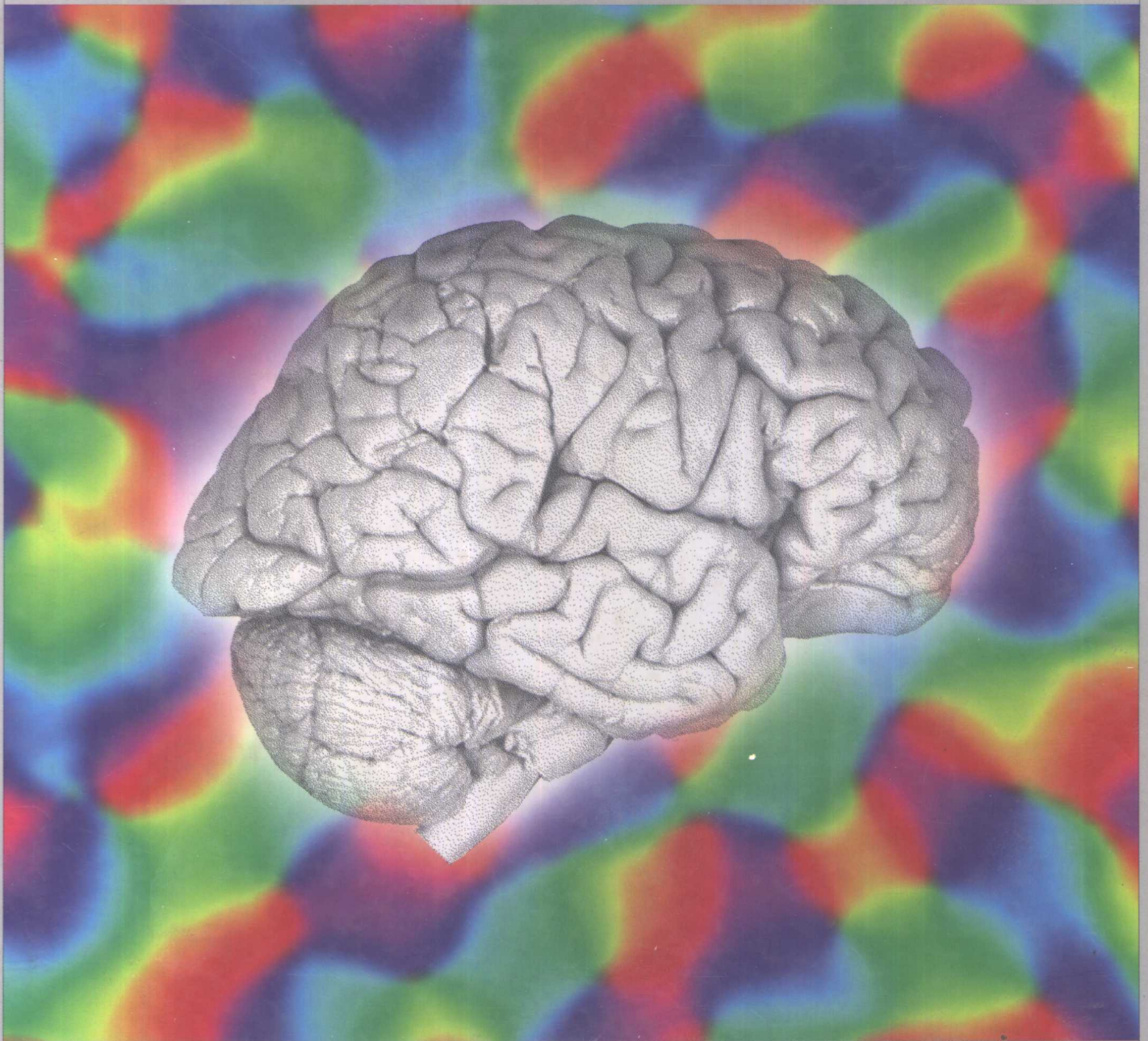


NEUROSCIENCE



DALE Purves

GEORGE J. AUGUSTINE DAVID FITZPATRICK LAWRENCE C. KATZ

ANTHONY-SAMUEL LAMANTIA JAMES O. MCNAMARA

EDITORS

92225

NEUROSCIENCE

Edited by

DALE PURVES

GEORGE J. AUGUSTINE

DAVID FITZPATRICK

LAWRENCE C. KATZ

ANTHONY-SAMUEL LAMANTIA

JAMES O. McNAMARA

Department of Neurobiology

Duke University Medical Center



SINAUER ASSOCIATES, INC.
PUBLISHERS
SUNDERLAND, MASSACHUSETTS

THE COVER

The background in the cover illustration is a pattern of orientation columns in the primary visual cortex revealed by optical imaging. (Courtesy of David Fitzpatrick; see Chapter 11.)

