

An Introduction to BEHAVIORAL ENDOCRINOLOGY

Fourth Edition



Randy J. Nelson

An Introduction to BEHAVIORAL

ENDOCRINOLOGY

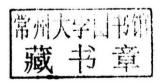
Fourth Edition







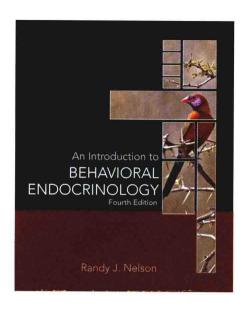
Randy J. Nelson
The Ohio State University











The Cover

The cover photo is a male violet-eared waxbill (*Uraeginthus granatina*), a brilliantly colored territorial finch that lives in male–female pairs. Violet-eared waxbills are native to West and South Africa. These birds have been used to identify the neuropeptides involved in social behaviors and social grouping. For example, mesotocin (an avian homologue of oxytocin) receptors are more prevalent in the dorsal lateral septum among flocking species than among violet-eared waxbills, a species that tends to avoid large groups. Understanding the receptor distribution of hormones in the nervous system is critical to understanding how hormones affect behavior.

An Introduction to Behavioral Endocrinology, Fourth Edition

Copyright @ 2011 by Sinauer Associates, Inc. All rights reserved. This book may not be reproduced in whole or in part without permission from the publisher.

For information, address:

Sinauer Associates, Inc., 23 Plumtree Road, Sunderland, MA 01375 U.S.A.

Fax: 413-549-1118

Email: publish@sinauer.com Internet: www.sinauer.com

Library of Congress Cataloging-in-Publication Data

Nelson, Randy Joe.

An introduction to behavioral endocrinology / Randy J. Nelson. -- 4th ed. p. cm.

ISBN 978-0-87893-620-5 (hardcover)

 Animal behavior--Endocrine aspects. 2. Human behavior--Endocrine aspects. I. Title.

QP356.45.N45 2011 612.4'05--dc22

2011014673

Behavioral Endocrinology

For Courtney, Morgan, and Justin...again.

Preface

It is the last day of May 2011 and it is a time for reflection. How has the field of behavioral endocrinology changed since I published the first edition of this book in 1995? As I submit the final parts of my fourth edition manuscript to the publisher, I think of how the genomic revolution has influenced this field. This edition has required updating in how genomics has influenced the approaches used in the study of behavioral endocrinology. No matter how well the genetics, molecular signaling pathways, or endocrine interactions are characterized, it is important to understand the antecedents of behavior. What is the role of the behavior in the context of how individuals have evolved to survive and reproduce in specific environmental and temporal niches?

The field of behavioral endocrinology is a truly interdisciplinary effort. It involves the study of phenomena ranging from genetic, molecular, and cellular levels of analysis to the study of individual and social behaviors. I had several goals when I began writing the fourth edition of this textbook, one of which was to continue to present information about the interactions between hormones and behavior from diverse perspectives. I also want to provide students with more-detailed information about the scientists who laid the foundation for our modern studies of behavioral endocrinology. I have tried to present current hypotheses and theories in the context of their historical origins. Naturally, after six years, the book needed some general updating to remain useful, and I have endeavored to update all chapters to reflect current studies and information. Some areas, such as body mass regulation and circadian rhythm research, are moving forward with rapid advances announced weekly.

One criticism that I have received in the past, especially from my colleagues teaching in Psychology departments, is that I have too much comparative work in the text. This is a criticism that I continue to happily ignore. The comparative perspective is what gives behavioral endocrinology great strength, and has revealed some of the most fascinating discoveries in our field using nontraditional animal models. I present this broad comparative approach in this edition. It is my hope that presenting adaptive function along with molecular and physiological mechanisms will yield greater understanding than presenting either approach alone.

