 1-4). Each system may be further subdivided. The *autonomic* division of the peripheral nervous system controls the glands and smooth muscle of the viscera and blood vessels, whereas the *somatic* division provides the sensory innervation of body tissues and the motor innervation of skeletal muscle. There are seven separate components of

- Anterior olfactory nucleus, 192–193, 200, 203, 451*f*
- Anterior perforated substance, 197, 203, 371
- Anterior pituitary hormones, 336*t*
- Anterior temporal lobe degeneration, 357–358, 358*f*
- Anterior thalamic nuclei, 366, 379, 440*f*–441*f*, 452*f*–453*f*, 461*f*
- Anterograde amnesia, 362
- Anterograde degeneration, 36
- Anterolateral system, 101, 115, 405*f*, 407*f*, 409*f*, 411*f*, 413*f*, 415*f*, 417*f*, 419*f*, 421*f*, 423*f*, 425*f*, 427*f*, 429*f*, 431*f*, 435*f*
- axons, 290*f*
- decussation of, 108*f*
- lesions, 251
- medial lemniscus and, 109
- pain pathways and, 113*f*
- projection neurons and, 106
- trigeminothalamic tract and, 129
- Anteroventral cochlear nucleus, 181
- Antidiuretic hormone (ADH), 336–337
- Aortic arch, 132
- Aphasia, 179–181
- global, 53
- Apraxias, 220
- Arachnoid granulations, 72*f*, 74
- Arachnoid mater, 21, 21*f*, 24, 68*f*
- Arachnoid villi, 73, 74
- Arbor vitae, 279
- Archicortex, 199, 377
- Arcuate fasciculus, 179
- Arcuate nucleus, 334*f*, 335, 345, 369, 417*f*, 421*f*
- Area postrema, 70*f*, 74, 401*f*
- Argyll Robertson pupils, 271
- Arterial blood supply, 55
- Ascending pathways, 30
- Association areas, 95
- Association cortex, 17, 43
- Associative loop, 314, 315*f*
- Astrocytes, 7, 8*f*, 9, 22, 127
- Ataxia, 169, 251, 287, 329, 331
- Friedreich, 277–278, 284
- Athetosis, 313
- Auditory axons, 175
- Auditory cortex
- defects, 179–181
- fMRI of, 178*f*
- higher-order areas, 171, 178*f*, 178–179, 181
- linguistics processing and, 179
- primary, 18, 171, 178*f*, 181
- Heschl's gyri and, 177
- secondary, 171, 178*f*, 178–179
- linguistics processing and, 179
- Auditory system
- functional anatomy of, 169–171
- organization of, 172*f*
- organs, 171–173
- regional anatomy of, 171–181
- sensitivity, 173–175
- Auricle, 172*f*
- Autism spectrum disorder, 289
- Autonomic control, 370*f*
- Autonomic division, of peripheral nervous system, 9–10, 22, 346
- Autonomic motor column, 239, 241–242
- Autonomic motor fibers. *See* Visceral motor fibers
- Autonomic nervous system, 332, 337–340
- autonomic motor column and, 241–242
- organization of, 339*f*
- Autonomic nuclei, 253
- Axial muscles, 215, 218–220, 231, 273
- bilateral control of, 218
- control, 262
- spinocerebellum and, 284
- Axons, 6, 6*f*, 22. *See also specific reflex axon types*
- ascending, 46*f*
- auditory, 175
- degeneration, 237
- descending, 43–44, 46*f*
- dorsal column, 90
- large-diameter, 83, 96
- mechanoreceptors, 89–90
- motor, 11
- in peripheral nerves, 10
- sensory, 11
- small-diameter, 83, 115
- terminals, 6, 6*f*, 22
- unmyelinated, 191
- B**
- Babinski's sign, 222
- Bait shyness, 187–188
- Balance, 82, 126
- Ballistic movements, 314
- Bare nerve endings, 83, 105, 115
- Basal cells, 188, 194
- Basal cerebral vein, 67*f*
- Basal forebrain, 17, 197
- acetylcholine and, 32–33
- cholinergic systems in, 373–374
- components of, 371–374
- ventral amygdalofugal pathway and, 376
- Basal ganglia, 13*f*, 14, 17*f*, 23, 304
- blood supply of, 56*t*, 62, 323
- components of, 305, 305*t*
- development of, 305–308, 307*f*
- emotional loop of, 359
- functional anatomy of, 308–314
- functional circuits in, 312*f*–313*f*
- horizontal section, 317*f*
- information integration in, 314, 315*f*
- input-output loops of, 314
- internal capsule and, 44
- intrinsic circuitry of, 311
- limbic loop of, 369*f*, 370
- motor system functional anatomy and, 211
- neurotransmitters and, 310*f*, 311
- nuclei, 306*f*
- organization of, 305–308
- parallel circuits in, 314
- pathways in, 308–309, 310*f*
- pedunculo-pontine nucleus and, 322
- regional anatomy of, 314–323
- Basal nucleus, 32*f*, 368, 371, 373*f*, 374
- Basilar artery, 55, 58*f*, 59*f*, 74, 247*f*
- brain stem blood supply and, 57, 60
- Basis pedunculi, 38, 38*f*, 40, 48, 216, 224*f*, 227*f*, 246*f*, 295, 393*f*, 397*f*, 399*f*, 429*f*, 431*f*, 433*f*, 463*f*
- corticospinal tract and, 41, 225
- posterior cerebral artery occlusion and, 267
- Basket neurons, 293
- Basolateral nuclei, 364*f*, 366–368
- Bell's palsy, 243
- Benign positional vertigo, 264
- β-endorphin, 345
- Bilateral muscular control, 218
- Bilateral projection, 243
- Binocular inputs, 157
- Bipolar cells, 150, 153*f*, 181
- Bipolar neurons, 6–7, 22, 125, 201
- Bitemporal heteronymous hemianopia, 163
- Bladder control, 347, 349*f*

- Cerebellar cortex (*Cont.*):  
 neurons of, 293*t*  
 Purkinje layer of, 291, 292*f*
- Cerebellar folium, 292*f*
- Cerebellar glomerulus, 293
- Cerebellar hemisphere, 279, 280*f*, 389*f*, 395*f*
- Cerebellar lobes, 281*f*
- Cerebellar nuclei, 282*f*
- Cerebellar peduncles, 279, 399*f*, 401*f*, 423*f*
- Cerebellar tentorium, 279
- Cerebellopontine angle, 266
- Cerebellothalamic fibers, 431*f*, 433*f*
- Cerebellothalamic tract, 295
- Cerebellum, 10, 12, 17*f*, 23  
 blood supply of, 56*t*  
 circuitry, 282*f*  
 damage to, 287–289  
 efferent projections of, 289*f*  
 functional anatomy of, 279–289  
 functional divisions of, 279, 282, 283*f*, 284  
 gross anatomy of, 279  
 inhibitory circuitry of, 293  
 lateral surface of, 388*f*–389*f*  
 midsagittal section through, 394*f*–395*f*  
 motor system functional anatomy and, 211  
 nodulus of, 423*f*  
 nonmotor functions of, 295  
 oblique section of, 456*f*–457*f*  
 output path of, 296*f*  
 posterior circulation and, 57  
 regional anatomy of, 289–297  
