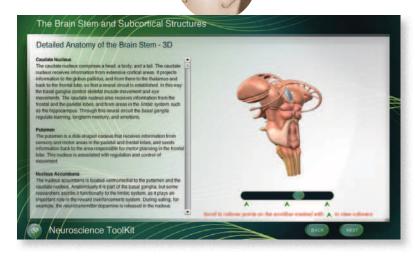


Witness Neuroscience Firsthand



Available at www.macmillanhighered.com/launchpadsolo/neurotk

The CounchPadSolo for Neuroscience is a powerful web-based tool for learning the core concepts of behavioral neuroscience—by witnessing them firsthand. These thirty interactive tutorials allow students to see the nervous system in action via dynamic illustrations, animations, and models that demystify the neural mechanisms behind behavior. Each activity is accompanied by a set of carefully crafted multiple choice questions for assessment that is easy to assign and instantly graded. Based on Worth Publishers'



groundbreaking Foundations of Behavioral Neuroscience CD-ROM, the LounchPodSolo for Neuroscience is a valuable accompaniment to

any course.

TOPICS AND ACTIVITIES

Neural Communication

Structure of a Neuron

The Membrane Potential

Conduction of the Action Potential

Synaptic Transmission

Neural Integration

Central Nervous System

Subdivisions of the Central Nervous System

Subcortical Structures

Sensory Systems-Vision

Sensory Systems-Audition

Sensory Systems-Somatosenses

Sensory Systems-Olfaction

Motor System

Limbic System

Language

The Cortex

Brain Stem

The Spinal Cord

Visual System

The Eye

Retina

Optic Chiasm

Lateral Geniculate Nucleus

Superior Colliculus

Primary Visual Cortex

Higher Order Visual Areas

Control of Movement

Organization of the Motor Systems

Muscle and Receptor Anatomy

Muscle Contraction

Spinal Reflexes

Descending Motor Tracts

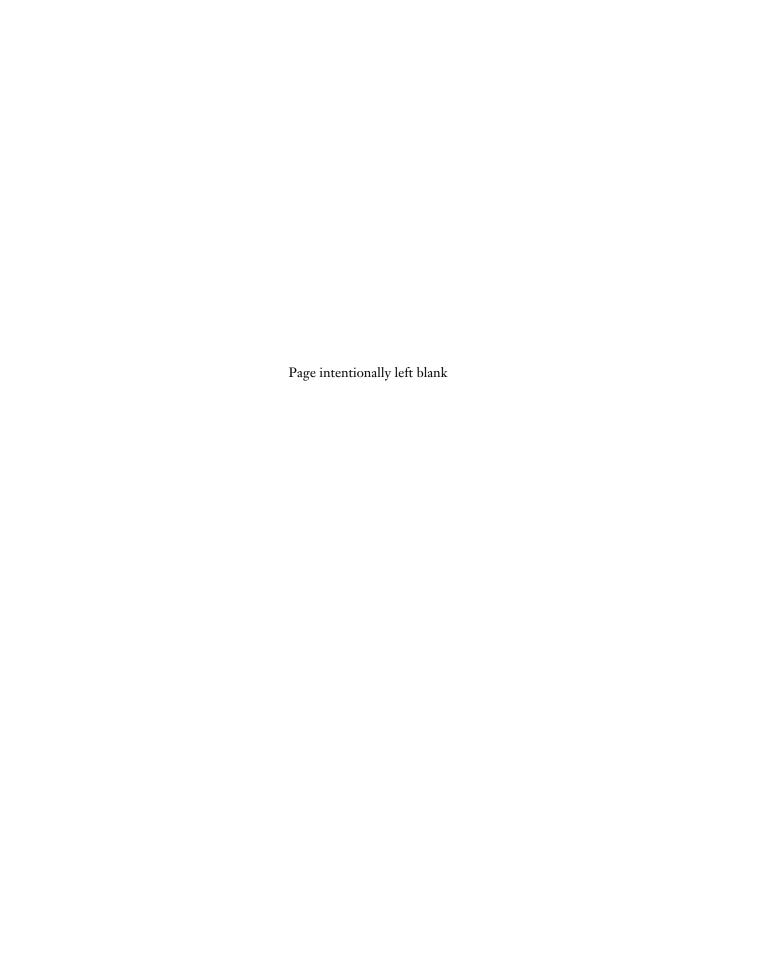
Primary Motor Cortex

Higher Order Motor Cortex

Basal Ganglia

Cerebellum





Fundamentals of **HUMAN NEUROPSYCHOLOGY**

SEVENTH EDITION

BRYAN KOLB & IAN Q. WHISHAW

University of Lethbridge



Publisher: Rachel Losh

Senior Acquisitions Editor: Daniel DeBonis Development Editor: Barbara Brooks Assistant Editor: Nadina Persaud Editorial Assistant: Katie Pachnos

Executive Marketing Manager: Katherine Nurre Executive Media Editor: Rachel Comerford

Director of Editing, Design, and Media Production for the Sciences

and Social Sciences: Tracey Kuehn Managing Editor: Lisa Kinne

Project Editors: Enrico Bruno, Andrew Roney, and Janice Stangel

Production Manager: Sarah Segal Associate Media Editor: Anthony Casciano

Photo Editor: Cecilia Varas Photo Researcher: Richard Fox Art Director: Diana Blume

Interior Designer: Tamara Newnam

Cover Designer: Kevin Kall Art Manager: Matthew McAdams Illustrations: Dragonfly Media

Composition: Northeastern Graphic, Inc. Printing and Binding: RR Donnelley Cover Art: *Orla* by Cian McLoughlin

Library of Congress Preassigned Control Number: 2014946473

ISBN-10: 1-4292-8295-9 ISBN-13: 978-1-4292-8295-6

© 2015, 2009, 2003 by Worth Publishers; © 1996, 1990, 1985, 1980 by W. H. Freeman and Company All rights reserved.

Printed in the United States of America

Worth Publishers 41 Madison Avenue New York, NY 10010 www.worthpublishers.com To all the students whose interest in how the brain produces the mind and controls behavior makes this book possible.

ABOUT THE AUTHORS



Bryan Kolb received his Ph.D. from The Pennsylvania State University and conducted postdoctoral work at the University of Western Ontario and the Montreal Neurological Institute. In 1976 he moved to the University of Lethbridge, Alberta, where he is a professor of neuroscience and holds a Board of Governors Chair in Neuroscience. His current research examines how perinatal factors—including tactile stimulation, psychoactive drugs, stress, and injury—

modify the developing cerebral cortex and how these changes are related to behavior. Kolb is a fellow of the Royal Society of Canada, the Canadian Psychological Association (CPA), the American Psychological Association, and the Association of Psychological Science. Currently a senior fellow of the Child Brain Development program of the Canadian Institute for Advanced Research, he is a recipient of the Hebb Prize from the CPA and from the Canadian Society for Brain, Behaviour, and Cognitive Science (CSBBCS). He has received honorary doctorates from the University of British Columbia, Thompson Rivers University, and Concordia University. He is a recipient the Ingrid Speaker Gold Medal for research, the distinguished teaching medal from the University of Lethbridge, and the Key to the City of Lethbridge. He and his wife train and show horses in Western riding performance events.



lan Q. Whishaw received his Ph.D. from Western University and is a professor of neuroscience at the University of Lethbridge. He has held visiting appointments at the University of Texas, the University of Michigan, the University of Cambridge, and the University of Strasbourg. He is a fellow of Clair Hall, Cambridge, the Canadian Psychological Association, the American Psychological Association, and the Royal Society of Canada. He is a recipient the Ca-

nadian Humane Society Bronze Medal for bravery, the Ingrid Speaker Gold Medal for research, the distinguished teaching medal from the University of Lethbridge, and the Donald O. Hebb Prize. He has received the Key to the City of Lethbridge and has honorary doctorates from Thompson Rivers University and the University of Lethbridge. His research addresses the neural basis of skilled movement and the neural basis of brain disease. The Institute for Scientific Information includes him in its list of most-cited neuroscientists. His hobby is training and showing horses for Western performance events.

BRIEF CONTENTS

Preface xix Media and Supplements xxiii PART I Background CHAPTER 1 The Development of Neuropsychology 1 CHAPTER 2 Research on the Origins of the Human Brain and Behavior 28 CHAPTER 3 **Nervous System Organization 53** The Structure and Electrical Activity of Neurons 85 CHAPTER 5 Communication Between Neurons 115 CHAPTER 6 The Influence of Drugs and Hormones on Behavior 139 CHAPTER 7 Imaging the Brain's Activity 174 **PART II Cortical Organization** Organization of the Sensory Systems 202 Organization of the Motor System 232 CHAPTER 10 Principles of Neocortical Function 255 CHAPTER 11 Cerebral Asymmetry 283 CHAPTER 12 Variations in Cerebral Asymmetry 316

PART III Cortical Functions

CHAPTER 13
The Occipital Lobes 350

CHAPTER 14 The Parietal Lobes 374 CHAPTER 15 The Temporal Lobes 400 CHAPTER 16 The Frontal Lobes 427 CHAPTER 17 Cortical Networks and Disconnection Syndromes 462 **PART IV Higher Functions** CHAPTER 18 Learning and Memory 480 CHAPTER 19 Language 515 CHAPTER 20 Emotion and the Social Brain 548 CHAPTER 21 Spatial Behavior 575 CHAPTER 22 Attention and Consciousness 607 **PART V Plasticity and Disorders** CHAPTER 23 Brain Development and Plasticity 635 CHAPTER 24 Neurodevelopmental Disorders 670 CHAPTER 25 Plasticity, Recovery, and Rehabilitation of the Adult Brain 699 CHAPTER 26 Neurological Disorders 730