I appreciate that many behavioral endocrinology students will be psychology majors. Thus, I have tried to keep the conceptual issues clear, and provide only sufficient details and examples that support the concepts. New to this edition is an outline and discussion of the main points for each chapter

to help guide students through the text. My assumption is that psychology students will have taken a course in biopsychology or neuroscience by the time they encounter this textbook, but again, I have tried to keep discussions of endocrine physiology and biochemistry to a minimum level necessary to understand the hormone–behavior interactions being discussed. Because students are likely to be familiar with the behavior of common animals such as dogs and rabbits, I have continued to use these animals as examples to help explain many concepts in this text. New to this edition is a student website that contains some wonderful videos and animations, which I hope help illustrate some of the behavioral and physiological concepts discussed in the text. Also new to this edition is the addition of color graphics that I hope will help clarify principles.

Several topics had to be omitted or curtailed in the text. I assume that professors will use additional readings to make up for any deficiencies. Some topics covered in the text are controversial and will likely stimulate class discussions. At the end of each chapter are some questions for discussion that I hope will be potential starting points for such exchanges. A short, updated list of suggested readings is also provided at the end of each chapter where students can find reasonably current and more detailed information on the material in each chapter.

This is a very exciting time to be studying this field, either as a student or as a researcher in behavioral endocrinology. I hope that I have captured for the reader at least a fraction of the excitement of this field that I have enjoyed.

Randy J. Nelson May 2011

Acknowledgments

Completion of a textbook requires input from students, colleagues, editors, artists, production editors, photo editors, composers, and friends. There are so many people to thank who provided remarkable assistance to me as I worked on this edition. I remain profoundly grateful to the reviewers and colleagues who provided feedback and assistance that shaped the first three editions. These individuals include: Elizabeth Adkins-Regan, Gregory Ball, Jacques Balthazart, Tim Bartness, George Bentley, Dan Bernard, Staci Bilbo, Eric Bittman, Elliott Blass, Jeff Blaustein, Joan Blom, Robert Bridges, Sue Carter, Joe Casto, Silvana Chiavegatto, Nicky Clayton, Lique Coolen, Tara Craft, David Crews, James Dabbs, Greg Demas, Courtney DeVries, Don Dewsbury, Debbie Drazen, Lori Flanagan-Cato, Alison Fleming, Nancy Forger, Karyn Frick, Stephen Gammie, Erica Glasper, Paul Gold, Bruce Goldman, Elizabeth Gould, David Gubernick, Tom Hahn, Joyce Hairston, Andrew Hotchkiss, Elaine Hull, Sabra Klein, Rosemary Knapp, Lance Kriegsfeld, Michael Leon, Joe Lonstein, Vicky Luine, Margaret McCarthy, Martha McClintock, Jim McGaugh, Lynn Martin, Chris Moffatt, Celia Moore, Michael Moore, Gretchen Neigh, Kathie Olsen, David Olton, Deb Olster, Vladimir Pravosudov, Brian Prendergast, Leah Pyter, Emilie Rissman, Mike Romero, Jay Rosenblatt, Ed Roy, Ben Sachs, Randall Sakai, Jen Sartor, Jill Schneider, Barbara Sherwin, David Shide, Rae Silver, Cheryl Sisk, Chuck Snowdon, Judith Stern, Brian Trainor, Anjali Trasy, George Wade, John Wingfield, Amy Wisniewski, Ruth Wood, Pauline Yahr, Kelly Young, Zachary Weil, and Irving Zucker.