 sagittal section of  
 near midline, 458*f*–459*f*  
 through amygdaloid complex, 464*f*–465*f*  
 through mamillothalamic tract, 460*f*–461*f*  
 through ventral posterior lateral nucleus, 462*f*–463*f*  
 smooth pursuit movements and, 264
- Cerebral angiography, 64, 65*f*–66*f*
- Cerebral aqueduct, 10, 19, 24, 41, 393*f*, 395*f*, 427*f*, 429*f*, 431*f*, 433*f*
- Cerebral arteries, 74
- Cerebral cortex, 23, 96–97  
 anterolateral system and, 115  
 basolateral nuclei and, 366–368  
 blood supply of, 57*t*, 63–64  
 cerebrocerebellum and, 284  
 columnar organization of, 156  
 contralateral, 285  
 cranial motor nuclei control and, 242–243  
 cytoarchitectonic map of, 45, 49*f*  
 eye movement control and, 273  
 input-output organization of, 45  
 layers of, 48*f*  
 lobes of, 15–19  
 neuronal organization of, 45  
 olfactory system and, 191–194  
 subcortical structures of, 41–43  
 visual field and, 151
- Cerebral hemisphere, 10, 14, 23  
 blood supply of, 60*f*–61*f*, 61  
 coronal section of  
 through anterior limb of internal capsule, 446*f*–449*f*  
 through anterior thalamic nuclei, 440*f*–441*f*  
 through head of caudate nucleus, 450*f*–451*f*  
 through intraventricular foramen, 442*f*–443*f*  
 through posterior limb of internal capsule, 434*f*–437*f*
- C-shaped development of, 20
- dorsal surface of, 19*f*
- horizontal section of, 454*f*–455*f*  
 through anterior thalamic nuclei, 452*f*–453*f*
- inferior surface of, 392*f*
- lateral surface of, 16*f*, 388*f*–389*f*
- lateral view of, 141*f*
- limbic system and, 359*t*
- medial surface of, 17*f*, 394*f*–395*f*
- midsagittal section of, 361*f*
- oblique section of, 438*f*–439*f*, 444*f*–445*f*, 456*f*–457*f*
- olfactory bulb and, 121
- organization of, 48
- sagittal section of  
 near midline, 458*f*–459*f*  
 through amygdaloid complex, 464*f*–465*f*  
 through mamillothalamic tract, 460*f*–461*f*  
 through ventral posterior lateral nucleus, 462*f*–463*f*
- superior surface of, 390*f*–391*f*
- at thalamus, 46*f*, 47*f*  
 ventral surface of, 18*f*, 362*f*
- Cerebral palsy, 227*f*
- Cerebral peduncle, 40, 225
- Cerebral vasculature, 64
- Cerebral veins, 64–67, 67*f*
- Cerebrocerebellum, 283*f*, 284–287  
 connections to, 287*f*  
 pontine nuclei and, 291
- Cerebrospinal fluid, 10, 24, 74  
 central nervous system cavities containing, 19  
 circulation of, 71  
 functions of, 67–71  
 lumbar cistern and, 71  
 MRI and, 36  
 production of, 71  
 removal of, 73*f*  
 return path of, 73–74
- Cervical flexure, 10
- Cervical spinal cord  
 degeneration, 277
- Cholinergic neurons, 33
- Cholinergic systems, 373–374
- Chorda tympani nerve, 189
- Chorea, 313
- Choroid epithelium, 71
- Choroid plexus, 10, 19, 70*f*, 71, 74
- Ciliary ganglion, 253, 270*f*, 271
- Ciliary muscle, 241
- Cingulate cortex, 361*f*, 368  
 pain pathways and, 113*f*
- Cingulate gyrus, 17, 360, 395*f*, 435*f*, 437*f*, 439*f*, 441*f*, 443*f*, 445*f*, 447*f*, 449*f*, 451*f*, 453*f*, 457*f*, 461*f*, 463*f*  
 subgenual region of, 360
- Cingulate motor area, 218*f*, 220, 221*f*, 222
- Cingulate sulcus, 17*f*, 395*f*
- Cingulum, 361, 374, 435*f*, 437*f*, 439*f*, 441*f*, 443*f*, 445*f*, 447*f*, 449*f*, 451*f*, 453*f*, 457*f*, 461*f*
- Circadian responses, 342–344, 343*f*
- Circle of Willis, 61, 74
- Circumvallate papillae, 189*f*
- Circumventricular organs, 69, 74, 337  
 blood-brain barrier and, 70*f*
- Cisterna magna, 71
- Cisterns, 71, 72*f*
- Clarke's column, 278
- Clarke's nucleus, 284, 290, 409*f*, 411*f*
- Clastrum, 437*f*, 439*f*, 441*f*, 443*f*, 445*f*, 447*f*, 449*f*, 451*f*, 453*f*, 455*f*, 457*f*, 465*f*
- Climbing fibers, 279, 294*f*  
 from inferior olivary nuclear complex, 291  
 inferior olivary nucleus and, 291

- Descending motor pathways (*Cont.*):  
 organization of, 215  
 parallel, 213  
 posture and, 218–220  
 regional anatomy of, 220–229  
 somatotopic organization of, 213f  
 spinal cord and, 228–229
- Descending pathways, 30
- Descending projection neurons,  
 45, 95
- Descending projections, 97, 137
- Descending visceromotor pathways,  
 340
- Diabetes insipidus, 345
- Diagonal band of Broca, 371, 449f, 455f,  
 461f  
 nucleus of, 32f
- Diencephalon, 10, 14, 15f, 16f, 17f, 23,  
 332f  
 acetylcholine and, 32–33  
 blood supply of, 56t, 61  
 coronal section of  
 through anterior thalamic nuclei,  
 440f–441f  
 through intraventricular foramen,  
 442f–443f  
 through posterior limb of internal  
 capsule, 434f–437f  
 cranial motor nuclei control and,  
 242–243  
 horizontal section of  
 at anterior commissure,  
 454f–455f  
 through anterior thalamic nuclei,  
 452f–453f  
 inferior surface of, 392f–393f  
 limbic system and, 359t  
 midbrain juncture, 432f–433f  
 midsagittal section through,  
 394f–395f  
 oblique section of, 438f–439f,  
 444f–445f, 456f–457f  
 organization of, 48  
 sagittal section of  
 near midline, 458f–459f  
 through mamillothalamic tract,  
 460f–461f  
 through ventral posterior lateral  
 nucleus, 462f–463f  
 ventral surface, 18f
- Diffuse-projecting neurons, 31
- Diffuse-projecting nuclei, 42, 48
- Diffusion tensor imaging (DTI), 27, 28f,  
 36, 37f, 179  
 of corticopontine projection, 295
- Diffusion-weighted imaging (DWI),  
 54f
- Diplopia, 257–259
- Disinhibition, 311
- Distal muscles, 284
- Dopamine, 7, 32f, 47, 311, 346  
 amacrine cells and, 150  
 in modulatory systems, 33  
 prolactin and, 335  
 schizophrenia and, 371  
 striatal neurons and, 311  
 substantia nigra pars compacta and,  
 321
- Dorsal cochlear nucleus, 173, 175
- Dorsal column-medial lemniscal  
 system, 30–31, 31f, 96, 108f  
 HGPPS and, 29  
 mechanical sensations and, 82  