Psychiatric and Related Disorders 761

Neuropsychological Assessment 793

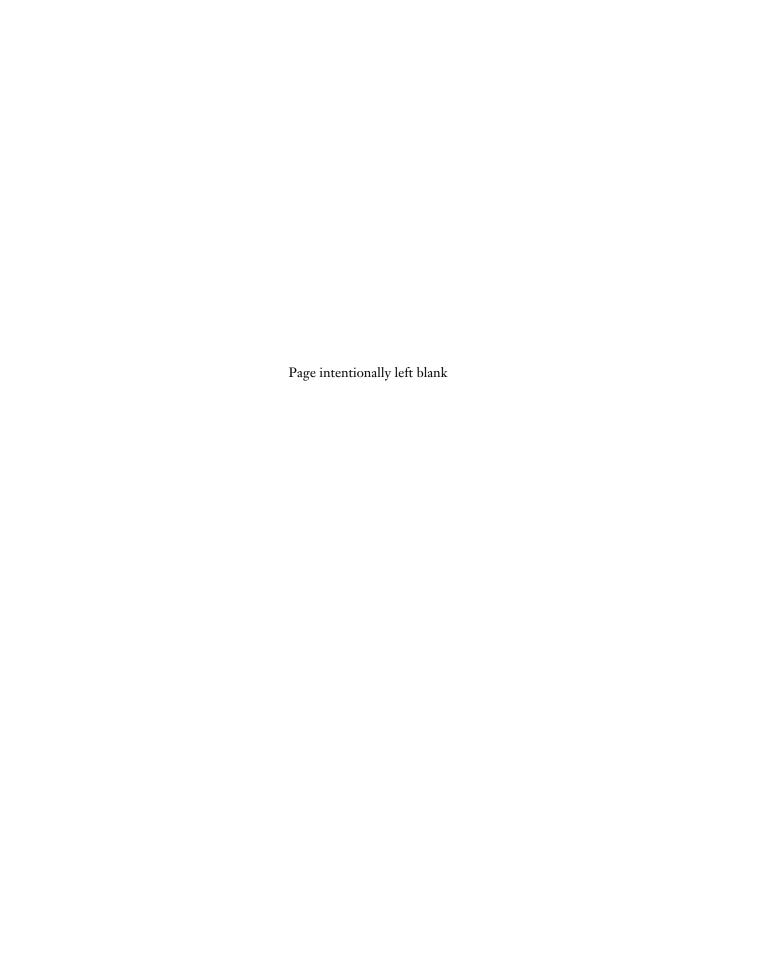
CHAPTER 27

CHAPTER 28

Glossary G-1

Name Index NI-1

Subject Index SI-1



CONTENTS

Preface xix

Media and Supplements xxiii

PART I Background

CHAPTER 1

The Development of Neuropsychology

PORTRAIT Living with Traumatic Brain Injury 1

1.1 The Brain Theory 2What Is the Brain? 2How Does the Brain Relate to the Rest of the Nervous System? 4

1.2 Perspectives on the Brain and Behavior 5 Aristotle: Mentalism 5 Descartes: Dualism 5 Darwin: Materialism 7 Contemporary Perspectives 8

1.3 Brain Function: Insights from Brain Injury 8 Localization of Function 8 Lateralization of Function 10 Neuroplasticity 13 Hierarchical Organization 13

SNAPSHOT ® The Dilemma in Relating Behavior and Consciousness 14

1.4 The Neuron Theory 17Nervous System Cells 17Identifying the Neuron 18

- Relating Electrical Activity in Neurons to Behavior 19
- © Connections Between Neurons As the Basis of Learning 20
- 1.5 Contributions to Neuropsychology from Allied Fields 21
 Neurosurgery 22
 Psychometrics and Statistical Evaluation 23
 Brain Imaging 24

© Coverage links neuropsychological theory and assessment

CHAPTER 2

Research on the Origins of the Human Brain and Behavior

PORTRAIT Evolving a Capacity for Language 28

2.1 Human Origins and the Origins of Larger Brains 29 Research on Hominid Evolution 29 Evolution of the Human Brain and Behavior 31 Relating Brain Size and Behavior 32 The Meaning of Human Brain-Size Comparisons 37

© 2.2 Comparative Research in Neuropsychology 39 Understanding Brain Mechanisms 40 Designing Animal Models of Disorders 40

The Acquisition of Culture 39

Describing Evolutionary Adaptations 41

2.3 Genes, Environment, and Behavior 41SNAPSHOT ® A Genetic Diagnosis 42

Mendelian Genetics and the Genetic Code 43
Applying Mendel's Principles 44
Genetic Engineering 47
Phenotypic Plasticity and the Epigenetic Code 49

CHAPTER 3 Nervous System Organization

- **OPERANT** Stroke 53
- 3.1 Neuroanatomy: Finding Your Way Around the Brain 54 Describing Location in the Brain 54 A Wonderland of Nomenclature 56
- 3.2 Overview of Nervous System Structure and Function 57 Support and Protection 58 Blood Supply 59 Neurons and Glia 59 Gray, White, and Reticular Matter 61 Layers, Nuclei, Nerves, and Tracts 62

Electrical Charges 97

3.3 Origin and Development of the Central Nervous System 623.4 The Spinal Cord 64	The Resting Potential 99 Graded Potentials 102 The Action Potential 103
Spinal-Cord Structure and Spinal Nerve Anatomy 64 Spinal-Cord Function and the Spinal Nerves 65 Cranial Nerve Connections 67 Autonomic Nervous System Connections 69 3.5 The Brainstem 70 The Hindbrain 70 The Midbrain 71 The Diencephalon 72	 4.3 Sending a Message Along an Axon 106 The Nerve Impulse 106 Saltatory Conduction and Myelin Sheaths 107
	SNAPSHOT © Diagnosing MS 108 © 4.4 How Neurons Integrate Information 109 Excitatory and Inhibitory Postsynaptic
3.6 The Forebrain 72 The Basal Ganglia 73 The Limbic System 74 The Neocortex 75 Fissures, Sulci, and Gyri 76 Cortical Organization in Relation to Inputs, Outputs, and Function 77 Cellular Organization in the Cortex 78	Potentials 109 Voltage-Sensitive Channels and the Action Potential 110 Summation of Inputs 110 The Versatile Neuron 112 4.5 Stimulating and Recording with Optogenetics 112
Cortical Connections 80	CHAPTER 5 Communication Between Neurons
SNAPSHOT ® Brainbow and Clarity 81 3.7 The Crossed Brain 82	PORTRAIT Otto Loewi's Dream Breakthrough 115
CHAPTER 4 The Structure and Electrical Activity of Neurons	 5.1 Neurotransmitter Discovery 116 5.2 The Structure of Synapses 117 © Chemical Synapses 117 Electrical Synapses 118
 PORTRAIT The Halle Berry Neuron 85 4.1 The Neuron's Structure 86 Overview of a Neuron 86 The Neuron as a Factory 87 The Cell Membrane: Barrier and Gatekeeper 88 The Nucleus: Blueprints for Proteins 90 Protein Synthesis: Transcription and Translation 91 Applying Epigenetic Mechanisms 92 Proteins: The Cell's Products 93 Golgi Bodies and Microtubules: Protein Packaging and Shipment 93 Crossing the Cell Membrane: Channels, Gates, and Pumps 94 4 2 The Neuron's Electrical Activity 95 	 5.3 Neurotransmission in Four Steps 119 Step 1: Transmitter Synthesis and Storage 120 Step 2: Neurotransmitter Release 120 Step 3: Receptor-Site Activation 121 Step 4: Neurotransmitter Deactivation 121 5.4 Types of Synapses 122 Synaptic Variations 122 Excitatory and Inhibitory Messages 123 5.5 Varieties of Neurotransmitters 124 Four Criteria for Identifying Neurotransmitters 124 Three Classes of Neurotransmitters 125 Peptide Transmitters 127 Transmitter Gases 128 5.6 Excitatory and Inhibitory Receptors 129
4.2 The Neuron's Electrical Activity 95 Recording from an Axon 96 How the Movement of Ions Creates	Ionotropic Receptors and Excitation 129 Metabotropic Receptors and Inhibition 129

Excitatory and Inhibitory Receptor Effects 131

§ 5.7 Neurotransmitter Activating Systems and Behavior 131

> Neurotransmission in Peripheral Nervous System Divisions 131

Activating Systems of the Central Nervous System 132

SNAPSHOT ® Neurochemical Links Between SIDS and Sleep Apnea 136

CHAPTER 6 The Influence of Drugs and Hormones on Behavior

- **PORTRAIT** The Case of the Frozen Addict 139
- 6.1 Principles of Psychopharmacology 140
 Routes of Drug Administration 140
 Routes of Drug Removal 141
 Revisiting the Blood-Brain Barrier 142
 Drug Routes and Dosage 143

Sensitization 146

Can Drugs Cause Brain Damage? 148

6.3 Grouping Psychoactive Drugs 150

Group I: Antianxiety Agents and Sedative Hypnotics 150

Group II: Antipsychotic Agents 152

Group III: Antidepressants and Mood Stabilizers 153

Group IV: Opioid Analgesics 155 Group V: Psychotropics 156

SNAPSHOT © Cognitive Enhancement 158

General Stimulants 160

6.4 Individual Responses and Influences on Addiction 160
 Behavior on Drugs 160
 Addiction and Dependence 161
 Sex Differences in Addiction 162
 Wanting-and-Liking Theory 162
 Treating Drug Abuse 163

6.5 Hormones 164

Hierarchical Control of Hormones 165

© Classes and Functions of Hormones 165

Homeostatic Hormones 166 Gonadal Hormones 167

Anabolic-Androgenic Steroids 168

- Glucocorticoids and Stress 168
- © Ending a Stress Response 169

CHAPTER 7 Imaging the Brain's Activity

- **PORTRAIT** Angelo Mosso 174
- 7.1 Recording the Brain's
 Electrical Activity 175
 Single-Cell Recording 175
 Electroencephalographic Recording 177
 Event-Related Potentials 181
 Magnetoencephalography 183
- 7.2 Brain Stimulation 183Deep Brain Stimulation 184Transcranial Magnetic Stimulation 184
- 7.3 Static Imaging Techniques 185Imaging by X-Ray 185Computed Tomography 186
- 7.4 Dynamic Brain Imaging 187
 Positron Emission Tomography 187
 Magnetic Resonance Imaging 189
 Magnetic Resonance Spectroscopy 191
 Diffusion Tensor Imaging 192
 Functional Magnetic Resonance Imaging 193
 Resting-State fMRI 194
 Optical Tomography 195

SNAPSHOT © Tuning in to Language 196

T.5 Comparing Brain-Imaging Techniques and Uses 197

Imaging Techniques, Pro and Con 198 Toward Multimodal Brain Atlases 199

PART II Cortical Organization

CHAPTER 8 Organization of the Sensory Systems

- PORTRAIT Phantoms of the Brain 202
- 8.1 General Principles of Sensory-System Function 203Sensory Receptors and Neural Relays 203

Neural Relays Determine the Hierarchy of Motor Responses 207

Central Organization of Sensory Systems 208

8.2 Sensory Receptors and Pathways 211

Vision 211

Hearing 214

Body Senses 217

The Chemical Senses: Taste and Smell 223

SNAPSHOT Watching the Brain Make Flavor 225

 8.3 Perception 228 Illusions 228 Synesthesia 229 Sensory Synergies 229

CHAPTER 9 Organization of the Motor System

- © PORTRAIT Mind in Motion 232
- 9.1 The Neocortex: Initiating Movement 233 Mapping the Motor Cortex Using Electrical Stimulation 235 Multiple Representations in the Motor Cortex 236 The Movement Lexicon 239 Mirroring Movement 242