I am especially grateful for assistance during the preparation of this fourth edition by many colleagues, who provided helpful, insightful, direct, critical, and immensely kind comments including Elizabeth Adkins-Regan, Noah Ashley, Greg Ball, Jacques Balthazart, Andy Bass, Tracy Bedrosian, Jeff Blaustein, Frances Champagne, Nicky Clayton, David Crews, Jill Daniel, Greg Demas, Courtney DeVries, Gary Dohanich, Alison Fleming, Laura Fonken, Karyn Frick, Stephen Gammie, Jim Goodson, Achikam Haim, Eric Herzog, Kim Huhman, Ellen Ketterson, Kelly Klump, Lance Kriegsfeld, Al Lewy, Joe Lonstein, Vicky Luine, Bob Mason, Ignacio Moore, John Morris, Karl Obrietan, Michael Romero, Heather Rupp, Randall Sakai, Jill Schneider, Brian Trainor, Sari van Anders, Amy Wisniewski, James Walton, Zachary Weil, Gary Wenk, John Wingfield, and Irving Zucker. I attempted to incorporate virtually all of these reviewers' suggestions for changes into this new edition. Occasionally, because of stubbornness, laziness, or other negative traits on my part, I failed to address my friends' and colleagues' suggestions. Any and all remaining errors, sources of confusion, or other shortcomings in this new edition remain my sole responsibility.

I also thank Tracy Bedrosian, Laura Fonken, Greg Demas, Courtney DeVries, Lance Kriegsfeld, Brian Trainor, James Walton, and Zachary Weil for helping to track down various materials for the revised book manuscript. I remain especially grateful to my many colleagues who kindly provided reprint or preprint copies of their papers, as well as my colleagues and friends who generously provided permission to use their graphic or photographic material in the book or website. Special thanks to Jim Goodson for suggesting the use of the beautiful violet-eared waxbill for the cover image. I am profoundly grateful to individuals who provided extensive reviews and helpful updated text including Jill Daniel, Greg Demas, Gary Dohanich, Jim Goodson, Ellen Ketterson, Jill Schneider, and Zachary Weil who also provided much help in reading and re-reading proofs. Of course, I remain singularly grateful to my colleague, collaborator, and wife, Courtney DeVries, who has been supportive during the preparation of all four editions and remains critical only while reading chapter manuscripts, and uncritical at all other times.

I also thank the very hard-working folks at Sinauer Associates. Although only my name appears on the cover, this book is the result of helpful and talented people. I remain grateful for the friendship and guidance provided to me during the first two editions by Pete Farley, and during production of the third edition by Graig Donini. Graig started with the fourth edition of this book, but was completed with the remarkably kind and talented book editor, Sydney Carroll, who assured me that we were "right on schedule" no matter how many deadlines passed. She also led the effort to change format and add color to the production of this edition.

I am grateful to Chelsea Holabird, the production editor, whose excellent eye for detail has helped improve the book. Others who deserved special thanks at Sinauer include Chris Small, production manager; Joanne Delphia, book designer; Joan Gemme, compositor; Elizabeth Morales, artist; David McIntyre, photo editor; and Laura Green, production editor. I remain grateful for having the same outstanding copy editor for the first three editions, Norma Roche, who taught me about clear writing. A new copy editor, Lou Doucette, kindly stepped in to gently fix-up my prose in this edition. I also thank Jason Dirks, the media editor, for his help in designing and implementing the website. This Fourth Edition of the textbook is much improved because of their unrelenting hard work and uncompromising standards.

Finally, I thank the hundreds of undergraduate students who have taken my course in Behavioral Endocrinology over the past 25 years. They have provided many helpful suggestions on improving the textbook. The study of the interactions among hormones, brain, and behavior is a fascinating field. If I'm able to convey just a small part of the excitement in this discipline to students, then I'll consider this book a success.

Brief Contents

CHAPTER 1	The Study of Behavioral Endocrinology 1		
CHAPTER 2	The Endocrine System 37		
CHAPTER 3	Sex Differences in Behavior: Sex Determination and Differentiation 89		
CHAPTER 4	Sex Differences in Behavior: Animal Models and Humans 143		
CHAPTER 5	Male Reproductive Behavior 201		
CHAPTER 6	Female Reproductive Behavior 275		
CHAPTER 7	Parental Behavior 335		
CHAPTER 8	Hormones and Social Behavior 391		
CHAPTER 9	Homeostasis and Behavior 453		
CHAPTER 10	Biological Rhythms 511		
CHAPTER 11	Stress 579		
CHAPTER 12	Learning and Memory 625		
CHAPTER 13	Hormones and Affective Disorders 671		