NEUROSCIENCE

Copyright © 1997 by Sinauer Associates, Inc.

All rights reserved.

This book may not be reproduced
in whole or in part without permission.

Address inquiries and orders to
Sinauer Associates, Inc., PO Box 407,
23 Plumtree Road, Sunderland, MA 01375 U.S.A.

FAX: 413-549-1118

email: publish@sinauer.com

Library of Congress Cataloging-in-Publication Data

Neuroscience / edited by Dale Purves . . . [et al.].

p. cm.

Includes bibliographical references and index.

ISBN 0-87893-747-1 (alk. paper)

1. Neurosciences. 2. Neurophysiology. 3. Neurology. I. Purves, Dale.

[DNLM: 1. Nervous systems—physiology. 2. Neurochemistry. WL 102
N4996 1997]

QP355.2.N487 1997

612.8—dc20

DNLM/DLC

for Library of Congress

CIP

96-43031

Printed in U.S.A.

5 4 3 2 1

Contributors

George J. Augustine, Ph.D.

Nell B. Cant, Ph.D.

John H. Casseday, Ph.D.

Gillian Einstein, Ph.D.

David Fitzpatrick, Ph.D.

Lawrence C. Katz, Ph.D.

Anthony-Samuel LaMantia, Ph.D.

Julie Kauer, Ph.D.

Donald C. Lo, Ph.D.

James O. McNamara, M.D.

Richard D. Mooney, Ph.D.

Miguel A. L. Nicolelis, M.D., Ph.D.

Dale Purves, M.D.

Peter H. Reinhart, Ph.D.

Sidney A. Simon, Ph.D.

All the contributors are associated with the Department of
Neurobiology at Duke University Medical Center.

THE COVER

The background in the cover illustration is a pattern of orientation columns in the primary visual cortex revealed by optical imaging. (Courtesy of David Fitzpatrick; see Chapter 11.)

NEUROSCIENCE

Copyright © 1997 by Sinauer Associates, Inc.

All rights reserved.

This book may not be reproduced
in whole or in part without permission.

Address inquiries and orders to
Sinauer Associates, Inc., PO Box 407,
23 Plumtree Road, Sunderland, MA 01375 U.S.A.

FAX: 413-549-1118

email: publish@sinauer.com

Library of Congress Cataloging-in-Publication Data

Neuroscience / edited by Dale Purves . . . [et al.].

p. cm.

Includes bibliographical references and index.

ISBN 0-87893-747-1 (alk. paper)

1. Neurosciences. 2. Neurophysiology. 3. Neurology. I. Purves, Dale.

[DNLM: 1. Nervous systems—physiology. 2. Neurochemistry. WL 102
N4996 1997]

QP355.2.N487 1997

612.8—dc20

DNLM/DLC

for Library of Congress

CIP

96-43031

Printed in U.S.A.

5 4 3 2 1

Acknowledgments

We are grateful to numerous colleagues who provided helpful criticisms and suggestions as we were writing this book. We particularly wish to thank David Amaral, Gary Banker, Ursula Bellugi, Dan Blazer, Robert Burke, John Chapin, Milt Charlton, Michael Davis, Robert Desimone, Allison Doupe, Sascha du Lac, Jens Eilers, Peter Eimas, Everett Ellinwood, Robert Erickson, Howard Fields, Bob Fremeau, Michela Gallagher, Steve George, Pat Goldman-Rakic, Mike Haglund, Zach Hall, Bill Henson, John Heuser, Jonathan Horton, Alan Humphrey, Jon Kaas, Herb Kilackey, Len Kitzes, Arthur Lander, Story Landis, Darrell Lewis, Alan Light, Steve Lisberger, Arthur Loewy, Eve Marder, Robert McCarley, Jim McIlwain, Ron Oppenheim, Scott Pomeroy, Rodney Radtke, Louis Reichardt, Steve Roper, John Rubenstein, David Rubin, Josh Sanes, Cliff Saper, Lynn Selemon, Carla Shatz, Larry Squire, John Staddon, Peter Strick, Warren Strittmatter, Joe Takahashi, and Christina Williams. It is understood, of course, that any remaining errors are in no way attributable to our critics. We also thank the first-year students at Duke University Medical School, who from 1991 through 1996 read and criticized earlier drafts of this text that were used in introducing them to neuroscience. Finally, we owe special thanks to Polly Garner, Dana Hall, Robert Reynolds, and Cathy Wooton, who labored long and hard to put the manuscript together, and to Andy Sinauer and John Woolsey and their staffs for turning the manuscript into such a lovely book.