SNAPSHOT @ Recording Mirror Neuron Activity 244

- § 9.2 The Brainstem: Motor Control 245 The Basal Ganglia and Movement Force 245 The Cerebellum and Motor Learning 247
- § 9.3 Communicating with the Spinal Cord 250 Spinal-Cord Pathways 250 Spinal Motor Neurons 251

CHAPTER 10 **Principles of Neocortical Function**

- PORTRAIT Hemispherectomy 255
- 10.1 A Hierarchy of Function from Spinal Cord to Cortex 256

The Spinal Cord: Reflexes 258 The Hindbrain: Postural Support 258 The Midbrain: Spontaneous Movement 260 The Diencephalon: Affect and Motivation 261 The Basal Ganglia: Self-Maintenance 262

The Cortex: Intention 263

 10.2 The Structure of the Cortex 264 Cortical Cells 264

SNAPSHOT @ Mapping the Human Cortex 265

Cortical Layers, Efferents, and Afferents 266 Cortical Columns, Spots, and Stripes 268 Multiple Representations: Mapping Reality 270 Cortical Systems: Frontal Lobe, Paralimbic Cortex, and Subcortical Loops 272 Cortical Connections, Reentry, and the Binding Problem 273

© 10.3 Functional Organization of the Cortex 275

A Hierarchical Model of Cortical Function 275 Evaluating the Hierarchical Model 276 A Contemporary Model of Cortical Function 278

 10.4 Do Human Brains Possess Unique Properties? 279

CHAPTER 11 **Cerebral Asymmetry**

- © PORTRAIT Words and Music 283
- 11.1 Anatomical Asymmetries in the Human Brain 284 Cerebral Asymmetry 284 Neuronal Asymmetry 288 Genetic Asymmetry 288
- 11.2 Asymmetries in Neurological Patients 289 Patients with Lateralized Lesions 289 Commissurotomy Patients 291 **Brain Stimulation 294** Carotid Sodium Amobarbital Injection 296
- 11.3 Behavioral Asymmetries in the Intact Brain 298 Asymmetry in the Visual System 298 Asymmetry in the Auditory System 299 Asymmetry in the Somatosensory System 300 Asymmetry in the Motor System 301 What Do Laterality Studies Tell Us about
 - Brain Function? 303
- 11.4 Neuroimaging and Asymmetry 304
- 11.5 Theoretical Arguments: What Is Lateralized? 306 Specialization Models 306

Interaction Models 308
Preferred Cognitive Mode 309

SNAPSHOT @ Imaging the Brain's Plasticity 310

Measuring Behavior in Neuropsychology 311

CHAPTER 12 Variations in Cerebral Asymmetry

PORTRAIT Individual Responses to Injury 316

12.1 Handedness and
 Functional Asymmetry 316
 Anatomical Studies 317
 Functional Cerebral Organization in Left-Handers 318
 Theories of Hand Preference 319

SNAPSHOT © Genetic Influences on Brain Structure 321

12.2 Sex Differences in
Cerebral Organization 323
Sex Differences in Children's Behavior 323
Sex Differences in Adult Behavior 324
Sex Differences in Brain Structure 328
The Homosexual Brain 330
Sex Differences Revealed in Functional
Imaging Studies 331
Research with Neurological Patients 332

Research with Neurological Patients 332

Explanations for Sex Differences 333

12.3 Environmental Effects
 on Asymmetry 338
 Language and Culture 338
 Sensory or Environmental Deficits 340

12.4 Asymmetry in Nonhuman Animals 343
Asymmetry in Birds 344
Asymmetry in Nonhuman Primates 344

PART III Cortical Functions

CHAPTER 13 The Occipital Lobes

PORTRAIT An Injured Soldier's Visual World 350

13.1 Occipital Lobe Anatomy 350 Subdivisions of the Occipital Cortex 351 Connections of the Visual Cortex 353 13.2 A Theory of Occipital-Lobe Function 353 Visual Functions Beyond the Occipital Lobe 354 Visual Pathways Beyond the Occipital Lobe 357 Imaging Studies of Dorsal and Ventral Streams 359

Top-Down Predictions in Vision 360

13.3 Disorders of Visual Pathways 360

13.4 Disorders of Cortical Function 362
 Case B.K.: V1 Damage and a Scotoma 362
 Case D.B.: V1 Damage and Blindsight 364
 Case G.Y. and Related Cases: V1 Damage
 and Conscious Vision 364

Case J.I.: V4 Damage and Loss of Color Vision 364

Case P.B.: Conscious Color Perception in a Blind Patient 365

Case L.M.: V5 (MT) Damage and the Perception of Movement 365

Case D.F.: Occipital Damage and Visual Agnosia 366

Case V.K.: Parietal Damage and Visuomotor Guidance 367

Cases D. and T.: Higher-Level Visual Processes 367

Conclusions from the Case Studies 368

13.5 Visual Agnosia 368
 Object Agnosias 368
 Other Visual Agnosias 369

13.6 Visual Imagery 370

SNAPSHOT © Generating Mental Images 371

CHAPTER 14 The Parietal Lobes

PORTRAIT Varieties of Spatial Information 374

14.1 Parietal Lobe Anatomy 374 Subdivisions of the Parietal Cortex 375 Connections of the Parietal Cortex 376 Anatomy of the Dorsal Stream 377

14.2 A Theory of Parietal-Lobe Function 378
 Behavioral Uses of Spatial Information 379
 The Complexity of Spatial Information 382
 Other Parietal-Lobe Functions 382

SNAPSHOT © Spatial Cognition and White-Matter Organization 383

 14.3 Somatosensory Symptoms of Parietal Lesions 384 Somatosensory Thresholds 384 Somatoperceptual Disorders 385 Numb Touch 385 Somatosensory Agnosias 386

14.4 Symptoms of Posterior
 Parietal Damage 387
 Bálint's Syndrome 387
 Contralateral Neglect and Other Symptoms of Right Parietal Lesions 388
 The Gerstmann Syndrome and Other Left Parietal Symptoms 390
 Apraxia and the Parietal Lobe 391
 Drawing 392
 Spatial Attention 392
 Disorders of Spatial Cognition 393

 14.5 Major Symptoms and Their Assessment 394

Clinical Neuropsychological Assessment 395

Left and Right Parietal Lobes Compared 394

CHAPTER 15 The Temporal Lobes

PORTRAIT Living with Temporal-Lobe Damage 400

15.1 Temporal-Lobe Anatomy 400 Subdivisions of the Temporal Cortex 401 Connections of the Temporal Cortex 402 Anatomy of the Ventral Stream 403

15.2 A Theory of Temporal-Lobe Function 404 The Superior Temporal Sulcus and Biological Motion 406 Visual Processing in the Temporal Lobe 406 Are Faces Special? 409

Auditory Processing in the Temporal Lobe 411

Saymmetry of Temporal-Lobe Function 415

 15.3 Symptoms of Temporal-Lobe Lesions 416
 Disorders of Auditory and Speech Perception 417
 Disorders of Music Perception 417

SNAPSHOT (a) Imaging Auditory Hallucinations 418

Disorders of Visual Perception 419
Disturbance of Visual- and AuditoryInput Selection 420
Impaired Organization and Categorization 420

Inability to Use Contextual Information 421 Memory Impairment 421 Altered Affect and Personality 422 Changes in Sexual Behavior 423

 15.4 Clinical Neuropsychological Assessment of Temporal-Lobe Damage 423

CHAPTER 16 The Frontal Lobes

- **PORTRAIT** Losing Frontal-Lobe Functions 427
- 16.1 Frontal-Lobe Anatomy 427 Subdivisions of the Frontal Cortex 428 The Connectome and the Frontal Cortex 430
- 16.2 A Theory of Frontal-Lobe Function 431 Functions of the Premotor Cortex 432 Functions of the Prefrontal Cortex 433 Asymmetry of Frontal-Lobe Function 435 Heterogeneity of Frontal-Lobe Function 435

SNAPSHOT Heterogeneity of Function in the Orbitofrontal Cortex 436

© 16.3 Symptoms of Frontal-Lobe Lesions 437
Disturbances of Motor Function 437
Loss of Divergent Thinking 440
Environmental Control of Behavior 443
Poor Temporal Memory 446
Impaired Social and Sexual Behavior 449
Does a Spatial Deficit Exist? 452
Clinical Neuropsychological Assessment of Frontal-Lobe Damage 452

16.4 Intelligence and the Frontal Lobes 454

16.5 Imaging Frontal-Lobe Function 455

16.6 Disorders Affecting
 the Frontal Lobe 457

CHAPTER 17 Cortical Networks and Disconnection Syndromes

- **PORTRAIT** At Cross Purposes 462
- 17.1 Disconnecting Cognitive Functions 463
- 17.2 Anatomy of Cerebral Connections 464
- © 17.3 Cortical Networks and Hubs 466
- 17.4 Behavioral Effects
 of Disconnection 468

- 17.5 Hemispheric Disconnection 470 Commissurotomy 470 Callosal Agenesis and Early Transections 471
- © 17.6 Disconnecting Sensorimotor Systems 472 Olfaction 472 Vision 473 Somatosensory Functions 474 Audition 474 Movement 475 Effects of Partial Disconnection 476

SNAPSHOT @ An fMRI Study of Disconnection 476

17.7 Lesion Effects Reinterpreted As Disconnection Syndromes 477 Apraxia 477 Agnosia and Alexia 477 Contralateral Neglect 478 Hubs and Connectivity in Brain Dysfunction 478

PART IV Higher Functions

CHAPTER 18 Learning and Memory

- **PORTRAIT** The Mystery of Memory 480
- 18.1 Learning, Memory,
 and Amnesia 481
 Varieties of Amnesia 482
 Anterograde and Retrograde Amnesia 484
 Time-Dependent Retrograde Amnesia 484
 Three Theories of Amnesia 485
- 18.2 Long-Term Explicit Memory 486
 Episodic Memory 486
 Autonoetic Awareness of Time 487
 Semantic Memory 488
 Neural Substrates of Explicit Memory 489
 Hemispheric Specialization for Explicit Memory 495
- 18.3 Long-Term Implicit Memory 497
 Sparing of Implicit Memory in Amnesia 497
 Neural Substrates of Implicit Memory 498
- 18.4 Long-Term Emotional Memory 501
 Evoking Negative Emotions 501
 Neural Substrates of Emotional Memory 501