Contents

Chapter 2

Chemical Communication 38

Steroid Hormones 56

Monoamine Hormones

Lipid-Based Hormones 65

The Major Vertebrate Hormones 42

Protein and Peptide Hormones 43

General Features of the Endocrine System 39

BOX 2.1 The Discovery of Secretin 53

Preface xv

Historical Roots of Behavioral Endocrinology 3	Ablation and Replacement 19		
Berthold's Experiment 4	Bioassays 19		
BOX I.I The Hijras of India 5 What Are Hormones? 7	Immunoassays 21 Immunocytochemistry 23		
 BOX 1.2 Frank A. Beach and the Origins of the Modern Era of Behavioral Endocrinology 8 	Autoradiography 24 Blot Tests 24 Autoradiography Using In Situ Hybridization 24		
BOX 1.3 Neural Transmission versus Hormonal Communication 10	Stimulation and Recording 25		
The Study of Behavior II Problems of Behavioral Research 11 The Simple System Approach 12 Levels of Analysis 13 How Might Hormones Affect Behavior? 15 How Might Behavior Affect Hormones? 16 Classes of Evidence for Determining Hormone— Behavior Interactions 18 Common Techniques in Behavioral Endocrinology 19	Pharmacological Techniques 25 Microdialysis 26 Brain Imaging 26 Genetic Manipulations 28 Gene Arrays 31 A Case Study: Effects of Leptin on Behavior 31 Summary 34 Questions for Discussion 35 Suggested Readings 35		

37

How Hormones Are Regulated 66

Cellular and Molecular Mechanisms of Hormone Action 68

Hormone Receptor Types 68

Events 72

Endocrine Glands 75

Evolution of Hormones 74

Transcription, Translation, and Posttranslational

The Endocrine System

Hypothalamus 76

Pituitary Gland 77	Gonads 83		
Thyroid Gland 79	Placenta 85		
Pancreas 80			
Gastrointestinal Tract 80	Summary 86		
Adrenal Glands 81	Questions for Discussion 88		
	Suggested Readings 88		
Chapter 3 Sex Differences in Behavior:	Soy Determination and Differentiation on		
Sex Differences in Berlavior	Sex Determination and Differentiation 89		
Sex Determination and Differentiation 95	BOY 2.2 Mailing C.V.		
Ultimate Causes of Sex Differences 96	BOX 3.2 William C. Young 119		
BOX 3.1 Behavioral Sex Role Reversals 98	Sexual Differentiation and Behavior 127		
Proximate Causes of Sex Differences 99	Early Effects of Androgens on Brain and Behavior Are Mediated by Activation of Estrogen and Androgen		
Mammalian Sexual Differentiation 100	Receptors 128		
	Environmental Influences on Mammalian Sexual		
Anomalous Mammalian Sexual Differentiation 103 Sexual Differentiation in Birds 110	Differentiation of the Nervous System 129		
	BOX 3.3 Epigenetic Effects on Sexual Dimorphism:		
Alternative Reproductive Tactics and Male Polymorphism 111	Direct Maternal Provisioning of Steroids to		
	Offspring 130		
Environmental Sex Determination in Reptiles and Fishes 115	Conclusions 137		
	Summary 138		
The Effects of Hormones on Sexually Dimorphic Behaviors 118	Questions for Discussion 141		
The Organizational/Activational Hypothesis 118	Suggested Readings 141		
- 110			
Chapter 4 Sex Differences in Behavior:	Animal Models and Humans 143		
BOX 4.1 Sex Ratio of Litter Affects Adult Behavior 146	Gender Role 174		
Neural Bases of Mammalian Sex Differences 147	Gender Identity 176		
BOX 4.2 The Spinal Nucleus of the Bulbocavernosus	Sexual Orientation/Sexual Preference 177		
Muscle 149	BOX 4.5 Hormonal Influences on Mate Choice 179		
Molecular Sex Differences in the Brain 154	Sex Differences in Cognitive Abilities 183		
Animal Models for Sexually Dimorphic	Perception and Sensory Abilities 184		
Behaviors 158	Lateralization of Cognitive Function 189		
Birdsong 158	Verbal Skills 191		
BOX 4.3 The Organization of Avian	Mathematical Reasoning and Visuospatial		
Copulatory Behavior 159	Abilities 192		
Courtship Behavior of the Plainfin	Conclusions 195		
Midshipman Fish 164	BOX 4.6 Hormones, Sex Differences, and Art 196		
Urinary Posture in Canines 166	Summary 198		
Rough-and-Tumble Play in Primates 168	Questions for Discussion 199		
Sex Differences in Human Behavior 170			
BOX 4.4 Ambiguous Genitalia: Which Course of Treatment? 171	Suggested Readings 200		