 organization of, 84f  
 pathway, 85f  
 touch receptors and, 31
- Dorsal columns, 30–31, 38f, 47, 80f  
 axons, 90  
 decussation of, 90  
 mechanoreceptor axons and, 89  
 nuclei, 30–31, 39f, 48, 82, 85f, 96,  
 416f–417f  
 mechanoreceptor axons and, 89  
 somatic organization of, 90  
 somatotopic organization of, 91f  
 visceral pain and, 101, 105, 115
- Dorsal cortex, 176, 181
- Dorsal horn, 33, 47, 89, 115  
 anterolateral system and, 101  
 anterolateral system projection  
 neurons and, 106–107  
 base of, 405f, 407f, 411f, 413f  
 pain pathways and, 113f  
 primary sensory axon terminals in,  
 106f  
 spinal trigeminal nucleus and,  
 133–135  
 superficial laminae of, 105  
 visceral pain and, 101, 105
- Dorsal intermediate septum, 90,  
 413f
- Dorsal intermediate sulcus,  
 401f, 413f
- Dorsal longitudinal fasciculus, 346,  
 348f, 419f, 423f, 425f, 427f,  
 431f, 459f
- Dorsal median septum, 90, 405f, 407f,  
 409f, 411f, 413f
- Dorsal median sulcus, 401f, 405f, 407f,  
 409f, 411f, 413f
- Dorsal medulla, 130
- Dorsal motor nucleus of vagus, 241, 253,  
 347, 368, 417f, 419f
- Dorsal raphe nucleus, 342, 371, 429f
- Dorsal root, 11, 12f, 33, 96, 115, 399f,  
 401f, 405f
- Dorsal root ganglion, 84f  
 limb proprioception and, 80  
 neurons, 33, 82–83, 96  
 central branches of, 83
- Dorsal spinocerebellar tract, 284,  
 290f, 291, 409f, 411f, 413f, 415f,  
 417f
- Dorsal stream, 164  
 spatial localization and, 160
- Dorsal tegmental nucleus, 427f
- Dorsal trigeminothalamic tract, 128
- Dorsolateral medulla, 119
- Dorsolateral prefrontal association  
 cortex, 361f
- Dorsolateral prefrontal cortex, 179, 371
- Dorsolateral tegmentum, 340
- Dorsomedial nucleus, 334f
- Dorsoventral axis, 22, 24
- Drug abuse, 368
- DTI. *See* Diffusion tensor imaging
- Dura mater, 19, 21, 23f, 24, 68f  
 dural sinuses and, 66
- Dural sinuses, 24, 55, 66, 67f, 74  
 return path of cerebrospinal fluid  
 and, 73–74
- DWI. *See* Diffusion-weighted imaging
- Dynorphin, 310f
- Dysdiadochokinesia, 329, 331
- Dysphagia, 250
- Dystonia, 304
- ## E
- Ear  
 ipsilateral, 173  
 structure of, 172f
- Ectodermal origin, 345
- Edinger-Westphal nucleus, 241, 253,  
 270f, 271, 431f, 433f, 437f,  
 457f
- Effector systems, 368–370, 370f
- Efferent neurons, 38
- Electrical synapses, 7
- Electrocoagulation, 322
- Emboliform nucleus, 279, 289f
- Emetics, 188
- Emotions, 359, 371–381
- Encapsulated axon terminals, 84
- Endocrine hormones, 332

- Genu (*Cont.*):  
 of internal capsule, 44, 224*f*, 225, 316  
 blood supply of, 225  
 lesion of, 246  
 voluntary eye movements and, 263
- Ghrelin, 345
- Girdle muscles, 215, 218–220, 231  
 bilateral control of, 218
- Glia, 5, 22  
 cell types, 7–9  
 glomerulus and, 197
- Glial capsule, 293
- Globose nucleus, 279, 289*f*
- Globus pallidus, 306*f*, 320*f*, 321*f*, 437*f*, 439*f*, 441*f*, 443*f*, 445*f*, 447*f*, 449*f*, 451*f*, 453*f*, 455*f*, 457*f*, 463*f*  
 external segment of, 305  
 anterior commissure and, 319  
 putamen neurons and, 311  
 internal segment of, 305, 310*f*, 311, 321, 322*f*  
 posterior limb of internal nucleus and, 316  
 ventral pallidum and, 308
- Glomerulus, 192, 197, 292*f*
- Glossopharyngeal nerve, 124, 127, 131, 140–141, 189, 253, 397*f*, 399*f*, 401*f*, 421*f*  
 exiting fibers of, 249*f*  
 gustatory innervation and, 190*f*  
 nucleus ambiguus and, 239–240  
 parasympathetic postganglionic neurons and, 241  
 rostral medulla and, 248–249  
 sensory axons from, 127  
 taste and, 187  
 taste buds and, 201
- Glutamate, 7  
 corticostriatal neurons and, 310
- Glycine, 7
- Golgi neuron, 293
- Golgi staining, 34*f*
- Golgi tendon organ, 86*f*, 96  
 termination of, 106
- Golgi tendon receptor, 83
- Gonadotropin-releasing hormone, 335
- Gracile fascicle, 85*f*, 90, 96, 115, 405*f*, 407*f*, 409*f*, 411*f*, 413*f*, 415*f*, 417*f*, 459*f*
- Gracile nucleus, 85*f*, 90, 92*f*, 115, 415*f*, 417*f*, 459*f*
- Gracile tubercle, 401*f*
- Granular layer, of cerebellar cortex, 291, 292*f*
- Granule cells, 197, 201
- Granule neurons, 293
- Gray matter, 11, 12*f*  
 central, 415*f*  
 mechanoreceptor axons in, 89  
 MRI and, 36  
 periventricular, 425*f*, 435*f*, 459*f*  
 spinal cord, 89  
 spinal cord organization of, 231*f*
- Great cerebral vein (of Galen), 65
- GSM fibers. *See* General somatic motor (GSM) fibers
- GSS fibers. *See* General somatic sensory (GSS) fibers
- Gustatory cortex, 188*f*
- Gustatory information, 190–191, 200
- Gustatory innervation, 190*f*
- Gustatory receptors, 201
- Gustatory system, 191*f*  
 organization of, 188*f*  
 pathway lesion of, 186*f*  
 pathways, 187–188  
 regional anatomy of, 188–191
- GVM fibers. *See* General visceral motor (GVM) fibers
- GVS fibers. *See* General visceral sensory (GVS) fibers
- Gyri, 23. *See also specific gyrus*
- Gyrus rectus, 197, 393*f*
- H**
- Habenula, 373, 401*f*, 435*f*, 439*f*, 445*f*, 455*f*
- Habenulointerpeduncular tract, 431*f*, 433*f*, 435*f*, 437*f*, 457*f*, 459*f*
- Hair cells, 169, 181  
 basal, 172  
 inner, 171  
 olivocochlear system and, 175  
 organ of Corti and, 171–172  
 outer, 171
- Hand weakness, 99–100
- Head movements, 287
- Hearing, 126  
 unilateral loss of, 167
- Hemiparesis, 237–238, 238*f*
- Hemineglect, 146
- Hemiparesis, 237–238, 238*f*
- Hemiplegic cerebral palsy, 225
- Hemorrhagic stroke, 55, 74
- Heschl's gyri, 171, 172*f*, 177, 178*f*, 181
- HGPPS. *See* Horizontal gaze palsy with progressive scoliosis
- Hierarchical organization, 147
- Hindbrain, 10  
 segmented structure of, 87*f*
- Hippocampal formation, 14, 15*f*, 23, 360*f*, 363*f*, 377*f*, 443*f*, 447*f*, 455*f*  
 Alzheimer disease and, 3  
 archicortex and, 199  