Unique Aspects of Emotional Memory 502

Short-Term Memory and the Temporal and Parietal Lobes 503

Short-Term Memory and the Frontal Lobes 503

Neuropsychological Testing for Short-Term Memory Function 503

SNAPSHOT © Disrupting Memory Formation 504

- 18.6 Neurological Diseases and Long-Term Memory 507 Transient Global Amnesia 507 Herpes Simplex Encephalitis 507 Alzheimer's Disease 508 Korsakoff's Syndrome 508 Neurotransmitter Activating Systems and Memory 509

CHAPTER 19 Language

- PORTRAIT Multilingual Meltdown 515
- 19.1 What Is Language? 516 Language Structure 516 Producing Sound 517 Core Language Skills 518
- 19.2 Searching for the Origins of Language 519

SNAPSHOT © Genetic Basis for an Inherited Speech and Language Disorder 520

Continuity Theory 520
Discontinuity Theory 523
Experimental Approaches to Language
Origins 524

19.3 Localization of Language 526
Anatomical Areas Associated with
Language 527

Speech Zones Mapped by Brain Stimulation and Surgical Lesions 529

Speech Zones Mapped by Brain-Imaging Techniques 531

- Neural Networks for Language 533
- 19.4 Language Disorders 536
 Fluent Aphasias 536

Nonfluent Aphasias 538 Pure Aphasias 538

19.5 Localization of Lesions in Aphasia 538 Cortical Language Components 539 Subcortical Language Components 540 Right-Hemisphere Contributions to Language 540

¶
19.6 Neuropsychological Assessment of Aphasia 541

Assessing Developmental Language Disorders 542

CHAPTER 20 Emotion and the Social Brain

- **PORTRAIT** Agenesis of the Frontal Lobe 548
- 20.1 The Nature of Emotion 549
 What Are Emotions? 549
 Components of Emotion 549
- 20.2 Historical Views 550
 Investigating the Anatomy of Emotion 550
 The Emotional Brain 551
 Cortical Connections of Emotion 551
- 20.3 Candidate Structures in Emotional Behavior 553
 Processing Emotional Stimuli 553
 Brain Circuits for Emotion 554
- 20.4 Neuropsychological Theories of Emotion 556 Appraisal Theories of Emotion 556

SNAPSHOT © Brain Activation in Social Cognition 558

Cognitive–Emotional Interactions 559 Cognitive Asymmetry and Emotion 561

- © 20.5 Asymmetry in Emotional Processing 562 Producing Emotional Behavior 562 Interpreting Emotional Behavior 564 Temporal-Lobe Personality 566
- 20.6 The Social Brain and Social Cognition 567 Frontal Lesions in Monkeys 567 Cerebral Lesions in Humans 568 Social Neural Networks 569 The Self and Social Cognition 570 Cognitive Control of Emotion 571

CHAPTER 21 Spatial Behavior

- **PORTRAIT** Lost in Space 575
- 21.1 Spatial Behavior and Spatial Impairments 576 Explaining Spatial Behavior 577
 - © Clinical Descriptions of Spatial Impairments 577

Topographic Disorientation 578

21.2 Dorsal- and Ventral-Stream Contributions to Spatial Behavior 581 The Dorsal Stream in Parietal Cortex 581 The Dorsal Stream in Frontal Cortex 584 The Dorsal and Ventral Streams in Temporal Cortex 585

SNAPSHOT © Imaging the Hippocampi of London Taxi Drivers 586

21.3 Experimental Models of Spatial Behavior 587 Route Following 588 Piloting 588 Caching Behavior 590 Dead Reckoning 591

Neuropsychological Tests of Spatial Behavior 593

Single-Cell Recording and Spatial Behavior 594 Location of Spatial Cells 597

- © 21.4 Individual Differences in Spatial Abilities 598 Sex-Related Differences 598 Handedness and Spatial Ability 601
- © 21.5 Episodic Memory, Scene Construction, and Theory of Mind 601
 Spatial Activity in Episodic Memory 601
 Spatial Memory as Distinct from
 Episodic Memory 602
 Spatial and Episodic Memory as
 Hippocampal Functions 602
 Theory of Mind 603

CHAPTER 22 Attention and Consciousness

- **PORTRAIT** A Curious Case of Neglect 607
- © 22.1 Defining Attention and Consciousness 608

Automatic and Conscious Processing Compared 609

Neurophysiological Evidence of Attention 612 Parallel Processing of Sensory Input 615

Functional Imaging and Attention 615 Networks of Attention 618

Mechanisms of Attention 621

Absence of Visual Attention 622 Sensory Neglect 624

© 22.4 Consciousness 625 The Neural Basis of Consciousness 627 Cerebral Substrates of Consciousness 629

SNAPSHOT Stimulating Nonconscious Emotion 630

Emotion and Consciousness 630 Nonconscious Processing 632

PART V Plasticity and Disorders

CHAPTER 23

Brain Development and Plasticity

- © PORTRAIT Plasticity and Language 635
- 23.1 Approaches to Studying Brain Development 635
- 23.2 Development of the Human Brain 636 Neuron Generation 638 Cell Migration and Differentiation 639 Neural Maturation 640 Synapse Formation and Pruning 641 Glial Development 643 The Adolescent Brain 643
- 23.3 Imaging Studies of Brain Development 644
- © 23.4 Development of Problem-Solving Ability 647
- © 23.5 Environmental Effects on Brain Development 650 Developmental Effects of Aversive Environments 651

Environmental Influences on Brain Organization 652

Experience and Neural Connectivity 654 Plasticity of Representational Zones in the Developing Brain 655

© 23.6 Brain Injury and Plasticity 656 Effects of Age 657 Effects of Brain Damage on Language 657

SNAPSHOT © Distinct Cortical Areas for Second Languages 658

Reorganization of Language 660 Absence of Language After Bilateral Lesions 662

© 23.7 Studying Plasticity After Early Brain Injury 662

Effects of Early Brain Lesions on Behaviors Later in Life 663

Effects of Early Brain Lesions on Brain Structure Later in Life 665

Factors Influencing Plasticity After Early Cortical Injury 665

CHAPTER 24 **Neurodevelopmental Disorders**

- **PORTRAIT** Life Without Reading 670
- © 24.1 Neurodevelopmental Disorders 671 Historical Background and Evolution of Understanding 671 Incidence of Neurodevelopmental Disorders 673 Types of Neurodevelopmental Disorders 673
- 24.2 Learning Disorders That Affect Reading 674 Types of Reading 674 Causes of Reading Disorders 675

SNAPSHOT © Imaging Sound Perception in Controls and Subjects with Dyslexia 678

- Meuropsychological Evaluation 679
- Disorders 681 Attention-Deficit/Hyperactivity Disorder 681 Cerebral Palsy 683 Hydrocephalus 685 Autism Spectrum Disorders 686 Fragile-X Syndrome 689 Fetal Alcohol Spectrum Disorder 690
- © 24.4 Developmental Influences on Neurodevelopmental Disorders 692 Structural Damage and Toxic Effects 692 Hormonal Effects: The Geschwind-Galaburda Theory 693

Environmental Deprivation 694 The Birthday Effect 694

 24.5 Adult Outcome of Neurodevelopmental Disorders 695

CHAPTER 25

Plasticity, Recovery, and Rehabilitation of the Adult Brain

- © PORTRAIT Concussion 699
- © 25.1 Principles of Brain Plasticity 700

Principle 1: Plasticity is common to all nervous systems, and the principles are conserved. 700

Principle 2: Plasticity can be analyzed at many levels. 700

Principle 3: The two general types of plasticity derive from experience. 707

Principle 4: Similar behavioral changes can correlate with different plastic changes. 707

Principle 5: Experience-dependent changes interact. 707

Principle 6: Plasticity is age-dependent. 708

Principle 7: Plastic changes are timedependent. 708

Principle 8: Plasticity is related to an experience's relevance to the animal. 708

Principle 9: Plasticity is related to the intensity or frequency of experiences. 709

Principle 10: Plasticity can be maladaptive. 709

© 25.2 Can Plasticity Support Functional Recovery After Injury? 709

Compensation Compared with Recovery 710 What Happens When a Brain Is Injured? 711

© 25.3 Examples of Functional Restitution 712

> Recovery from Motor-Cortex Damage 712 Recovery from Aphasia 712 Recovery from Traumatic Lesions 713 Recovery from Surgical Lesions 714

Return to Daily Life 715

 25.4 Research on Plasticity in the Injured Brain 717 Functional Imaging After Cerebral Injury 717

SNAPSHOT (a) Using Imaging to Study Recovery 718

Physiological Mapping After Cerebral Injury 719

- © 25.5 Variables Affecting Recovery 720
- © 25.6 Therapeutic Approaches to Recovery After Brain Damage 721

Rehabilitation 722

Pharmacological Therapies 724

Electrical Stimulation 725

Brain-Tissue Transplants and Stem-Cell Induction 725

Diet 726

CHAPTER 26 **Neurological Disorders**

- PORTRAIT Posttraumatic Stress Disorder 730
- © 26.1 The Neurological Examination 731 The Patient's History 731 The Physical Examination 731
- 26.2 Cerebral Vascular Disorders 733 Types of Cerebral Vascular Disease 733 Treating Cerebral Vascular Disorders 735
- © 26.3 Traumatic Brain Injuries 736 Open Head Injuries 737 Closed Head Injuries 737 Behavioral Assessment of Head Injury 739 Recovering from and Preventing Head Injury 741
- 26.4 Epilepsy 741 Classifying Seizures 742 Treating Epilepsy 743
- 26.5 Tumors 743
- 26.6 Headache 745 Types of Headache 745 Treating Headache 747
- 26.7 Infections 747 Types of CNS Infection 748

Treating CNS Infection 749

© 26.8 Disorders of Motor Neurons and the Spinal Cord 750

> Myasthenia Gravis 750 Poliomyelitis 751 Multiple Sclerosis 751 Paraplegia 752

Brown-Séquard Syndrome 752 Hemiplegia 753

© 26.9 Sleep Disorders 753 Narcolepsy 755 Insomnia 756

SNAPSHOT © Restless Legs Syndrome 757

CHAPTER 27 Psychiatric and Related Disorders

- **PORTRAIT** Losing Touch with Reality 761
- 27.1 The Brain and Behavior 761
- 27.2 Schizophrenia 762

Structural Abnormalities in Schizophrenic Brains 763

Biochemical Abnormalities in the Brains of People with Schizophrenia 764

- Schizophrenia as a Neurodevelopmental Disorder 765
- © Cognitive Symptoms in Schizophrenia 765
- 27.3 Mood Disorders 767