About the Book

Editor: Andrew D. Sinauer

Project Manager: Carol J. Wigg

Copy Editor: Janet Greenblatt

Production Manager: Christopher Small

Book Layout and Production: Michele Ruschhaupt

Art Editing and Illustration Program: J/B Woolsey Associates

Book Design: Rodelinde Graphic Design

Cover Design: Mickey Boisvert

Color Separations: Vision Graphics, Inc.

Cover Manufacturer: Henry Sawyer Company, Inc.

Book Manufacturer: The Courier Companies, Inc.

Contents in Brief

1 The Organization of the Nervous System

-
- 2 Electrical Signals of Nerve Cells
 - 3 Voltage-Dependent Membrane Permeability
 - 4 Channels and Pumps
 - 5 Synaptic Transmission
 - 6 Neurotransmitters
 - 7 Neurotransmitter Receptors and Their Effects
-

I. Neural Signaling

-
- 8 The Somatic Sensory System
 - 9 Pain
 - 10 Vision: The Eye
 - 11 Central Visual Pathways
 - 12 The Auditory System
 - 13 The Vestibular System
 - 14 The Chemical Senses
-

II. Sensation and Sensory Processing

-
- 15 Spinal Cord Circuits and Motor Control
 - 16 Descending Control of Spinal Cord Circuitry
 - 17 Modulation of Movement by the Basal Ganglia
and Cerebellum
 - 18 Cellular Mechanisms of Motor Modulation
 - 19 Eye Movements and Sensory-Motor Integration
-

III. Movement and Its Central Control

-
- 20 Early Brain Development
 - 21 Construction of Neural Circuits
 - 22 Modification of Developing Brain Circuits
by Neural Activity
 - 23 Plasticity in the Adult Nervous System
-

IV. The Changing Brain

-
- 24 Cognition
 - 25 Language and Lateralization
 - 26 Sleep and Wakefulness
 - 27 Emotions
 - 28 Sex, Sexuality, and the Brain
 - 29 Human Memory
-