 blood supply of, 56*t*  
 circuits of, 363*f*, 363–366  
 components of, 363  
 cortical projections from, 366  
 C-shaped development of, 20  
 location of, 376–378  
 memory and, 359  
 memory consolidation and, 362–366  
 neurogenesis and, 201
- Hippocampal sulcus, 376
- Hippocampus, 363, 376, 435*f*, 437*f*, 441*f*, 457*f*, 465*f*
- Histamine, 83, 342, 346
- Hoffmann's sign, 222
- Homonymous hemianopsia, 145–146, 146*f*, 163, 164
- Horizontal cells, 150
- Horizontal gaze palsy with progressive scoliosis (HGPPS), 27–29, 28*f*
- Horizontal sections, 22, 23*f*, 24
- Hormone regulation, 334–336, 336*t*
- Horner syndrome, 251, 350–351, 351*f*
- Horner syndrome and, 251
- Huntington disease, 304, 313*f*, 313–314  
 medium spiny neurons and, 318
- Hydrocephalus, 10
- Hydrocephalus ex vacuo, 71
- Hyperalgesia, 105
- Hyperkinetic movement disorders, 313–314
- Hyperkinetic signs, 312*f*–313*f*, 313–314
- Hyperreflexia, 222  
 concurrent with muscle weakness, 238
- Hypocretins, 346
- Hypoglossal motor neurons, 251
- Hypoglossal nerve, 124, 140, 239, 252, 397*f*, 399*f*, 419*f*
- Hypoglossal nucleus, 239, 249*f*, 252, 417*f*, 419*f*, 459*f*  
 innervation of, 243
- Hypoglossal trigone, 401*f*
- Hypoglossus, 239

- Interstitial nucleus  
   of Cajal, 267, 433*f*  
   of the medial longitudinal fasciculus, 274  
 Interventricular foramen, 10, 19, 24, 443*f*  
 Intra-arterial pressure, 127  
 Intrafusal fibers, 86*f*  
 Intralaminar nuclei, 42, 43*f*, 44*t*, 48  
   pain processing and, 111  
 Intraparietal sulcus, 389*f*, 391*f*  
 Intra-ventricular foramen, 442*f*–443*f*, 453*f*, 457*f*  
 Intra-ventricular pressure, 70  
 Intrinsic nuclei, 305, 305*t*  
 Involuntary unilateral ballistic limb movements, 303–304, 304*f*  
 Ipsilateral pathway, 137  
 Ischemia, 55, 74  
 Ischemic stroke, 55, 74  
 Itch, 81*t*, 82, 83, 115  
   anterolateral system and, 101  
   cortical representations of, 113–115  
   processing, 111  
   small-diameter sensory fibers and, 105–106  
   trigeminal pathways for, 131*f*–132*f*  
   trigeminal sensory system and, 142  
 Itch-sensitive receptors, 105
- J**
- Jaw proprioception, 125, 139*f*  
 Jaw-jerk reflex, 137, 139*f*  
 Juvenile motor impairments, 277–278, 278*f*  
 Juxtarestiform body, 423*f*
- K**
- Knee-jerk reflex, 35  
 Koniocellular system, 156  
 Korsakoff syndrome, 380
- L**
- Lacrimal glands, 248, 253  
 Lamina terminalis, 371  
   organum vasculosum of, 337  
   vascular organ of, 70*f*, 74  
 Language, 54  
 Large-diameter fiber entry zone (spinal cord), 405*f*, 407*f*, 409*f*, 411*f*, 413*f*  
 Laryngeal closure reflex, 137  
 Laryngeal mucosa, 127  
 Laryngeal muscles, 330  
 Larynx, 130, 253  
   innervation of, 132  
   nucleus ambiguus and, 239  
 Lateral column, 35, 47, 229  
 Lateral corticospinal tract, 213, 215, 216*f*, 223*f*, 227–228, 229, 405*f*, 407*f*, 409*f*, 411*f*, 413*f*  
   axons, 227  
 Lateral dorsal nucleus, 435*f*, 437*f*  
 Lateral gaze palsy, 271  
 Lateral geniculate body, 399*f*, 401*f*  
 Lateral geniculate neurons, 156  
 Lateral geniculate nucleus, 147, 156*f*, 163, 177*f*, 431*f*, 433*f*, 435*f*, 437*f*  
   primary visual cortex and, 154  
   visual field defects and, 163  
 Lateral hemisphere, 284  
 Lateral hypothalamus, 443*f*, 447*f*  
 Lateral lemniscus, 170, 175, 181, 423*f*, 425*f*, 427*f*, 429*f*, 457*f*, 461*f*  
   nucleus of, 175, 427*f*  
 Lateral mammillary nucleus, 443*f*  
 Lateral medullary lamina, 439*f*, 441*f*, 443*f*, 445*f*, 447*f*, 455*f*, 457*f*  
 Lateral medullary syndrome, 109, 137, 250*f*, 251, 351  
   PICA occlusion and, 288  
 Lateral motor nuclei, 217*f*, 228–229  
 Lateral nuclei, 42, 43*f*, 44*t*, 48  
 Lateral olfactory stria, 197, 393*f*, 451*f*  
 Lateral posterior lateral nucleus, 463*f*  
 Lateral posterior nucleus, 154, 435*f*, 437*f*, 439*f*, 445*f*, 453*f*, 463*f*  
 Lateral prefrontal cortex, 315*f*  
 Lateral rectus motor neurons, 262  
 Lateral rectus muscle, 239, 252, 262, 263*f*, 268  
   abducens nerve lesion and, 271  
 Lateral reticular nucleus, 291, 417*f*, 419*f*  
 Lateral reticulospinal tract, 415*f*  
 Lateral sulcus, 16*f*, 18, 389*f*, 453*f*, 465*f*  
   blood supply of, 64*f*  
 Lateral superior olivary nucleus, 173  
 Lateral ventral horn, 215, 229  
 Lateral ventricle, 10, 19, 24, 321*f*, 433*f*, 435*f*, 437*f*, 439*f*, 441*f*, 443*f*, 445*f*, 447*f*, 449*f*, 451*f*, 453*f*, 455*f*, 457*f*, 461*f*, 463*f*, 465*f*  
   anterior horn, 4*f*, 20, 318*f*  
   atrium, 4*f*  
   inferior horn, 4*f*, 20  
   posterior horn, 20  
 Lateral vestibular nucleus, 262, 267, 273  
 Lateral vestibulospinal tract, 261*f*, 262, 267, 273, 405*f*, 407*f*, 409*f*, 411*f*, 413*f*, 415*f*, 417*f*  
 L-dopa, 312  
 Learning, 371–381  
 Lens, 149  
 Lenticular fasciculus, 319, 321*f*, 433*f*, 439*f*, 441*f*, 443*f*, 445*f*  
 Lenticular nucleus, 46*f*, 316  
 Lenticulostriate arteries, 62, 323  
 Lenticulostriate branches, 225  
 Leptin, 345  
 Levator palpebrae superioris muscle, 239, 252, 262  
 Limb control, 211–213  
 Limb motor signs, 288  
 Limb muscles, 215  
   descending motor pathways and, 215–218  
 Limb position sense, 108*f*  
 Limb proprioception, 79–80, 81*t*, 82  
 Limb withdrawal to noxious stimulation, 54  
 Limbic association area, 213  
 Limbic association cortex, 43, 359–362, 362*f*  
 Limbic loop, 314, 315*f*  
 Limbic system, 14, 24, 222, 358–359  
   association areas, 361*f*  
   brain stem components of, 380*f*  
   components of, 359*t*  
   neurotransmitter regulatory systems and, 370–371  
   regional anatomy of, 371–381  
   somatic senses and, 113–115  
   structures, 380*f*  
 Lingual gyri, 393*f*  
 Linguistic processing, 179, 180*f*  