Neurochemical Aspects of Depression 767 Neuropathological and Blood-Flow Abnormalities in Depression 768

SNAPSHOT © Cortical Metabolic and Anatomical Abnormalities in Mood Disorders 769

Neurobiological Aspects of Bipolar Disorder 770

- © 27.4 Anxiety Disorders 771
- 27.5 Psychiatric Symptoms of Cerebral Vascular Disease 772
- 27.6 Psychosurgery 773
- 27.7 Motor Disorders 774

Hyperkinetic Disorders 774
 Hypokinetic Disorders 778
 Causes of Parkinsonism 780

- Treating Parkinson's Disease 781
- Psychological Aspects of Parkinson's Disease 782
- **27.8** Dementias 783

Anatomical Correlates of Alzheimer's Disease 784

Putative Causes of Alzheimer's Disease 786

- © Clinical Symptoms and the Progression of Alzheimer's Disease 787
- © 27.9 Micronutrients and Behavior 788

CHAPTER 28

Neuropsychological Assessment

PORTRAIT Lingering Effects of Brain Trauma 793

- 28.1 The Changing Face of Neuropsychological Assessment 794 Functional Brain Imaging 794 Cognitive Neuroscience 795 Managed Care 796
- 28.2 Rationale Behind Neuropsychological Assessment 797

Factors Affecting Test Choice 798
Goals of Neuropsychological Assessment 798
Intelligence Testing in Neuropsychological
Assessment 799

Categories of Neuropsychological Assessment 801

- 28.3 Neuropsychological Tests and Brain Activity 802
- 28.4 The Problem of Effort 803
- © 28.5 Case Histories 804

Case 1: Epilepsy Caused by Left-Hemisphere Tumor 804

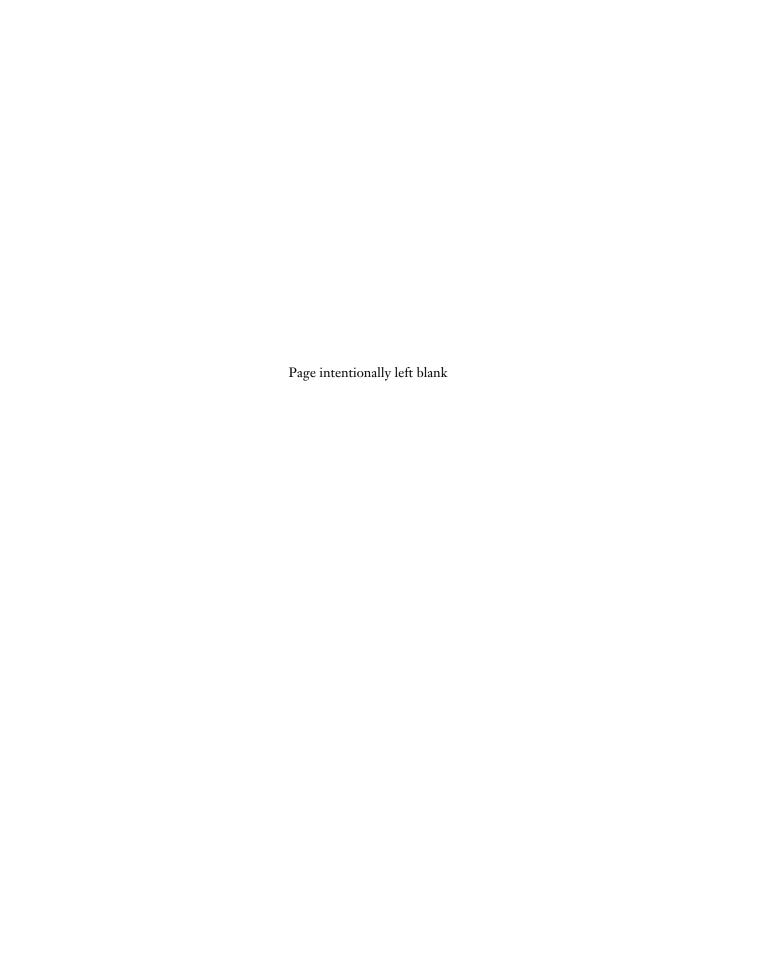
Case 2: Epilepsy Caused by Right-Hemisphere Infection 805

Case 3: Rehabilitation 805

Glossary G-1

Name Index NI-1

Subject Index SI-1



PREFACE

Looking back to 1980, when Fundamentals of Human Neuropsychology's first edition appeared, reminds us that in the 1970s, human neuropsychology did not yet exist as a unified body of knowledge about the human brain. The field had coalesced around hunches and inferences based on laboratory studies of monkeys, cats, and rats as well as on scattered studies of humans with assorted brain injuries. Over the past 40 years, as neuropsychology expanded, cognitive and social neuroscience have emerged as disciplines. Advances in and ever-more incisive use of noninvasive neuroimaging and abundant research innovations all have improved our understanding of brain anatomy.

Studies of nonhuman species remain central to human neuropsychology's core principles, especially in understanding the structure and connectivity of the primate brain, but are more focused on mechanisms than behavioral phenomena. Many researchers may share a bias that functional neuroimaging can replace studying brain-injured humans and laboratory animals. To others, this seems unlikely given the complexity of brain processes and the nature of subtraction methods used in imaging. The two approaches have become complementary, and this seventh edition reflects their intellectual evolution:

- Neuroimaging has led the renaissance in understanding neural networks and appreciating the brain's connectome. In this edition, we have expanded Chapter 7, Imaging the Brain's Activity, both to include new methods and to consider the pros and cons of different techniques in light of their relevant uses and costs (see Section 7.5). Coverage of dynamic neural networks appears throughout the book, especially in Chapters 10, 16 to 22, and 27.
- Epigenetics explains how our behaviors change our brains. We introduce basic genetics and epigenetic principles in Section 2.3 and highlight both factors throughout the book to reflect the expanding emphasis on epigenetics as a factor in cerebral organization.
- Neuropsychological assessment is vital for evaluating patients with focal brain injuries.
 One unexpected consequence of the cognitive neuroscience revolution is a declining appreciation for neuropsychological theory and clinical focus. In this new edition, we employ the venerable maze as a graphic icon (shown at right) to identify for the reader particular discussions, cases, tables, and figures that link theory and assessment throughout the book.



Content and Structure

Fundamentals differs from other textbooks of psychology, cognitive neuroscience, or neuroscience. In our experience, students find it helpful to see the brain from two organizational perspectives, anatomical and behavioral.

• We continue to provide the requisite basic background—about history, evolution, genetics and epigenetics, anatomy, physiology, pharmacology, and methodology—in Part I, Chapters 1 to 7.

- Equally fundamental to understanding subsequent material, Part II, Chapters 8 to 12, outlines the general organization and functions of the cerebral cortex.
- Part III, Chapters 13 to 17, focuses on the anatomically defined cortical regions. Understanding the organization of the cerebral cortex is central to appreciating how the brain functions to produce the complex processes that underlie complex behaviors.
- The psychological constructs presented in Part IV, Chapters 18 to 22, including language, memory, social behavior and affect, spatial behavior, and attention and consciousness, emerge from the neuronal networks explored in Part III. Shifting from anatomy to psychological processes naturally means revisiting material from earlier parts, but this time in the context of psychological theory rather than anatomy.
- Part V, Chapters 23 to 28, considers brain development and plasticity and includes more-detailed discussions of brain disorders introduced earlier in the book. Chapters on neurological and psychiatric disorders and on neuropsychological assessment continue the book's emphasis on approaching human brain functions from an interdisciplinary perspective.

We have updated all of the chapters and the glossary that follows, both to correspond to new material that reflects the changing face of neuropsychology and to include some unexpected topics—neuroeconomics in Section 22.4 and micronutrients in Section 27.9 are two. Maintaining a manageable length meant sacrificing some detail that may have been prominent in previous editions, sometimes reaching back to the first edition.

To address the challenge inherent in using a comprehensive text and to facilitate access to information, we added section numbers to each chapter's main headings. Readers can easily locate interrelated material relevant across several topics, refresh their knowledge, or jump ahead to learn more.

Acknowledgments

As in the past, we must sincerely thank many people who have contributed to the development of this edition. We are particularly indebted to colleagues from around the world who have been so supportive and have strongly encouraged us to include their favorite topics. We have done so wherever possible.

We also thank the reviewers solicited by our editors on the sixth edition of *Fundamentals*. Their anonymous comments contributed varied perspectives and valuable points of consensus that helped us shape the new edition.

Julie Alvarez Tulane University Marlene Behrmann Carnegie Mellon University Edward Castañeda The University of Texas at El Paso Pauline Dibbets Maastricht University

Peter Donovick The State University of New York at Binghamton Amanda Higley Point Loma Nazarene University Jamie Lillie Argosy University, Schaumburg

Salvatore Massa Marist College Taryn Myers Virginia Wesleyan College Martin Paczynski George Mason University Rosie Reid Dublin Business School

Tony Robertson
Vancouver Island University
Joe Wayand
Walsh University
Robin Wellington
St. John's University

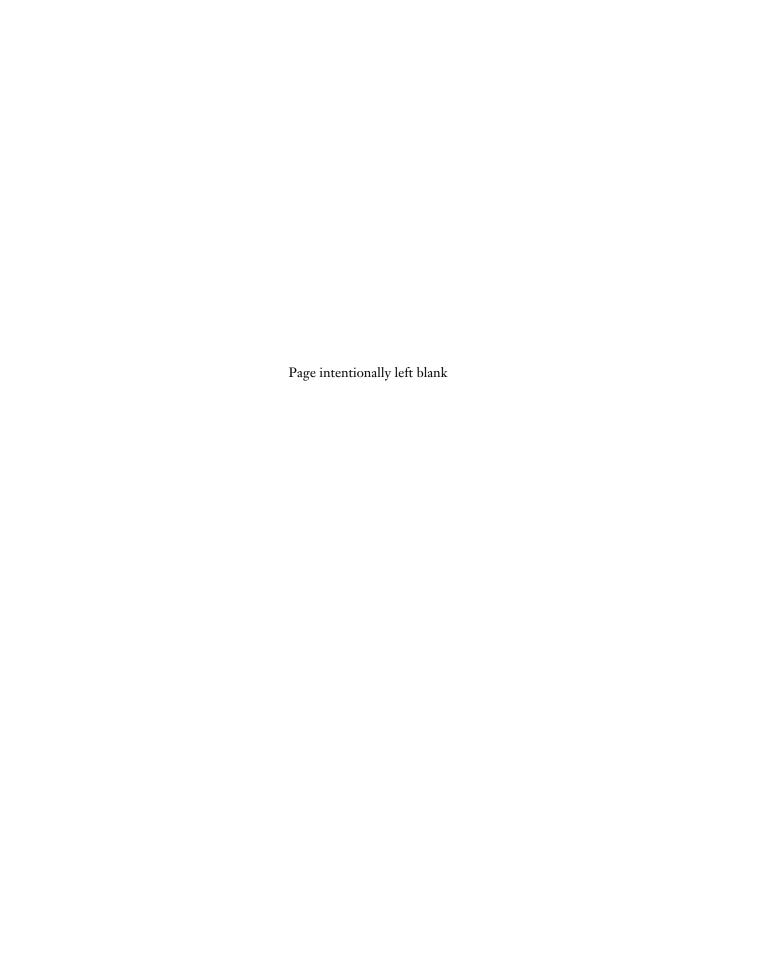
The staff at Worth Publishers and W. H. Freeman and Company are amazing and have made this task far more enjoyable than it would be without them. These folks include our sponsoring editor, Daniel DeBonis, assistant editor Nadina Persaud, and editorial assistant Katie Pachnos; our project editors, Enrico Bruno, Andrew Roney, and Janice Stangel; and our production manager, Sarah Segal. Our thanks to art director Diana Blume and interior designer Tamara Newnam for a fresh, inviting, accessible new book design, and to Kevin Kall for a striking cover.