V. Complex Brain Functions

Contents

Preface xviii

Acknowledgments xix

1. The Organization of the Nervous System 1

Overview 1

The Nervous System Is Made Up of Cells 1

Nerve Cells 2

Neuroglial Cells 4

Neural Circuits and Systems 5

The Basic Anatomical Subdivisions of the Nervous System 6

The External Anatomy of the Cerebral Hemispheres 10

The External Anatomy of the Diencephalon and Brainstem 13

The External Anatomy of the Spinal Cord 18

The Internal Anatomy of the Cerebral Hemispheres and Diencephalon 19

The Internal Anatomy of the Brainstem and Spinal Cord 24

The Ventricular System 25

The Meninges 27

The Blood Supply of the Brain and Spinal Cord 27

Summary 34

Additional Reading 34

BOX A The Autonomic Nervous System 8

BOX B Some Anatomical Terminology 12

BOX C Brain Imaging Techniques 22

BOX D The Blood-Brain Barrier 31

BOX E Imaging Techniques Based on Blood Flow: PET, SPECT, and fMRI 32

Unit I **Neural Signaling**

BOX A The Remarkable Giant Nerve Cells of Squid 46

BOX B Action Potential Form and Nomenclature 49

BOX A The Voltage Clamp Method 52

BOX B Toxins that Poison Ion Channels 57

2. Electrical Signals of Nerve Cells 37

Overview 37

Electrical Potentials Across Nerve Cell Membranes 37

How Ionic Movements Produce Electrical Signals 39

The Forces that Create Membrane Potentials 41

Electrochemical Equilibrium in a Multi-Ion Environment 43

The Ionic Basis of the Resting Membrane Potential 44

The Ionic Basis of Action Potentials 47

Summary 50

Additional Reading 50

3. Voltage-Dependent Membrane Permeability 51

Overview 51

Ionic Currents Across Nerve Cell Membranes 51

Two Types of Voltage-Dependent Ionic Current 53

Two Voltage-Dependent Membrane Conductances 56

Reconstruction of the Action Potential 58

Long-Distance Signaling by Means of Action Potentials 62
The Refractory Period 64
Increased Conduction Velocity as a Result of Myelination 66
Summary 66
Additional Reading 68

4. Channels and Pumps 69

Overview 69
Ion Channels Involved in Action Potential Propagation 69
Other Types of Ion Channels 73
The Molecular Structure of Ion Channels 74
The Diversity of Voltage-Gated Channels 76
Pumps Create and Maintain Ion Gradients 77
Functional Properties of the Na^+/K^+ Pump 80
The Molecular Structure of the Na^+/K^+ Pump 82
Summary 82
Additional Reading 84

5. Synaptic Transmission 85

Overview 85
Electrical Synapses 85
Chemical Synapses 87
Quantal Transmission at Neuromuscular Synapses 89
Release of Transmitters from Synaptic Vesicles 90
Local Recycling of Synaptic Vesicles 92
The Role of Calcium in Transmitter Secretion 94
Molecular Mechanisms of Transmitter Secretion 95
Summary 97
Additional Reading 98

6. Neurotransmitters 99

Overview 99
What Defines a Neurotransmitter? 99
Two Major Categories of Neurotransmitters 101
Neurons May Release More Than One Transmitter 104
Neurotransmitter Synthesis 104
The Packaging of Neurotransmitters 107
Neurotransmitter Release and Removal 108
Acetylcholine 108
Glutamate 109
GABA and Glycine 110
The Biogenic Amines 112
ATP and Other Purines 115

BOX C Threshold 61

BOX A The Patch Clamp Method 70

BOX B Expression of Ion Channels
in *Xenopus* Oocytes 75

BOX C Genetic Diseases that
Affect Voltage-Gated Ion
Channels 78

BOX A Toxins that Affect
Transmitter Release 97

BOX A Criteria that Define a
Substance as a
Neurotransmitter 100

BOX B Excitotoxicity in Acute
Neuronal Injury 113

Peptide Neurotransmitters 116
Nitric Oxide: New Mechanisms of Neurotransmitter Action 118
Summary 118
Additional Reading 119

BOX C Biogenic Amine
Neurotransmitters and
Psychiatric Disorders 114

7. Neurotransmitter Receptors and Their Effects 121

Overview 121
Neurotransmitter Receptors Alter Postsynaptic Membrane Permeability 121
Principles Derived from Studies of the Neuromuscular Junction 121
Excitatory and Inhibitory Postsynaptic Potentials 127
Summation of Synaptic Potentials 129
Two Families of Postsynaptic Receptors 130
Ligand-Gated Ion Channels: Fast-Acting Cholinergic Receptors 131
Ligand-Gated Ion Channels: Fast-Acting Glutamate Receptors 135
Ligand-Gated Ion Channels: GABA and Glycine Receptors 137
Other Ligand-Gated Ion Channels 138
Metabotropic Receptors and the Activation of G-Proteins 138
Direct Modulation of Ion Channels by G-Proteins 139
Indirect Modulation by Intracellular Messenger Pathways 140
Postsynaptic Responses Involving Gene Expression 141
Summary 143
Additional Reading 144

BOX A Neurotoxins that Act on
Postsynaptic Receptors 132

BOX B Myasthenia Gravis: An
Autoimmune Disease
of Neuromuscular
Synapses 136

8. The Somatic Sensory System 147

Overview 147
Cutaneous and Subcutaneous Somatic Sensory Receptors 147
Mechanoreceptors Specialized to Receive Tactile Information 149
Differences in Mechanosensory Discrimination Across the Body Surface 151
Mechanoreceptors Specialized for Proprioception 152
Active Tactile Exploration 154
The Major Mechanosensory Pathway: The Dorsal Column-Medial Lemniscus
System 154
The Trigeminal Portion of the Mechanosensory System 156
The Somatic Sensory Components of the Thalamus 158
The Somatic Sensory Cortex 159
Higher-Order Cortical Representations 162
Summary 162
Additional Reading 163