 Lissauer tract, 89, 105, 115, 405*f*, 407*f*, 409*f*, 411*f*, 413*f*  
   spinal trigeminal tract and, 135  
 Lithium chloride, 188  
 Lobules, 279  
 Locomotor control centers, 322  
 Locus ceruleus, 32*f*, 33, 371, 427*f*, 461*f*  
 Long circumferential branches, 57  
 Longitudinal axis, 22, 24  
 Lumbar cistern, 71, 73*f*  
 Lumbar tap, 71, 73*f*  
 Luteinizing hormone-releasing hormone, 335  
 Lymph nodes, 351*f*

- Memory, 359, 371–381  
 consolidation, 362–366  
 declarative, 365  
 episodic, 365  
 explicit, 362, 365  
 implicit, 362, 365  
 nondeclarative, 365  
 spatial, 365  
 working, 286
- Meningeal layers, 19, 21, 23*f*, 24, 68*f*
- Meperidine, 313
- Merkel's cells, 83
- Merkel's receptors, 96
- Mesencephalic trigeminal nucleus, 127, 131, 139*f*, 142, 425*f*, 429*f*, 431*f*, 457*f*, 461*f*
- Mesencephalic trigeminal tract, 137, 425*f*, 429*f*, 431*f*, 461*f*
- Mesencephalon, 10. *See also* Midbrain
- Mesodermal tissue, 83
- Mesolimbic dopaminergic system, 368
- Metabolism, 340
- Meyer's loop, 154, 156*f*, 163  
 visual field defects and, 162*f*
- MFB. *See* Medial forebrain bundle
- Microglia, 7, 22
- Microzones, 294
- Midbrain, 4*f*, 10, 12, 13*f*, 17*f*, 23, 110*f*, 395*f*  
 auditory centers, 176*f*  
 blood supply of, 56*t*, 59*f*, 60  
 colliculi and, 40–41  
 cross section, 18*f*  
 diencephalon juncture, 432*f*–433*f*  
 extraocular motor nuclei and, 267–270  
 eye control and, 147–149  
 eye movement control and, 163  
 limbic system and, 359*t*  
 MRI, 42*f*  
 myelin-stained, 42*f*  
 regions of, 40–41  
 rostral, 40  
 nuclei, 225  
 transverse section of, 430*f*–431*f*  
 tectum, 175–176  
 visual field and, 151
- Middle cerebellar peduncle, 279, 285, 291, 425*f*, 427*f*, 435*f*, 437*f*, 463*f*
- Middle cerebral artery, 58*f*, 60*f*, 61, 74, 146*f*, 246, 323, 451*f*  
 branches of, 63*f*  
 cerebral cortex and, 63  
 collateral circulation and, 62*f*  
 occlusion, 54*f*  
 through lateral sulcus, 64*f*  
 visual field defects and, 163
- Middle ear ossicles, 169, 172
- Middle frontal gyrus, 391*f*
- Middle hypothalamus, 447*f*
- Middle temporal gyrus, 18, 389*f*
- Midline grooves, 29
- Midline nuclei, 42, 43*f*, 44*t*
- Midline thalamic nuclei, 455*f*, 457*f*
- Midline thalamic tract, 459*f*
- Midmedulla, 39  
 cranial nerve nuclei in, 249
- Midsagittal sections, 22
- Mirror neurons, 220
- Mitral cells, 197
- Mixed nerves, 124
- MLF. *See* Medial longitudinal fasciculus
- Modulatory systems, 31–32
- Molecular layer, of cerebellar cortex, 291, 292*f*
- Monosynaptic stretch reflex, 89
- Mossy fibers, 279, 294*f*, 365  
 Purkinje neurons and, 293
- Motion pathway, 160*f*
- Motor axons, 11
- Motor control, 121  
 disproportionate complex impairment of, 238
- Motor cortex  
 cingulate area, 244*f*  
 face-controlling area of, 54  
 neurons, 31  
 primary, 213, 216*f*, 221*f*, 229, 244*f*  
 area 4, 295  
 corticobulbar tract and, 242  
 corticospinal tract and, 222  
 cytoarchitecture of, 49*f*  
 skeletomotor loop and, 315*f*  
 somatotopic organization of, 223*f*  
 ventral corticospinal tract and, 218  
 rubrospinal tract and, 295
- Motor homunculus, 222
- Motor innervation, 124–125, 126
- Motor neurons, 211  
 autonomic preganglionic, 229  
 descending motor pathways and, 215  
 gamma, 86*f*  
 muscle spindle organ and, 86*f*  
 somatic, 242*f*
- Motor nuclei, 231*f*, 232*f*, 405*f*, 407*f*, 413*f*
- Motor systems  
 functional anatomy of, 211–213  
 organization of, 212*f*  
 regional anatomy of, 220–229  
 rostral midbrain nuclei and, 225
- Motor thalamic nuclei, 314
- Motor units, 229
- Movement, planning of, 179
- Movement control, 212*f*  
 descending motor pathways for, 214*t*  
 visually guided, 213
- MRA. *See* Magnetic resonance angiography
- MRI. *See* Magnetic resonance imaging
- Müller cells, 151, 163
- Multiple sclerosis, 186*f*
- Multipolar neurons, 7, 22
- Muscle. *See also specific muscle*  
 reflexes, reduced, 222  
 skeletal, 337  
 control of, 338*f*  
 tongue, 239  
 weakness  
 contralateral, 238  
 hyperreflexia concurrent with, 238
- Muscle spindles, 86*f*, 96  
 receptors, 83, 105
- Muscle tone, 222
- Myelencephalon, 10
- Myelin basic protein (MBP), 8*f*
- Myelin sheath, 7, 8*f*
- Myelin staining, 34, 34*f*  
 midbrain, 42*f*  
 spinal cord, 35*f*  
 of striata, 320
- ## N
- Narcolepsy, 344
- Nasal hemiretina, 149, 151*f*  
 optic chiasm and, 151
- Nasal mucosa, 248  
 glands, 253
- Nasolabial fold, flattening of, 168–169, 238
- Neocortex, 45, 48, 197, 376
- Nerve endings, bare, 83, 105, 115
- Nervous system  
 cellular organization, 22  
 regional anatomy, 22–23
- Neural crest cells, 125
- Neural systems  
 components, 9–10  
 principal cellular constituents of, 5

- One-and-one-half syndrome, 257–259, 258*f*
- Onuf's nucleus, 350
- Operculum, 20, 187, 201  
gustatory information and, 191
- Ophthalmic artery, 61
- Ophthalmic division, 131, 140
- Ophthalmic vein, 67*f*
- Optic chiasm, 145, 147, 151, 163, 332*f*, 333*f*, 344*f*, 393*f*, 395*f*, 397*f*, 439*f*, 449*f*, 459*f*, 461*f*  
visual field defects and, 161–163, 162*f*
- Optic disk, 149, 150*f*
- Optic nerve, 121*f*, 121–124, 139, 147, 148*f*, 150*f*, 151, 163, 393*f*, 395*f*, 397*f*, 439*f*, 451*f*  
formation of, 151  
ipsilateral retina and, 151  
visual field defects and, 161, 162*f*
- Optic radiations, 146, 147, 154, 156*f*, 163, 433*f*  
visual field defects and, 162*f*, 163
- Optic tectum, 147, 149
- Optic tract, 121*f*, 145, 147, 163, 393*f*, 397*f*, 399*f*, 431*f*, 433*f*, 437*f*, 439*f*, 441*f*, 443*f*, 445*f*, 447*f*, 463*f*  
visual field defects and, 162*f*, 163
- Optokinetic reflexes, 262
- Oral nucleus, 129, 137, 141