Once again, Cecilia Varas coordinated photo research, ably assisted by researcher Richard Fox. They found photographs and other illustrative materials that we would not have found on our own. We remain indebted to art manager Matt McAdams and the artists at Dragonfly Media for their excellent work in expanding the illustration program and to Kate Scully and her team at Northeastern Graphic for their talents in translating the manuscript onto the page.

Our manuscript editor, Martha Solonche, has contributed to the book's clarity and consistency and proofreader Kate Daly to its accuracy. And as in the past, our gratitude to Barbara Brooks, our development editor, knows no bounds. She has provided a strong guiding hand to our thinking and organization and has done so with humor and a commitment to excellence that shows its stamp all over the book. Thank you, Barbara, for reminding us that the book is for students, not senior investigators, and thus requires us to write simply and clearly, and for keeping us abreast of topical news items that we might otherwise not encounter in our reading of the field's diverse literature.

Once again, errors remain solely attributable to us. In a field that has expanded so dramatically since our first edition, we hope that readers continue to acquire a breadth of knowledge in the ever-expanding world of human neuropsychology. Finally, we thank our students, who have motivated us to continue the journey of *Fundamentals of Human Neuropsychology* for nearly 40 years. Seeing the faces of students light up when they begin to understand how the marvelous brain can produce cognition and behavior continues to be rewarding and is what this endeavor is all about. Once again, we must thank our wives for putting up with us when we were distracted by deadlines and may not always have been our "usual" selves.

Bryan Kolb and Ian Q. Whishaw



MEDIA AND SUPPLEMENTS

Fundamentals of Human Neuropsychology, Seventh Edition, features a variety of supplemental materials for students and teachers of the text. For more information about any of the items below, please visit Macmillan's online catalog at http://www.macmillanhighered.com.



Available at www.macmillanhighered.com/launchpadsolo/neurotk

LaunchPad Solo is a powerful Web-based tool for learning the core concepts of behavioral neuroscience—by witnessing them firsthand. These 30 interactive tutorials allow students to see the nervous system in action via dynamic illustrations, animations, and models that demystify the neural mechanisms behind behavior. These interactive simulations enhance students' understanding of complex biological mechanisms, and carefully crafted multiple-choice questions make it easy to assign and assess each activity. Based on Worth Publishers' groundbreaking *Foundations of Behavioral Neuroscience* CD-ROM, LaunchPad Solo is a valuable accompaniment to any biopsychology course.

Topics and Activities

Neural Communication

Structure of a Neuron The Membrane Potential

Conduction of the Action Potential

Synaptic Transmission Neural Integration

Central Nervous System

Subdivisions of the Central Nervous System

Subcortical Structures

Sensory Systems—Vision

Sensory Systems—Audition

Sensory Systems—Somatosenses

Sensory Systems—Olfaction

Motor System

Limbic System

Language

The Cortex

Brain Stem and Subcortical Structures

The Spinal Cord

Visual System

The Eve

Retina

Optic Chiasm

Lateral Geniculate Nucleus

Superior Colliculus

Primary Visual Cortex

Higher Order Visual Areas

Control of Movement

Organization of the Motor Systems

Muscle and Receptor Anatomy

Muscle Contraction

Spinal Reflexes

Descending Motor Tracts

Primary Motor Cortex

Higher Order Motor Cortex

Basal Ganglia

Cerebellum

Fundamentals of Human Neuropsychology, Seventh Edition, can be ordered with LaunchPad Solo at no additional cost by using the following ISBNs.

Hardcover Text & LaunchPad Solo Access Card

ISBN-10: 1-3190-1715-0 / ISBN-13: 978-1-3190-1715-6

CourseSmart e-Book A complete electronic version of Fundamentals of Human Neuropsychology, Seventh Edition, can be previewed and purchased at www.coursesmart.com. Students can choose to view the CourseSmart e-Book online or download it to a personal computer or a portable media player such as a smartphone or iPad. This flexible, easy-to-use format makes the text more portable than ever before!

Psychology and the Real World: Essays Illustrating Fundamental Contributions to Society, Second Edition, is a superb collection of essays by major researchers that describes their landmark studies. Published in association with the not-for-profit FABBS Foundation, this engaging reader includes Bruce McEwen's work on the neurobiology of stress and adaptation, Elizabeth Loftus's own reflections on her study of false memories, and Jeremy Wolfe on his study of visual search. The new edition also features the new essay, "Can the Mind Be Read in the Brain Waves?" by Emanual Donchin, among many others. A portion of all proceeds is donated to FABBS to support societies of cognitive, psychological, behavioral, and brain sciences.

Revised! Test Bank Prepared by Tony Robertson of Vancouver Island University and Robin Wellington of St. John's University, the revised test bank includes over 50 questions per chapter including multiple-choice and shortanswer questions. Each item is keyed to the page in the textbook on which the answer can be found. All of the questions have been thoroughly reviewed and edited for accuracy and clarity.

PowerPoint Slide Sets For download on the book's catalog page (http://www. macmillanhighered.com/Catalog/product/fundamentalsofhumanneuropsychology-seventhedition-kolb/instructorresources) we offer two sets of Power-Point © presentations. For each chapter, there is a set that includes chapter art and illustrations and a final lecture presentation set that merges detailed chapter outlines with text illustrations and artwork from the book. Each set can be used directly or customized to fit your needs.

Course Management Aids The various resources for this textbook are available in the appropriate format for users of Blackboard, WebCT, Angel, Desire-2Learn, and other systems. For more information, please visit our Web site at www.macmillanhighered.com/lms.

The Development of Neuropsychology



PORTRAIT

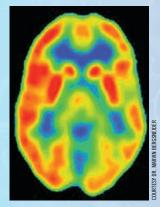
Living with Traumatic Brain Injury

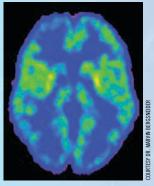
L.D., an aspiring golfer, had worked as a cook. Following brain damage, the lawyers negotiating his case puzzled over how L.D. continued to excel at golf but at the same time was unable to return to his former work as a cook.

Four years earlier, when he was 21, L.D. had been invited to participate in a sports promotion at a pub. He became ill and was helped onto a balcony by a pub employee. On the balcony, he slipped out of the employee's grasp and fell down five flights of stairs, striking his head against the stairs and wall. He was taken, unconscious, to the emergency ward of the local hospital, where his concussion was assessed on the Glasgow Coma Scale rating as 3, the lowest score on a scale from 3 to 15.

A computed tomography (CT) scan revealed bleeding and swelling on the right side of L.D.'s brain. A neurosurgeon performed a craniotomy (skull removal) over his right frontal cortex to relieve pressure and remove blood. A subsequent CT scan revealed further bleeding on the left side of his brain, and a second craniotomy was performed.

When discharged from the hospital 6 weeks later, L.D.'s recall of the events consisted only of remembering that he had entered the pub and then becoming





aware that he was in a hospital 3 weeks later. L.D. was unable to return to work because he found the multitasking involved in preparing meals too difficult. He was seeking compensation from the company that had hosted the sports promotion and from the pub where he had been injured.

We found that L.D. became frustrated and annoyed when attempting to cook. He had lost his sense of smell and taste and was not interested in socializing. He and his girlfriend had ended their 4-year relationship. We administered a comprehensive neuropsychological examination, and his scores on most tests were typical, except for tests of verbal memory and attention. Magnetic resonance imaging (MRI), a brain-scanning method that can reveal the brain's structure in detail, showed some diffuse damage to both sides of his brain. The accompanying positron emission tomography (PET) images contrast blood flow in a healthy brain (top) to blood flow in patients like L.D. (bottom).

Based on previous patients with traumatic brain injuries and behavioral and brain symptoms similar to L.D.'s, we recommended compensation, which L.D. did

receive, in addition to assistance in finding work less demanding than cooking. He was able to live on his own and successfully returned to playing golf.

According to National Institute of Neurological Disorders and Stroke estimates, 1.7 million U.S. residents receive medical attention each year after suffering traumatic brain injury (TBI), a wound to the brain that results from a blow to the head (detailed in Section 26.3, including *concussion*, the common term for mild TBI). TBI is a contributing factor in 30% of deaths due to accidents and can result from head blows while playing sports, from falls, and from vehicle accidents. While also the most common cause of discharge from military service

(Gubata et al., 2013), TBI most frequently occurs in children under the age of 6, young adults, and those over age 65. The number of people who endure TBI each year but do not report an injury is not known.

L.D. is not unusual in that, in his own view and in the view of acquaintances, he has mainly recovered, but lingering problems prevent him from resuming his former level of employment. L.D. is also not unusual in that he puzzles both friends and experts with his ability to do some things well while being unable to do other things that appear less difficult. Finally, L.D. is not unusual in that the diffuse brain injury revealed by brain-scanning methods (see Chapter 7) does not predict his abilities and disabilities well.

Neuropsychological testing is required to confirm that he has enduring cognitive deficits and to identify those deficits. L.D.'s poor scores on tests of memory and attention are associated with his difficulty in everyday problem solving, a mental skill referred to as executive function. Thus, L.D. can play golf at a high level because it requires that he execute only one act at a time, but he cannot prepare a meal, which requires him to multitask.