Pineal Gland 82



Male Reproductive Behavior 201

	BOX 5.1	Battle	of the '	'Sexes''	203	
The Pro	ximate l	Bases	of Ma	ale Sex	ual Beh	12

The Proximate Bases of Male Sexual Behavior 204 Historical Origins of Research on Male Sexual Behavior 207

Male Sexual Behavior in Rodents 211

Male Mating Behavior: A Description 211 Hormonal Correlates of Male Mating Behavior 215

BOX 5.2 Anatomy of the Penis 218

Brain Mechanisms of Male Mating Behavior 220

BOX 5.3 Just Say NO (Nitric Oxide) to Erectile Dysfunction with Viagra 234

Social Influences on Male Mating Behavior 236
Individual Differences in Male Mating Behavior 239

Male Sexual Behavior in Primates 242

The Strength of the Sex Drive in Human Males 243 Human Male Sexual Behavior: A Description 246 Nonhuman Primate Male Sexual Behavior: A Description 248 Hormonal Correlates of Primate Male Sexual Behavior 249

Brain Mechanisms of Primate Male Sexual Behavior 254

Social Influences on Men's Sexual Behavior 257 Individual Variation and Aging 258

Peptide Hormones and Male Sexual Behavior 259

BOX 5.4 Sodefrin, a Female-Attracting
Pheromone in Newts 260

Male Reproductive Behavior in Birds 261
Male Reproductive Behavior in Reptiles 267
Conclusions 270
Summary 271
Questions for Discussion 273
Suggested Readings 273

Chapter 6

Female Reproductive Behavior 275

Early Discoveries about Female Sexual Behavior 277

The Development of the Vaginal Cytological Assay 278 Research in the Twentieth Century 282

Mammalian Female Mating Behavior:

A Description 284

Rodents 284 Canines 284

Primates 286

Are Females Active Participants in Sexual Behavior? 287

Components of Female Sexual Behavior 289

Attractivity 292

BOX 6.1 Chemosignals and Courtship in the Red-Sided Garter Snake 295

Proceptivity 297 Receptivity 298

Female Reproductive Cycles 304

Types of Reproductive Cycles 305
The Ecology of Reproductive Cycles 307

Social and Environmental Effects on Reproductive Cycles 309

BOX 6.2 Human Pheromones 311

BOX 6.3 Illness Suppresses Female Sexual Behavior 312

Experimental Analyses of Female Sexual Behavior 313

Hormonal Correlates of Female Reproductive Cycles 314

Neural Mechanisms Mediating Female Sexual Behavior 319

BOX 6.4 Nongenomic Behavioral Effects of Steroid Hormones 324

Gene Knockouts 325

A Neural Model of Lordosis 326

Neural Mechanisms Underlying Primate Sexual Behaviors 328

Summary 330

Questions for Discussion 333

Suggested Readings 334

Parental Behavior 335

Par	ental	Investment	Theory	336

Sex Differences in Parental Behavior 339

Parental Behavior in Birds 341

Endocrine Correlates of Avian Parental Behavior 343

BOX 7.1 Daniel S. Lehrman 345

Parental Behavior in Mammals 349

Mammalian Maternal Behavior 349

Mammalian Paternal Behavior 353

Endocrine Correlates of Mammalian Parental Behavior 354

The Onset of Maternal Behavior 358

BOX 7.2 Maternal Behavior in Sheep 363

Maternal Aggression 365

BOX 7.3 Offspring Behavior and the Maintenance of Maternal Behavior 368

Endocrine Correlates of Primate Maternal Behavior 371

Paternal Behavior 375

Neural Changes Associated with Mammalian Parental Behavior 377

BOX 7.4 Nongenetic Transmission of Parenting Styles 383

Conclusions 387

Summary 388

Questions for Discussion 389

Suggested Readings 390

Chapter 8

Hormones and Social Behavior 39

Affiliation 393

Imaging Studies of Humans 393

Adaptive Function of Affiliation 395

Hormones and Affiliation 395

Evolutionary Basis for Social Effects of the

Nonapeptides 402

Opioids and Affiliation 404

BOX 8.1 Beneficial Effects of Social Support on Health 405

Aggression 406

Seasonal Changes in Social Behavior 410

Aggression and the Breeding Cycle: Red Deer 410

Signals of Social Rank: Harris's Sparrows 411

Aggression and Winter Survival: Rodents 414

Testosterone and the Energetic Costs of Aggression:

Lizards 418

Do Seasonal Hormonal Changes in Primates Correlate with Aggression? 419

BOX 8.2 How Much Testosterone? Just the Right Amount ... 420

Aggression Increases at Puberty 420

Social Influences on the Development of Aggressive Behavior 421

Is It Adaptive for Rodents to Be Aggressive at Puberty? 422

The Timing of Puberty: Birds 423

Hormones and Dispersal Strategies: Primates 424

Sex Differences in Social Behavior 425

The Organization and Activation of Aggression:

Mice 426

Sex Differences and Dispersal: Ground Squirrels 427

Hormones and Dominance Status: Canines 427

Sex Differences in Play Behavior: Primates 429

Sex Role Reversals 430

Individual Differences in Aggression 432

Social Experience Feeds Back to Influence Hormone Concentrations 434

The Challenge Hypothesis: Birds 435

Conditioned Social Defeat 439

Hormones, Competition, and Violent Behavior:

Humans 440

Physiological Mechanisms Mediating Hormonal Effects on Aggressive Behavior 443

Brain Regions Associated with Aggression 443

Brain Steroid Hormone Receptor 446

Estrogen Receptors 446

Androgen Receptors 446

Serotonin 447

Vasopressin 447

BOX 8.3 Nitric Oxide and Aggression 448

Conclusions 450

Summary 450

Questions for Discussion 45

Suggested Readings 452



Homeostasis and Behavior 453

Basic Concepts in Homeostasis 456

Fluid Balance 457

BOX 9.1 Vertebrate Renal Function 459

Endocrine Regulation of Fluid Balance and Thirst 463 Sodium Balance 466

How Do Hormones Regulate Drinking Behavior? 469

Energy Balance 470

Metabolism during the Well-Fed State 473 Metabolism during the Fasting State 474

Disordered Energy Metabolism 476

Primary Sensory Signals and Secondary Mediators 479

Control of Food Intake 479

Peripheral Signals 480

Central Signals: The Role of the Hypothalamus 483 Central Anabolic Effectors: Peptides That Promote Food Intake 487