- Orbital gyri, 17, 389*f*, 393*f*
- Orbitofrontal cortex, 187, 193, 198*f*, 203, 371  
flavor sensing and, 200  
limbic loop and, 315*f*  
piriform cortex and, 200
- Orbitofrontal gyrus, 361
- Orexins, 342, 344, 346
- Organ of Corti, 171, 172*f*, 181
- Orientation, 259–260
- Orientation columns, 156–158, 157*f*, 164
- Oropharynx, 190*f*
- Orthonasal olfaction, 200
- Orthostatic hypotension, 261
- Ossicles, 172, 172*f*
- Otic ganglion, 249, 253
- Otolith organs, 264
- Outer synaptic layer, 151
- Output nuclei, 305, 305*t*, 310*f*
- Oxytocin, 332, 336–337
- P**
- Pacinian corpuscles, 79, 83, 84*f*, 96
- PAG. *See* Periaqueductal gray matter
- Pain, 81*t*, 82, 115  
acute, 113–115  
anterolateral system and, 101  
contralateral loss of, 108*f*  
cortical representations of, 113–115  
cranial, 129–130  
ipsilateral loss of, 330  
loss of, 99–100  
    contralateral, 120  
    ipsilateral, 119–120  
matrix, 113–115, 114*f*  
modulatory system, 110*f*  
pathways, 102*f*–104*f*, 107*f*, 113*f*  
perception, 210  
periaqueductal gray and, 41  
processing, 111, 112*f*  
radicular, 88  
referred, 107  
small-diameter sensory fibers and, 105–106  
somatic sensory impairments and, 108  
spinal cord hemisection and, 210  
suppression pathways, 110  
transmission, 101  
trigeminal pathways for, 131*f*–132*f*  
trigeminal sensory system and, 142  
ventral posterior nucleus and, 111  
visceral, 101, 105, 115, 127
- Palate, 190*f*, 201
- Paleocortex, 199, 377
- Pallidotomy, 322–323
- Pancreas, 345
- Papillae, 189*f*
- Parabigeminal nucleus, 429*f*
- Parabrachial nucleus, 101, 110, 138*f*, 187, 190, 340, 368, 427*f*  
as viscerosensory integrative centers, 137–139
- Parafascicular nucleus, 321, 321*f*, 437*f*, 439*f*, 445*f*, 455*f*
- Parahippocampal gyrus, 198*f*, 199, 361, 393*f*, 435*f*
- Parallel fibers, 294
- Parallel organization, 147
- Paralysis  
facial muscle, 243  
flaccid, 222  
right side, 53–54  
spinal cord hemisection and, 210*f*
- Paramedian branches, 57
- Paramedian pontine reticular formation (PPRF), 257, 258*f*, 264, 274
- Paramedian reticular formation, 423*f*
- Parasagittal sections, 22
- Parasympathetic nervous system, 10, 242*f*  
autonomic motor column and, 241  
organization of, 339*f*  
origin of, 337–340
- Parasympathetic neurons, 346
- Parasympathetic nuclei, 346
- Parasympathetic postganglionic neurons, 241
- Parasympathetic preganglionic neurons, 241, 242*f*, 253, 339
- Paraterminal gyrus, 371, 395*f*
- Paraventricular nucleus, 337, 340  
organization of, 345*f*
- Paravertebral ganglia, 340
- Parietal lobe, 16*f*, 17, 17*f*, 23  
higher-order somatic sensory cortical areas in, 95–96  
higher-order visual cortical areas and, 159*f*  
superior, 30
- Parietal operculum, 96*f*  
higher-order somatic sensory cortical areas in, 95–96
- Parietal-temporal-occipital association areas, 154
- Parietal-temporal-occipital association cortex, 43, 361*f*  
cytoarchitecture of, 49*f*
- Parietooccipital sulcus, 17*f*, 17–18, 395*f*
- Parkinson disease, 213, 305, 311–313, 313*f*, 342  
dopaminergic neurons and, 33
- Parolfactory sulcus, 395*f*
- Parotid gland, 241, 249, 253
- Parvocellular cells, 151
- Parvocellular division, 187, 225, 231, 286, 295
- Parvocellular neurosecretory system, 333–334, 336*f*
- Parvocellular nucleus, 344–346  
periventricular portion of, 335
- Parvocellular system, 155–156, 157*f*
- PCNA. *See* Proliferating cell nuclear antigen
- Pedunculopontine nucleus, 322, 342, 371, 429*f*
- Penfield, Wilder, 94
- Peptides, 7
- Perception, 259–260
- Perforant pathway, 365
- Periamygdaloid cortex, 203, 451*f*

- Preoptic area, 337, 342–344, 344f, 449f, 459f, 461f
- Prepositus nucleus, 421f, 459f
- Prerubral field, 461f
- Pressor reflex response, 250
- Presynaptic neurons, 6f, 7
- Presynaptic terminal, 7
- Pretectal area, 461f
- Pretectal nuclei, 147, 163, 270f, 271
- Pretectal region, 433f
- Preventricular zone, 347f
- Prevertebral ganglia, 340
- Primary fissure, 279
- Primary olfactory neurons, 201
- Projection neurons, 7
- anterolateral system and, 106
  - retinal, 147
  - thalamocortical, 190
- Prolactin, 335
- Proliferating cell nuclear antigen (PCNA), 201, 202f
- Proopiomelanocortin, 345
- Proprioception, 83
- cervical spinal cord degeneration and, 277
  - jaw, 125
    - mesencephalic trigeminal nucleus and, 131
    - pathway, 129
  - limb, 120
  - loss of, 99–100
- Propriospinal neurons, 228
- Prosencephalon. *See* Forebrain
- Prosopagnosia, 161
- Proximal limb muscles, 273
- spinocerebellum and, 284
- Pruritic receptors, 83, 105
- Pruritic stimuli, 101
- Pseudoptosis, 350
- Psychostimulants, 368
- Pterygopalatine ganglion, 241, 248, 253
- Ptosis, 331
- Pulmonary aspiration, 250
- Pulvinar, 401f, 433f, 439f, 445f, 453f, 455f, 459f, 461f, 463f
- Pulvinar nuclei, 154
- Pupillary constriction, 242f, 331
- Horner syndrome and, 348, 350
- Pupillary dilation, 271
- Pupillary light reflex, 149, 270f, 270–271
- Purkinje cells, 34f, 282f, 294f
- of flocculonodular lobe, 291
  - inhibitory nature of, 293
- Purkinje layer, of cerebellar cortex, 291, 292f
- Putamen, 305, 318f, 320f, 321f, 397f, 401f, 433f, 437f, 439f, 441f, 443f, 445f, 447f, 449f, 451f, 453f, 455f, 457f, 465f
- anterior limb of internal capsule and, 316
  - neurons, 311
- Pyramidal decussations, 31, 39, 39f, 229, 229f, 252, 397f, 414f–415f
- Pyramidal neurons, 365
- Pyramidal signs, 227
- Pyramidal tract, 227
- Wallerian degeneration of, 228f
- Pyramids, 31, 38f, 47, 216, 224f, 397f, 399f, 415f, 417f, 419f, 421f, 435f, 437f, 459f, 461f
- on brain stem surface, 38
  - corticospinal axons in, 251
  - formation of, 227
- ## Q
- Quadrantanopia, 163
- Quadrigeminal cistern, 71, 433f
- ## R