This book's objective is to describe **neuropsychology**, the scientific study of the relations between brain function and behavior. Neuropsychology draws information from many disciplines—anatomy, biology, biophysics, ethology, pharmacology, physiology, physiological psychology, and philosophy among them. Neuropsychological investigations into the brain-behavior relationship can identify impairments in behavior that result from brain trauma and from diseases that affect the brain.

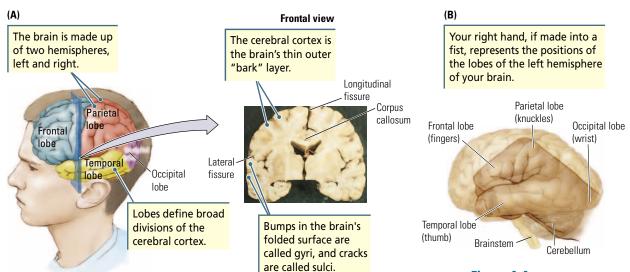
Neuropsychology is strongly influenced by two experimental and theoretical investigations into brain function: the **brain theory**, which states that the brain is the source of behavior; and the **neuron theory**, the idea that the unit of brain structure and function is the **neuron**, or nerve cell. This chapter traces the development of these two theories and introduces neuropsychology's major principles, which have emerged from investigating brain function and which we apply in subsequent chapters.

1.1 The Brain Theory

People knew what the brain looked like long before they had any idea of what it did. Early in human history, hunters must have noticed that all animals have brains and that the brains of different animals, including humans, although varying greatly in size, look quite similar. Over the past 2000 years, anatomists have produced drawings of the brain, named its distinctive parts, and developed methods to describe the functions of those parts.

What Is the Brain?

Brain is an Old English word for the tissue found within the skull (cranium). **Figure 1.1**A shows a human brain as oriented in the skull of an upright human. Just as your body is symmetrical, having two arms and two legs, so is your brain. Its two almost symmetrical halves are called **hemispheres**, one on the left side of the body and the other on the right, as shown in the frontal view. If you make your right hand into a fist and hold it up with the thumb pointing toward the front, the fist can represent the brain's left hemisphere as positioned within the skull (Figure 1.1B).



The brain's basic plan is that of a tube filled with salty fluid called **cerebro**spinal fluid (CSF), which cushions the brain and assists in removing metabolic waste. Parts of the tube's covering have bulged outward and folded, forming the more complicated-looking surface structures that initially catch the eye in Figure 1.1A. The brain's most conspicuous outer feature is the crinkled tissue that has expanded from the front of the tube to such an extent that it folds over and covers much of the rest of the brain (Figure 1.1A at right). This outer layer is the **cerebral cortex** (usually referred to as just the cortex). The word *cortex*, meaning "bark" in Latin, is apt, because the cortex's folded appearance resembles the bark of a tree and because, as bark covers a tree, cortical tissue covers most of the rest of the brain.

The folds, or bumps, in the cortex are called **gyri** (gyrus is Greek for "circle"), and the creases between them are called **sulci** (sulcus is Greek for "trench"). Some large sulci are called fissures: the **longitudinal fissure**, shown in the Figure 1.1 frontal view, divides the two hemispheres, and the lateral fissure divides each hemisphere into halves. (In our fist analogy, the lateral fissure is the crease separating the thumb from the other fingers.) Pathways called *commissures*, the largest of which is the **corpus callosum**, connect the brain's hemispheres.

The cortex of each hemisphere forms four lobes, each named after the skull bones beneath which they lie. The **temporal lobe** is located below the lateral fissure at approximately the same place as the thumb on your upraised fist (Figure 1.1B). Lying immediately above the temporal lobe is the **frontal lobe**, so called because it is located at the front of the brain beneath the frontal bones. The parietal lobe is located behind the frontal lobe, and the occipital lobe constitutes the area at the back of each hemisphere.

The cerebral cortex constitutes most of the forebrain, so named because it develops from the front part of the neural tube that makes up an embryo's primitive brain. The remaining "tube" underlying the cortex is the brainstem. The brainstem is in turn connected to the **spinal cord**, which descends down the back within the vertebral column. To visualize the relations among these parts of the brain, again imagine your upraised fist: the folded fingers represent the cortex, the heel of the hand represents the brainstem, and the arm represents the spinal cord.

Figure 1.1 ▲

The Human Brain (A) The human brain, as oriented in the head. The visible part of the intact brain is the cerebral cortex, a thin sheet of tissue folded many times and fitting snugly inside the skull. (B) Your right fist can serve as a guide to the orientation of the brain and its cerebral lobes. (Photograph: Arthur Glauberman/ Science Source.)

This three-part brain is conceptually useful evolutionarily, anatomically, and functionally. Evolutionarily, animals with only spinal cords preceded those with brainstems, which preceded those with forebrains. Anatomically, in prenatal development, the spinal cord forms before the brainstem, which forms before the forebrain. Functionally, the forebrain mediates cognitive functions; the brainstem mediates regulatory functions such as eating, drinking, and moving; and the spinal cord conveys sensory information into the brain and sends commands from the brain to the muscles to move.

How Does the Brain Relate to the Rest of the Nervous System?

The brains and spinal cords of mammals are encased in protective bones: the skull protects the brain, and vertebrae protect the spinal cord. Together, the brain and spinal cord are called the **central nervous system**, or CNS. The CNS is connected to the rest of the body through nerve fibers.

Some fibers carry information away from the CNS; others bring information into it. These nerve fibers constitute the **peripheral nervous system**, or PNS. One distinguishing feature between the central and peripheral nervous systems is that PNS tissue will regrow after damage, whereas the CNS does not regenerate lost tissue. Thus the long-term prospect for L.D. is that he will show little further recovery in higher brain functions such as planning, but his golf game may improve.

Nerve fibers that bring information to the CNS are extensively connected to sensory receptors on the body's surface and to muscles, enabling the brain to sense the world and to react. This subdivision of the PNS is called the **somatic nervous system** (SNS). Organized into **sensory pathways**, collections of fibers carry messages for specific senses, such as hearing, vision, and touch. Sensory pathways carry information collected on one side of the body mainly to the cortex in the *opposite* hemisphere. The brain uses this information to construct perceptions of the world, memories of past events, and expectations about the future.

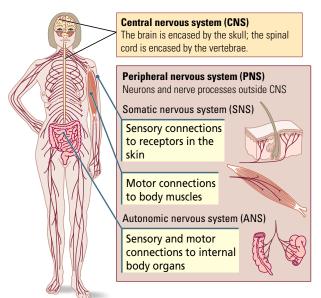
Motor pathways are groups of nerve fibers that connect the brain and spinal cord to the body's muscles through the SNS. Movements produced by motor pathways include the eye movements that you are using to read this book, the hand movements that you make while turning or scrolling through the pages, and your body's posture as you read. The parts of the cortex that produce movement mainly send information out via motor pathways to muscles on the opposite side of the body. Thus, one hemisphere uses muscles on the opposite side of the body to produce movement.

Sensory and motor pathways also influence the muscles of your internal organs—the beating of your heart, contractions of your stomach, raising and lowering of your diaphragm to inflate and deflate your lungs. The pathways that control these organs are a subdivision of the PNS called the **autonomic nervous system** (ANS). **Figure 1.2** diagrams these major divisions of the human nervous system.

Figure 1.2 ▼

Major Divisions of the Human Nervous System

The brain and spinal cord together make up the CNS. All the nerve processes radiating from it and the neurons outside it connect to the sensory receptors and muscles in the SNS and to internal organs in the ANS. This constitutes the peripheral nervous system (PNS).



1.2 Perspectives on the Brain and Behavior

The central topic in neuropsychology is how brain and behavior are related. We begin with three classic theories—mentalism, dualism, and materialism representative of the many attempts scientists and philosophers have made to relate brain and behavior. Then we explain why contemporary brain investigators subscribe to the materialist view. In reviewing these theories, you will recognize that some "commonsense" ideas you might have about behavior are derived from one or another of these perspectives (Finger, 1994).

Aristotle: Mentalism

The Greek philosopher Aristotle (384–322 B.C.E.) was the first person to develop a formal theory of behavior. He proposed that a nonmaterial psyche is responsible for human thoughts, perceptions, and emotions and for such processes as imagination, opinion, desire, pleasure, pain, memory, and reason.

The psyche is independent of the body but in Aristotle's view, works through the heart to produce action. As in Aristotle's time, heart metaphors serve to this day to describe our behavior: "put your heart into it" and "she wore her heart on her sleeve" are but two. Aristotle's view that this nonmaterial psyche governs behavior was adopted by Christianity in its concept of the soul and has been widely disseminated throughout the world. Mind is an Anglo-Saxon word for memory, and, when "psyche" was translated into English, it became *mind*.

The philosophical position that a person's mind is responsible for behavior is called *mentalism*, meaning "of the mind." Mentalism still influences modern neuropsychology: many terms—sensation, perception, attention, imagination, emotion, memory, and volition among them—are still employed as labels for patterns of behavior. (Scan some of the chapter titles in this book.) Mentalism also influences people's ideas about how the brain might work, because the mind was proposed to be nonmaterial and so have no "working parts." We still use the term *mind* to describe our perceptions of ourselves as having unitary consciousness despite recognizing that the brain is composed of many parts, and as we describe in Section 1.3, has many separate functions.

Descartes: Dualism

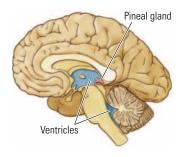
René Descartes (1596-1650), a French anatomist and philosopher, wrote what could be considered the first neuropsychology text in 1684. In it he gave the brain a prominent role. Descartes was impressed by machines made in his time, such as those encased in certain statues on display for public amusement in the water gardens of Paris. When a passerby stopped in front of one particular statue, for example, his or her weight depressed a lever under the sidewalk, causing the statue to move and spray water at the person's face. Descartes proposed that the body is like these machines. It is material and thus clearly has spatial extent, and it responds mechanically and reflexively to events that impinge on it (Figure 1.3).

Described as nonmaterial and without spatial extent, the mind, as Descartes saw it, was different from the body. The body

Figure 1.3 ▼

Descartes's Concept of Reflex Action In this mechanistic depiction, heat from the flame causes a thread in the nerve to be pulled, releasing ventricular fluid through an opened pore. The fluid flows through the nerve, causing not only the foot to withdraw but the eyes and head to turn to look at it, the hands to advance, and the whole body to bend to protect it. Descartes ascribed to reflexes behaviors that today are considered too complex to be reflexive, whereas he did not conceive of behavior described as reflexive today. (From Descartes, 1664. Print Collector/Getty Images.)





operated on principles similar to those of a machine, but the mind decided what movements the machine should make. Descartes located the site of action of the mind in the *pineal body*, a small structure high in the brainstem. His choice was based on the logic that the pineal body is the only structure in the nervous system not composed of two bilaterally symmetrical halves and moreover that it is located close to the ventricles. His idea was that the mind, working through the pineal body, controlled valves that allowed CSF to flow from the ventricles through nerves to muscles, filling them and making them move.