Unit II Sensation and Sensory Processing

BOX A Dermatomes 155

BOX B Patterns of Organization
within the Sensory Cortices:
Brain Modules 161

9. Pain 165

Overview 165
Nociceptors 165
The Perception of Pain 166

Hyperalgesia and Sensitization 167
Central Pain Pathways: The Spinothalamic Tract 168
The Nociceptive Components of the Thalamus and Cortex 170
Central Regulation of Pain Perception 173
The Placebo Effect 173
The Physiological Basis of Pain Modulation 174
Summary 176
Additional Reading 177

10. Vision: The Eye 179

Overview 179
The Formation of Images on the Retina 179
The Retina 182
Phototransduction 186
Specializations of the Rod and Cone Systems 187
Retinal Ganglion Cell Receptive Fields 193
Retinal Circuitry Underlying Ganglion Cell Receptive Field Properties 196
Summary 198
Additional Reading 198

11. Central Visual Pathways 199

Overview 199
Central Projections of Retinal Ganglion Cells 199
The Retinotopic Representation of the Visual Field 203
Visual Field Deficits 207
The Functional Organization of the Striate Cortex 208
The Columnar Organization of the Striate Cortex 211
Parallel Streams of Information from the Retina 213
The Functional Organization of Extrastriate Visual Areas 218
Summary 221
Additional Reading 222

12. The Auditory System 223

Overview 223
Sound 223
The Audible Spectrum 224
A Synopsis of Auditory Function 224
The External Ear 225
The Middle Ear 226
The Inner Ear 227
Hair Cells and the Mechanoelectrical Transduction of Sound Waves 229
Two Kinds of Hair Cells in the Cochlea 233
Tuning and Timing in the Auditory Nerve 233
How Information from the Cochlea Reaches Targets in the Brainstem 235

BOX A Referred Pain 171

BOX B Phantom Limbs and
Phantom Pain 172

BOX A Refractive Errors 181

BOX B Myopia and the Growth of
the Eye 185

BOX C Deficiencies in Color
Vision 192

BOX A The Blind Spot 201

BOX B Random Dot Stereograms and
Related Amusements 214

BOX C Optical Imaging of
Functional Domains in the
Visual Cortex 216

BOX A The World's Loudest Rock
and Roll Band 225

BOX B The Sweet Sound of
Distortion 234

Integrating Information from the Two Ears 236
Monaural Pathways from the Cochlear Nucleus to the Lateral Lemniscus 239
Integration in the Inferior Colliculus 240
The Auditory Thalamus 240
The Auditory Cortex 241
Summary 243
Additional Reading 243

13. The Vestibular System 245

Overview 245
The Vestibular Labyrinth 245
Vestibular Hair Cells 245
The Otolith Organs 250
How Otolith Neurons Sense Linear Forces 250
The Semicircular Canals 253
How Semicircular Canal Neurons Sense Angular Accelerations 255
Central Vestibular Pathways: Eye, Head, and Body Reflexes 256
Vestibular Pathways to the Thalamus and Cortex 258
Summary 262
Additional Reading 262

BOX A A Primer on (Vestibular) Navigation 246

BOX B Adaptation and Tuning of Vestibular Hair Cells 248

BOX C Throwing Cold Water on the Vestibular System 260

14. The Chemical Senses 263

Overview 263
The Organization of the Olfactory System 263
Olfactory Perception in Humans 263
The Olfactory Epithelium and Olfactory Receptor Neurons 266
The Transduction of Olfactory Signals 267
Specificity of Odorant Detection: Odorant Receptors 269
Neural Coding in the Olfactory System 269
Central Processing of Olfactory Signals 271
The Organization of the Taste System 273
Taste Perception in Humans 276
The Organization of the Peripheral Taste System 277
Responses to Tastants 279
Taste Receptors and the Transduction of Taste Signals 280
Neural Coding in the Taste System 282
Central Processing of Taste Signals 284
Trigeminal Chemoreception 284
Summary 287
Additional Reading 287