- Radicular arteries, 55, 74
- Radiological image convention, 40
- Radiological imaging
- after stroke, 54f
  - of cerebral vasculature, 64
- Ramón y Cajal, Santiago, 6–7
- Raphe nuclei, 32f, 33, 110, 115, 421f
- salient stimuli and, 321
- Rapid eye movement (REM) sleep, 342, 343f
- Rathke's pouch, 345
- Receptive membrane, 7
- Red nucleus, 41, 217, 217f, 289f, 393f, 431f, 433f, 437f, 457f, 459f
- dentate nucleus and, 286
  - magnocellular division of, 295
  - rubrospinal tract and, 225
- Region of cavernous sinus, 67f
- Regional neuroanatomy, 5
- Regulatory peptides, 334–336
- Regulatory systems, neurotransmitter-specific, 30
- Reinforcement, 369f
- Relay nuclei, 30, 42–43, 48
- REM sleep. *See* Rapid eye movement (REM) sleep
- Restless leg syndrome, 346
- Reticular formation, 38, 109, 115, 211, 232–233, 417f, 419f, 421f, 423f, 427f, 431f
- cortical projection to, 215
  - pain pathways and, 113f
  - salient stimuli and, 321
  - swallowing and, 250
- Reticular nuclei, 42, 43f, 44t, 435f, 437f, 439f, 441f, 443f, 445f, 453f, 455f, 457f, 463f
- Reticulospinal tracts, 215, 219, 232
- formation of, 225–227
  - projections to spinal cord, 215
- Retina, 149–151, 150f, 152f, 163
- detached, 151
  - ganglion cell layer of, 150
  - inner layer of, 149–150
  - ipsilateral, 151
  - lateral geniculate neurons and, 156
  - outer, 149–150, 151
- Retinal ganglion cells, 150–151
- Retinal interneurons, 153f
- Retinal-geniculate-calcarine pathway, 148f
- Retronasal olfaction, 200
- Reward, 359
- Rexed, Bror, 105
- Rexed laminae, 105, 228
- spinal cord nuclei and, 107t
- Rhinal sulcus, 200, 362f, 393f
- Rhodopsin, 150
- Rhombencephalon. *See* Hindbrain
- Rhombomeres, 87f, 126, 126f
- Right superior temporal gyrus, 181
- Rigidity, 312, 313
- RMS. *See* Rostral migratory stream
- Rod bipolar cells, 150
- Rods, 150, 163
- Rostral interstitial nucleus, of medial longitudinal fasciculus, 264
- Rostral migratory stream (RMS), 201
- Rostral solitary nucleus, 190
- Rostral spinal cord
- dorsal surface of, 400f–401f
  - lateral surface of, 388f–389f, 398f–399f
  - midsagittal section through, 394f–395f
  - ventral surface of, 396f–397f
- Rostrocaudal axis, 21, 24
- Rostrocaudal organization, 135–137
- Rostrum, 17f, 19

- Spinal cord (*Cont.*):  
 schematic of, 35*f*, 220*f*  
 second lumbar segment of, 291  
 segments, 83, 87, 290–291  
   organization, 89*f*  
   structure of, 87*f*  
 transverse section of  
   cervical segment (C7), 412*f*–413*f*  
   lumbar segment (L1), 408*f*–409*f*  
   lumbar segment (L2), 406*f*–407*f*  
   sacral segment (S1), 404*f*–405*f*  
   thoracic segment (T3),  
   410*f*–411*f*
- Spinal cord-medullary junction, 39,  
 135*f*
- Spinal mechanosensory system  
 functional anatomy of, 82  
 regional anatomy of, 82
- Spinal motor circuits, 211
- Spinal nerves, 11, 12*f*  
 primary sensory neurons in, 125  
 sensory axons in, 121
- Spinal protective systems  
 functional anatomy of, 101–105  
 regional anatomy of, 105–115
- Spinal roots, 241
- Spinal tap, 71, 73*f*
- Spinal trigeminal nucleus, 127, 133–135,  
 141–142, 284, 414*f*–415*f*, 417*f*,  
 419*f*, 423*f*  
 cranial pain and, 129–130  
 lesions, 251  
 rostrocaudal organization of,  
 135–137
- Spinal trigeminal oral nucleus, 421*f*
- Spinal trigeminal tract, 120, 127,  
 135, 141, 415*f*, 417*f*, 419*f*,  
 421*f*, 423*f*  
 lesions, 251, 330  
 organization of, 134*f*  
 rostrocaudal organization of,  
 135–137
- Spinocerebellum, 283*f*, 284  
 lateral, 285*f*  
 vermis and, 286*f*
- Spinomesencephalic tract, 101, 110
- Spinoreticular tract, 101, 109
- Spinothalamic tract, 102*f*–104*f*,  
 109, 115  
 pain pathways and, 113*f*
- Spiral ganglion, 169, 181
- Splenium, 17*f*, 19
- SSS fibers. *See* Special somatic sensory  
 (SSS) fibers
- Stapes, 172
- Stellate neurons, 293
- Stem cells, 188  
 neurogenesis and, 201
- Sternocleidomastoid muscle, 241
- Straight sinus, 66, 67*f*
- Stretch receptors, 125
- Stria medullaris, 380, 401*f*, 421*f*, 435*f*,  
 437*f*, 439*f*, 441*f*, 443*f*, 445*f*, 453*f*,  
 455*f*, 457*f*, 459*f*, 461*f*
- Stria of Gennari, 156
- Stria terminalis, 368, 375, 401*f*, 433*f*,  
 435*f*, 437*f*, 439*f*, 441*f*, 443*f*,  
 445*f*, 447*f*, 449*f*, 453*f*, 461*f*,  
 465*f*  
 bed nucleus of, 366, 375, 455*f*
- Striatal cell bridges, 316, 318*f*, 435*f*,  
 451*f*, 453*f*
- Striatal neurons, 311
- Striate cortex, 147
- Striatum, 14, 15*f*, 305, 308*f*  
 compartmental organization of, 320  
 components of, 316–317  
 C-shaped development of, 20  
 information integration in basal  
   ganglia and, 316*f*  
 input nuclei and, 310*f*  
 myelin-stained, 320  
 striosome-matrix organization of,  
 319*f*
- Striosome-matrix organization, 319*f*
- Striosomes, 320
- Stroke. *See also* Hemorrhagic stroke;  
 Ischemic stroke  
 dysphagia and, 250  
 internal capsule, 230*f*  
 internal capsule and, 225  
 neuroradiological imaging after, 54*f*  
 unilateral ventral pontine, 238*f*
- Styloglossus, 239
- Stylopharyngeus muscle, 249
- Subarachnoid space, 21, 24, 68*f*, 74,  
 451*f*, 453*f*  
 capacity of, 69–70  
 cerebrospinal fluid circulation and,  
 71
- Subcallosal area, 395*f*
- Subcommissural organ, 70*f*, 74
- Subcortical structures, 62  
 atrophy of, 5
- Subdural hematoma, 21
- Subdural space, 21
- Subfornical organ, 70*f*, 74, 337
- Subgranular zone (SGZ), 201
- Subiculum, 363, 377, 435*f*, 437*f*, 441*f*,  
 457*f*, 465*f*
- Submandibular ganglion, 241, 248,  
 253
- Submodality, 156
- Substance P, 310*f*, 311
- Substantia gelatinosa, 405*f*, 407*f*, 409*f*,  
 411*f*, 413*f*, 415*f*
- Substantia innominata, 449*f*
- Substantia nigra, 32*f*, 33, 41, 225,  
 306*f*, 393*f*, 429*f*, 431*f*, 433*f*, 437*f*,  