For Descartes, the cortex was not functioning neural tissue but merely a covering for the pineal body. People later argued against Descartes's hypothesis by pointing out that no obvious changes in behavior occur when the pineal body is damaged. Today, the pineal body, now called the pineal gland, is known to influence daily and seasonal biorhythms. And the cortex became central to understanding behavior as scientists began to discover that it performs the functions Descartes attributed to a nonmaterial mind.

Descartes's position that mind and body are separate but can interact is called **dualism**, to indicate that behavior is caused by two things. Dualism originated a quandary known as the **mind-body problem**: for Descartes, a person is capable of consciousness and rationality only because of having a mind, but how can a nonmaterial mind produce movements in a material body?

To understand the mind-body problem, consider that for the mind to affect the body, it must expend energy, adding new energy to the material world. The spontaneous creation of new energy violates a fundamental law of physics, the law of conservation of matter and energy. Thus, dualists who argue that mind and body interact causally cannot explain how.

Other dualists avoid this problem by reasoning either that the mind and body function in parallel, without interacting, or that the body can affect the mind but the mind cannot affect the body. These dualist positions allow for both a body and a mind by sidestepping the problem of violating the laws of physics.

Descartes's theory also spawned unforeseen and unfortunate consequences. In proposing his dualistic theory of brain function, Descartes also proposed that animals do not have minds and therefore are only machinelike, that the mind develops with language in children, and that mental disease impairs rational processes of the mind. Some of his followers justified the inhumane treatment of animals, children, and the mentally ill on the grounds that they did not have minds: an animal did not have a mind, a child developed a mind only at about 7 years of age when able to talk and reason, and the mentally ill had "lost their minds." Likewise misunderstanding Descartes's position, some people still argue that the study of animals cannot be a source of useful insight into human neuropsychology.

Descartes himself, however, was not so dogmatic. He was kind to his dog, Monsieur Grat. He suggested that whether animals had minds could be tested experimentally. He proposed that the key indications of the presence of a mind are the use of language and reason. He suggested that, if it could be demonstrated that animals could speak or reason, then such demonstration would indicate that they have minds. Exciting lines of research in modern experimental neuropsychology, demonstrated throughout this book, are directed toward the comparative study of animals and humans with respect to language and reason.

Darwin: Materialism

By the mid-nineteenth century, our contemporary perspective of materialism was taking shape. The idea is that rational behavior can be fully explained by the workings of the nervous system. No need to refer to a nonmaterial mind. Materialism has its roots in the evolutionary theories of two English naturalists, Alfred Russel Wallace (1823-1913) and Charles Darwin (1809-1892).

Evolution by Natural Selection

Darwin and Wallace looked carefully at the structures of plants and animals and at animal behavior. Despite the diversity of living organisms, the two were struck by their many similarities. For example, the skeleton, muscles, internal organs, and nervous systems of humans, monkeys, and other mammals are similar. These observations support the idea that living things must be related, an idea widely held even before Wallace and Darwin. More importantly, these same observations led to the idea that the similarities could be explained if all animals had evolved from a common ancestor.

Darwin elaborated his theory in On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life, originally published in 1859. He argued that all organisms, both living and extinct, are descended from an ancestor that lived in the remote past. Animals have similar traits because those traits are passed from parents to their offspring. The nervous system is one such trait, an adaptation that emerged only once in animal evolution. Consequently, the nervous systems of living animals are similar because they are descendants of that first nervous system. Those animals with brains likewise are related, because all animals with brains descend from the first animal to evolve a brain.

Natural selection is Darwin's theory for explaining how new species evolve and how they change over time. A species is a group of organisms that can breed among themselves but usually not with members of other species. Individual organisms within a species vary in their **phenotype**, the traits we can see or measure. Some are big, some are small, some are fat, some are fast, some are light colored, some have large teeth. Individual organisms whose traits best help them to survive in their environment are likely to leave more offspring that feature those traits.

Natural Selection and Heritable Factors

Beginning about 1857, Gregor Mendel (1822-1884), an Austrian monk, experimented with plant traits, such as the flower color and height of pea plants, and determined that such traits are due to heritable factors we now call genes (elaborated in Section 2.3). Thus, the unequal ability of individual organisms to survive and reproduce is related to the different genes they inherit from their parents and pass on to their offspring.

Mendel realized that the environment plays a role in how genes express traits: planting tall peas in poor soil reduces their height. Likewise, experience affects gene expression: children who lack educational opportunities may not adapt as well in society as children who attend school. The science that studies differences in gene expression related to environment and experience is epigenetics (see Section 2.3). Epigenetic factors do not change the genes individuals inherit, but they do affect whether a gene is active—turned on or off—and in this way influence an individual's phenotypic traits.

Environment and experience play an important role in how animals adapt and learn. Adaptation and learning are in turn enabled by the brain's ability to form new connections and pathways. This **neuroplasticity** is the nervous system's potential for physical or chemical change that enhances its adaptability to environmental change and its ability to compensate for injury. Epigeneticists are especially involved in describing how genes express the brain's plastic changes under the influence of environment and experience.

Contemporary Perspectives

As a scientific theory, contemporary brain theory is both materialistic and neutral with respect to beliefs, including religious beliefs. Science is not a belief system but rather a set of procedures designed to allow investigators to confirm answers to questions independently. Behavioral scientists, both those with and those without religious beliefs, use the scientific method to examine relations between the brain and behavior and to *replicate* (repeat) others' work on brainbehavior relationships. Today, when neuroscientists use the term *mind*, most are not referring to a nonmaterial entity but using it as shorthand for the collective functions of the brain.

1.3 Brain Function: Insights from **Brain Injury**

You may have heard statements such as, "Most people use only 10% of their brains" or "He put his entire mind to the problem." Both statements arise from early suggestions that people with brain damage often get along quite well. Nevertheless, most people who endure brain damage will tell you that some behavior is lost and some survives, as it did for L.D., whose case begins this chapter. Our understanding of brain function has its origins in individuals with brain damage. We now describe some fascinating neuropsychological concepts that have emerged from studying such individuals.

Localization of Function

The first general theory to propose that different parts of the brain have different functions was developed in the early 1800s by German anatomist Franz Josef Gall (1758–1828) and his partner Johann Casper Spurzheim (1776–1832) (Critchley, 1965). Gall and Spurzheim proposed that the cortex and its gyri were functioning parts of the brain and not just coverings for the pineal body. They supported their position by showing through dissection that the brain's most distinctive motor pathway, the *corticospinal* (cortex to spinal cord) *tract*, leads from the cortex of each hemisphere to the spinal cord on the opposite side of the body. Thus, they suggested, the cortex sends instructions to the spinal cord to command muscles to move. They also recognized that the two symmetrical hemispheres of the brain are connected by the corpus callosum and can thus interact.

Gall's ideas about behavior began with an observation made in his youth. Reportedly, he observed that students with good memories had large, protruding eyes and surmised that a well-developed memory area of the cortex located behind the eyes would cause them to protrude. Thus, he developed his hypothesis, called **localization of function**, that a different, specific brain area controls each kind of behavior.

Gall and Spurzheim furthered this idea by collecting instances of individual differences that they related to other prominent features of the head and skull. They proposed that a bump on the skull indicated a well-developed underlying cortical gyrus and therefore a greater capacity for a particular behavior; a depression in the same area indicated an underdeveloped gyrus and a concomitantly reduced faculty.

Thus, just as a person with a good memory had protruding eyes, a person with a high degree of musical ability, artistic talent, sense of color, combativeness, or mathematical skill would have large bumps in other

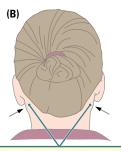
areas of the skull. **Figure 1.4** shows where Gall and Spurzheim located the trait of amativeness (sexiness). A person with a bump there would be predicted to have a strong sex drive, whereas a person low in this trait would have a depression in the same region.

Gall and Spurzheim identified a long list of behavioral traits borrowed from the English or Scottish psychology of the time. They assigned each trait to a particular part of the skull and, by inference, to the underlying brain part. Spurzheim called this study of the relation between the skull's surface features and a person's mental faculties **phrenology** (*phren* is a Greek word for "mind"). **Figure 1.5** shows the resulting phrenological map that he and Gall devised.

Some people seized on phrenology as a means of making personality assessments. They developed a method called *cranioscopy*, in which a device was placed around the skull to measure its bumps and depressions. These measures were then correlated with the phrenological map to determine the person's likely behavioral traits. The faculties described in phrenology—characteristics such as faith, self-love, and veneration—are impossible to define and to quantify objectively. Phrenologists also failed to recognize that the superficial features on the skull reveal little about the underlying brain. Gall's notion of localization of function, although inaccurate scientifically, laid the conceptual foundation for modern views of functional localization, beginning with the localization of language.

Among his many observations, Gall gave the first account of a case in which frontal-lobe brain damage was followed by loss of the ability to speak. The patient was a soldier whose brain was pierced by a sword driven through his eye. Note that, on the phrenological map in Figure 1.5, language is located below the eye. Gall gave the





Gall correlated bumps in the region of the cerebellum with the brain's "amativeness" center.

Figure 1.4 ◀

Gall's Theory Depressions
(A) and bumps (B) on the skull indicate the size of the underlying area of brain and thus, when correlated with personality traits, indicate the part of the brain controlling the trait. While examining a patient (who because of her behavior became known as "Gall's Passionate Widow"), Gall found a bump at the back of her neck that he thought located the center for "amativeness" in the cerebellum. (Research from Olin, 1910.)

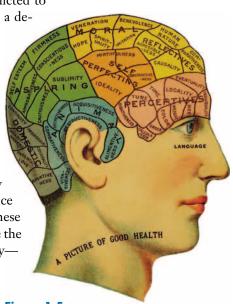


Figure 1.5 ▲

Phrenology Bust Originally, Gall's system identified putative locations for 27 faculties. As the study of phrenology expanded, the number of faculties increased. Language, indicated at the front of the brain, below the eye, actually derived from one of Gall's case studies. A soldier had received a knife wound that penetrated the frontal lobe of his left hemisphere through the eye. The soldier lost the ability to speak. (Mary Evans Picture Library/Image Works.)