BOX A Mapping the Sense of Smell 274

BOX B Capsaicin 285

15. Spinal Cord Circuits and Motor Control 291

Overview 291
Neural Structures Responsible for Movement 291

Unit III
Movement and Its Central Control

The Topography of Motor Neuron-Muscle Relationships 293
The Motor Unit 294
The Regulation of Muscle Force 296
The Lower Motor Neuron Syndrome 299
The Spinal Cord Circuitry Underlying Sensorimotor Reflexes 300
Flexion Reflex Pathways 306
Spinal Cord Circuitry and Locomotion 307
Summary 308
Additional Reading 309

BOX A Amyotrophic Lateral Sclerosis 299

BOX B Muscle Tone 305

16. Descending Control of Spinal Cord Circuitry 311

Overview 311
The Organization and Descending Control of Medial and Lateral Spinal Cord Circuitry 311
Some General Points About Brainstem Projections to the Spinal Cord 312
The Vestibular Nucleus and Reticular Formation: Maintaining Balance and Posture 312
The Motor Cortex 315
Descending Projections from the Motor Cortex 319
Damage to Descending Motor Pathways: The Upper Motor Neuron Syndrome 325
Summary 327
Additional Reading 327

BOX A What do Motor Maps Represent? 317

BOX B Sensorimotor Talents and Cortical Space 318

BOX C Descending Projections to Cranial Nerve Motor Nuclei 322

17. Modulation of Movement by the Basal Ganglia and Cerebellum 329

Overview 329
Sensory Information and Motor Commands 329
Basal Ganglia Lesions: Deficits in the Initiation of Movement 331
Cerebellar Lesions: Deficits in Coordinating and Terminating Movements 332
The Structural Elements of the Basal Ganglia and Cerebellum 335
Projections to the Basal Ganglia 336
Projections to the Cerebellum 339
Projections from the Basal Ganglia 340
Projections from the Cerebellum 342
Summary 343
Additional Reading 344

BOX A Can Gene Therapy Help Parkinson's Patients? 333

BOX B Huntington's Disease 334

18. Mechanisms of Motor Modulation 345

Overview 345
Neurons and Circuits in the Basal Ganglia and Cerebellum 345
Disinhibition: Direct and Indirect Pathways Through the Basal Ganglia 348
An Explanation of Parkinson's and Huntington's Diseases in Terms of Basal Ganglia Circuitry 350

Cerebellar Circuitry and the Coordination of Ongoing Movement 352
Motor Learning and Memory in the Basal Ganglia and Cerebellum 356
Summary 358
Additional Reading 359

BOX A Genetic Analysis of
Cerebellar Function 354

19. Eye Movements and Sensory-Motor Integration 361

Overview 361
What Eye Movements Accomplish 361
The Actions and Innervation of Extraocular Muscles 362
Types of Eye Movements and Their Functions 365
The Neural Control of Saccadic Eye Movements 367
Neural Control of Smooth Pursuit Movements 371
The Role of the Cerebellum and Basal Ganglia in Eye Movements 371
Summary 373
Additional Reading 374

BOX A The Perception of Stabilized
Retinal Images 363

20. Early Brain Development 377

Overview 377
The Initial Formation of the Nervous System: Gastrulation and
Neurulation 377
The Molecular Basis of Neural Induction 379
The Formation of the Major Brain Subdivisions 381
The Initial Differentiation of Neurons and Glia 385
The Generation of Neuronal Diversity 386
Neuronal Migration 391
Summary 393
Additional Reading 394

Unit IV **The Changing Brain**

BOX A Retinoic Acid: Teratogen and
Inductive Signal 380

BOX B Homeotic Genes and Human
Brain Development 382

BOX C Rhombomeres 384

BOX D Neuronal Birthdating 389

21. Construction of Neural Circuits 395

Overview 395
Axon Outgrowth and Pathfinding 395
Fixed Signals for Axon Guidance: Extracellular Matrix and Cell Surface Molecules 396
Diffusible Signals for Axon Guidance: Chemotropic Factors 398
Negative Regulation of Axon Growth: Inhibitors and Chemorepellents 400
The Formation of Topographical Maps: Recognition Molecules 401
Selective Synapse Formation 406
Trophic Interactions and the Ultimate Size of Neuronal Populations 407
Trophic Interactions and the Formation of Neuronal Connections 410
A Molecular Paradigm for Trophic Interactions: The Neurotrophins 410
Neurotrophin Receptors 413
The Effect of NGF on the Differentiation of Neuronal Form 415
A General Scheme for the Action of Trophic Molecules 416