 441*f*, 457*f*, 461*f*, 463*f*  
 anatomical divisions of, 321–322  
 pars compacta, 305, 309, 321, 368  
 pars reticulata, 305, 321
- Subthalamic nucleus, 305, 306*f*, 433*f*,  
 437*f*, 439*f*, 441*f*, 457*f*, 463*f*  
 circuitry, 303–304  
 lesion, 304*f*, 313*f*, 314, 321
- Subventricular zone (SVZ), 201
- Sulci, 23  
 widening, 4*f*, 5
- Sulcus limitans, 127, 128*f*, 140, 401*f*
- Superior cerebellar artery, 59*f*, 60
- Superior cerebellar peduncle, 279, 284,  
 291, 295, 296*f*, 425*f*, 427*f*, 429*f*,  
 435*f*, 437*f*, 457*f*, 461*f*
- Superior cerebellar peduncle  
 decussation, 459*f*
- Superior colliculus, 38, 147, 163, 233,  
 323*f*, 395*f*, 399*f*, 401*f*, 430*f*–431*f*,  
 433*f*, 459*f*  
 brachium of, 147, 153, 163, 176, 270,  
 401*f*, 431*f*, 433*f*, 461*f*  
 eye movement control centers and,  
 267  
 ocular motor control and, 153–154  
 pain pathways and, 113*f*  
 spinomesencephalic tract and,  
 110  
 tectospinal tract and, 219, 225  
 voluntary eye movements and, 263
- Superior frontal gyrus, 391*f*
- Superior ganglia, 131, 141, 189
- Superior medullary velum, 401*f*,  
 427*f*
- Superior nasal concha, 195*f*
- Superior oblique muscle, 239, 262,  
 263*f*
- Superior olivary complex, 170, 181,  
 423*f*, 425*f*  
 horizontal sound localization and,  
 173  
 ventral cochlear nucleus and, 175*f*
- Superior olivary nuclei, 175
- Superior parietal lobule, 17, 389*f*, 391*f*,  
 395*f*

- Tourette syndrome, 304  
 DBS and, 323
- Tractography, 36
- Tracts, 11
- Transcellular movement, of compounds, 67
- Transcranial magnetic stimulation (TMS), 28, 222
- Transduction, 83
- Transient ischemic attack (TIA), 55, 74
- Transient receptor potential (TRP) receptors, 105
- Transverse, 22, 24
- Transverse sinuses, 67, 67f
- Trapezius muscle, 241
- Trapezoid body, 173, 181, 423f  
 nucleus of, 173
- Tremors, 287, 312
- Treponema pallidum*, 79
- Trigeminal ganglion, 131
- Trigeminal lemniscus, 128, 137, 189–190, 423f, 425f, 427f, 429f, 431f, 433f
- Trigeminal mesencephalic nucleus, 129
- Trigeminal motor nucleus, 239, 252–253, 425f  
 trigeminal sensory nucleus and, 246
- Trigeminal nerve, 124, 139, 239, 253, 397f, 399f  
 divisions, 140  
 fascicles of, 425f  
 functional anatomy of, 127  
 pathways, 127–130, 131f–132f  
 peripheral innervation territories of, 134f
- Trigeminal nucleus, 127  
 cortical control of, 244f  
 innervation of, 243
- Trigeminal sensory nucleus, 127–128, 130f, 425f  
 trigeminal motor nucleus and, 246
- Trigeminal spinal nucleus, 249
- Trigeminal system, 140–142  
 functional anatomy of, 127  
 regional anatomy of, 131–139  
 somatotopic organization of, 134f
- Trigeminocerebellar pathways, 284
- Trigeminothalamic tract, 129
- Trochlear nerve, 139, 239, 252, 262, 397f, 399f, 401f, 427f  
 fascicles of, 429f
- Trochlear nucleus, 239, 252, 262, 429f, 457f, 459f  
 in caudal midbrain, 268  
 extraocular muscle control and, 264f
- TRP receptors. *See* Transient receptor potential (TRP) receptors
- Trunk muscles, 238
- Tuber cinereum, 333f, 393f, 397f
- Tubercles, 38  
 dorsal column, 38f
- Tuberomammillary nucleus, 342, 346
- Tufted cells, 197
- Tympanic membrane, 169, 173
- Tympanum, 172f
- ## U
- Uncinate fasciculus, 179, 374, 443f, 447f, 449f
- Uncus, 393f, 433f, 449f
- Unipolar neurons, 6, 22
- Upper extremity analgesia, 99–100
- Urination, 347
- Utricle, 171, 259, 273
- ## V
- Vagal trigone, 401f
- Vagus nerve, 124, 127, 131–132, 140–141, 189, 239, 253, 397f, 399f, 401f, 419f  
 gustatory innervation and, 190f  
 sensory axons from, 127  
 somatotopic organization of, 134f  
 taste and, 187  
 taste buds and, 201
- Vascular organ of lamina terminalis, 70f, 74
- Vasopressin, 332, 336–337
- Vein of Labbé, 67f
- Venograms, 64
- Ventral amygdalofugal pathway, 366–368, 375, 447f
- Ventral anterior nucleus, 314, 320, 321f, 443f, 453f, 455f, 457f, 461f, 463f
- Ventral anterior thalamic nuclei, 220
- Ventral brain surface, 197
- Ventral cochlear nucleus, 173  
 superior olivary complex and, 175f
- Ventral column, 47, 231
- Ventral commissure, 115, 405f, 407f, 409f, 411f, 413f  
 anterolateral system projection neurons and, 106–107
- Ventral corticospinal tract, 213, 218f, 218–219, 223f, 229, 231, 411f, 413f
- Ventral horn, 33, 47, 89, 211, 228–229, 231f  
 somatotopic organization of, 213f
- Ventral lateral nucleus, 319, 437f, 441f, 453f, 455f, 457f, 463f
- Ventral lateral sulcus, 397f
- Ventral lateral thalamic nuclei, 220
- Ventral medial nucleus, 375
- Ventral medial posterior nucleus, 113f
- Ventral median fissure, 397f, 405f, 407f, 409f, 411f, 413f
- Ventral pallidum, 305, 306f, 320f, 368, 371, 449f, 463f  
 anterior commissure and, 319  
 globus pallidus and, 308  
 limbic loop and, 314
- Ventral pons, 238f
- Ventral posterior lateral nucleus, 82, 85f, 93, 96, 112f, 115, 272f, 435f, 437f, 439f, 445f, 455f, 462f–463f  
 mechanosensory information and, 137  
 pain pathways and, 113f  
 spinothalamic projection to, 101
- Ventral posterior medial nucleus, 93, 112f, 129, 137, 142, 201, 437f, 439f, 445f, 455f, 461f  
 parvocellular division of, 137, 187  
 parvocellular portion of, 190, 193f  
 primary somatic sensory cortex and, 129  
 trigeminal lemniscus and, 128
- Ventral posterior medial parvocellular nucleus, 139
- Ventral posterior nucleus, 93, 93f, 94f, 142, 259, 271–273, 272f  
 visceral pain and, 111
- Ventral roots, 11, 12f, 33, 240f, 397f, 399f
- Ventral spinocerebellar tract, 290f, 291, 409f, 411f, 413f, 415f, 417f, 419f, 421f, 423f
- Ventral stream, 164, 366  
 objection recognition and, 160
- Ventral striatum, 371  
 addiction and, 369f  
 information integration in basal ganglia and, 317