BOX 9.2 Cannabinoids and the "Munchies" 488

Central Catabolic Effectors: Peptides That Inhibit Food Intake 490

Hindbrain and Brain Stem 491

Protein Hormones That Stop Food Intake 492

BOX 9.3 Comfort Food 496

Other Factors That Influence Food Intake 497

Gonadal Steroid Hormones, Food Intake, and Body Mass 498

Estrogens and Progestins 499

Androgens 502

Seasonal Body Mass Cycles 503

Inhibition of Reproduction to Maintain Energy Balance 504

Specific Hungers 505

Final Thoughts 506

Summary 507

Questions for Discussion 509

Suggested Readings 509

Chapter 10

Biological Rhythms 511

Exogenous versus Endogenous Control of Biological Clocks 513

BOX 10.1 Jet Lag 514

Types of Biological Clocks and Rhythms 516

Examples of Biological Rhythms in Behavior 522 Adaptive Function of Biological Clocks 525

Circadian Clocks 527

Localization and Characterization of Circadian Clocks 527

BOX 10.2 Molecular Mechanisms of Biological Clocks 528

Molecular Mechanisms of Circadian Clocks 530 SCN as Master Circadian Clock 532

BOX 10.3 Effects of Light on Gene Transcription 536

SCN Inputs and Outputs 539

Circadian Rhythms, Hormones, and Behavior 544

Effects of Hormones on the SCN 544

Effects of the SCN on Hormones 545 Circadian Regulation of Food Intake 549

Circannual and Seasonal Rhythms 552

Ultimate and Proximate Factors Underlying Seasonality 553

Neuroendocrine Mechanisms Underlying Seasonality 554

Timing Mechanisms 555

Neural Mechanisms of Endogenous and Exogenous Seasonal Timekeeping 560

Activational Aspects of Timing Mechanisms 563

Conclusions 575

Summary 575

Questions for Discussion 577

Suggested Readings 577

Chapter II Stress 579

Stress and its Consequences 580 The Stress Response 581

General Adaptation Syndrome 584 What Is "Stress"? 585

BOX II.I Allostatic Load 586

Physiological Effects of the Stress Response 587
Pathological Effects of the Stress Response 592
Factors That Affect Stress Responsiveness 596

Perinatal Stress 596 Reproductive Dysfunction 604 Stress and Social Behavior 609

Seasonal Fluctuations in Stress Responses 615

Psychological Factors in Stress and Coping 618

Control, Predictability, Habituation, and Outlets for Frustration 619

Stress and Drug Abuse 620

Summary 622

Questions for Discussion 623

Suggested Readings 623

Chapter 12 Learning and Memory 625

Components of Learning and Memory 627

Non-Associative Learning 627 Associative Learning 628 Memory 631

The Effects of Hormones on Learning and Memory 632

Epinephrine 632 Insulin 638 Glucocorticoids 642

Sex Differences in Learning and Memory 648

Sex Differences and Stress 650

Effects of Estrogens 653 Effects of Androgens 656

Seasonal Fluctuations in Learning and Memory 658

Adrenocorticotropic Hormone (ACTH) 658 Vasopressin and Oxytocin 662 Endogenous Opioids 664

Cholecystokinin 666

Summary 668

Questions for Discussion 669

Suggested Readings 670

Chapter 13 Hormones and Affective Disorders 671

Androgens and Affective Disorders 673

BOX 13.1 Anabolic Steroids: An Edge that Cuts Two Ways 674

Perimenstrual Syndrome 681

The Social Context of PMS 681 What Is PMS? 682

BOX 13.2 Diagnostic Criteria for Late Luteal Phase Dysphoric Disorder 685 Hormonal Correlates of PMS 686 Cognitive Features of PMS 691

Hormones and Depression 692

Thyroid Hormones 693 Growth Hormone and Prolactin 694

Cortisol 694 Estrogen 696

Postpartum Depression 697

Seasonal Affective Disorder 699 Hormones and Eating Disorders 706

Anorexia Nervosa 706 Bulimia Nervosa 708 Summary 710

Questions for Discussion 712

Suggested Readings 712

Glossary G-1

Illustration Credits IC-I

References R-I

Index I-I