BOX A Why Aren't We More Like
Fish and Frogs? 402

BOX B Molecular Signals that
Promote Synapse
Formation 408

Summary 416
Additional Reading 417

22. Modification of Developing Brain Circuits by Neural Activity 419

Overview 419
Insights From the Development of Peripheral Synapses 419
Development of Ocular Dominance Columns in the Visual Cortex 420
Effects of Visual Deprivation on Ocular Dominance 425
How Neuronal Activity Affects the Development of Neural Circuits 429
Molecular Mechanisms of Activity-Driven Competition 433
The Significance of Critical Periods 434
Critical Periods for the Development of Human Behavior 435
Summary 436
Additional Reading 437

23. Plasticity in the Adult Nervous System 439

Overview 439
Short-Term Synaptic Plasticity 439
Long-Term Potentiation 440
The Molecular Basis of LTP 447
Long-Term Depression 449
LTP and Epilepsy 451
Mechanisms of Synaptic Plasticity in "Simple" Nervous Systems 451
Common Themes in Adult Plasticity 457
Cortical Plasticity in Adult Animals 458
Summary 461
Additional Reading 461

24. Cognition 465

Overview 465
The Association Cortices 465
Differences Between the Association Cortices and the Rest
of the Neocortex 467
Lesions of the Parietal Lobe: Attention Deficits 470
Lesions of the Temporal Lobe: Deficits of Recognition 472
Lesions of the Frontal Lobe: Planning Deficits 474
"Attention Neurons" in the Parietal Cortex 474
"Recognition Neurons" in the Temporal Cortex 478
"Planning Neurons" in the Frontal Cortex 479
Summary 480
Additional Reading 482

BOX A Why Neurons Have
Dendrites 421

BOX B Direct Observation of
Synaptic Rearrangement in
Developing Muscle 422

BOX C Transneuronal Labeling with
Radioactive Amino Acids 424

BOX D Prenatal Activity and
Circuit Formation 431

BOX E Built-In Behaviors 435

BOX A Why the Hippocampus? 442

BOX B Brain Slices 444

BOX C Long-Term Depression in the
Cerebellum 452

BOX D Epilepsy 454

Unit V

Complex Brain Functions

BOX A A More Detailed Look at
Cortical Lamination 468

BOX B Neuropsychological
Testing 476

25. Language and Lateralization 483

Overview 483

Language is Both Localized and Lateralized 483

Aphasias 484

A Dramatic Confirmation of Language Lateralization 485

Anatomical Asymmetries Between the Right and Left Hemispheres 487

Mapping Language Function 490

The Development of Language Skills 493

Sign Language 494

Summary 495

Additional Reading 496

BOX A Do Apes Have Language? 489

BOX B Handedness 492

26. Sleep and Wakefulness 497

Overview 497

Sleep as an Active State 497

Non-REM Sleep 497

REM Sleep 499

Dreaming and the Possible Functions of REM Sleep 501

Sleep Deprivation 503

Styles of Sleep Among Different Species 503

Biological Clocks 504

Brainstem Mechanisms of Sleep and Wakefulness 506

Summary 511

Additional Reading 511

BOX A Electroencephalography 500

BOX B Molecular Mechanisms of
Biological Clocks 507

BOX C Sleep Factors 508

BOX D Consciousness 510

27. Emotions 513

Overview 513

Physiological Changes Associated with Emotion 513

The Integration of Emotional Behavior 514

The Limbic System 518

The Influence of the Amygdala on Emotional Behavior 521

The Neocortex and Emotional Expression 524

Summary 526

Additional Reading 527

BOX A The Hypothalamus 516

BOX B The Amygdala 520

BOX C The Reasoning Behind an
Important Discovery 522

BOX D Affective Disorders 525

28. Sex, Sexuality, and the Brain 529

Overview 529

Sexually Dimorphic Behavior 529

Definitions of Sex 531

Hormonal Influences on Sexual Dimorphism 532

The Effect of Estrogens on Neural Circuitry 535

Central Nervous System Dimorphisms Related to Relatively Simple Sexual
Behaviors 536

BOX A The Development of Male
and Female Phenotypes 530

BOX B The Actions of Sex
Hormones 534