SECOND EDITION

HANDBOOK OF Psychology

VOLUME 3
Behavioral Neuroscience

Randy J. Nelson
Sheri J. Y. Mizumori
Volume Editors

Irving B. Weiner
Editor-in-Chief

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Editorial Board

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Handbook of Psychology Preface

The first edition of the 12-volume *Handbook of Psychology* was published in 2003 to provide a comprehensive overview of the current status and anticipated future directions of basic and applied psychology and to serve as a reference source and textbook for the ensuing decade. With 10 years having elapsed, and psychological knowledge and applications continuing to expand, the time has come for this second edition to appear. In addition to well-referenced updating of the first edition content, this second edition of the *Handbook* reflects the fresh perspectives of some new volume editors, chapter authors, and subject areas. However, the conceptualization and organization of the *Handbook*, as stated next, remain the same.

Psychologists commonly regard their discipline as the science of behavior, and the pursuits of behavioral scientists range from the natural sciences to the social sciences and embrace a wide variety of objects of investigation. Some psychologists have more in common with biologists than with most other psychologists, and some have more in common with sociologists than with most of their psychological colleagues. Some psychologists are interested primarily in the behavior of animals, some in the behavior of people, and others in the behavior of organizations. These and other dimensions of difference among psychological scientists are matched by equal if not greater heterogeneity among psychological practitioners, who apply a vast array of methods in many different settings to achieve highly varied purposes. This 12-volume *Handbook of Psychology* captures the breadth and diversity of psychology and encompasses interests and concerns shared by psychologists in all branches of the field. To this end, leading national and international scholars and practitioners have collaborated to produce 301 authoritative and detailed chapters covering all fundamental facets of the discipline.

Two unifying threads run through the science of behavior. The first is a common history rooted in conceptual and empirical approaches to understanding the nature of behavior. The specific histories of all specialty areas in psychology trace their origins to the formulations of the classical philosophers and the early experimentalists, and appreciation for the historical evolution of psychology in all of its variations transcends identifying oneself as a particular kind of psychologist. Accordingly, Volume 1 in the *Handbook*, again edited by Donald Freedheim, is devoted to the *History of Psychology* as it emerged in many areas of scientific study and applied technology.

A second unifying thread in psychology is a commitment to the development and utilization of research methods suitable for collecting and analyzing behavioral data. With attention both to specific procedures and to their application in particular settings, Volume 2, again edited by John Schinka and Wayne Velicer, addresses *Research Methods in Psychology*.

Volumes 3 through 7 of the *Handbook* present the substantive content of psychological knowledge in five areas of study. Volume 3, which addressed *Biological Psychology* in the first edition, has in light of developments in the field been retitled in the second edition to cover *Behavioral Neuroscience*. Randy Nelson continues as editor of this volume and is joined by Sheri Mizumori as a new co-editor. Volume 4 concerns *Experimental Psychology* and is again edited by Alice Healy and Robert Proctor. Volume 5 on *Personality and Social Psychology* has been reorganized by two new co-editors, Howard Tennen and Jerry Suls. Volume 6 on *Developmental Psychology* is again edited by Richard Lerner, Ann Easterbrooks, and Jayanthi Mistry. William Reynolds and Gloria Miller continue as co-editors of Volume 7 on *Educational Psychology*.

Volumes 8 through 12 address the application of psychological knowledge in five broad areas of professional practice. Thomas Widiger and George Stricker continue as co-editors of Volume 8 on *Clinical Psychology*. Volume 9 on *Health Psychology* is again co-edited by Arthur Nezu, Christine Nezu, and Pamela Geller. Continuing to co-edit Volume 10 on *Assessment Psychology* are John Graham and Jack Naglieri. Randy Otto joins the Editorial Board as the new editor of Volume 11 on *Forensic Psychology*. Also joining the Editorial Board are two new co-editors, Neal Schmitt and Scott Highhouse, who have reorganized Volume 12 on *Industrial and Organizational Psychology*.

The *Handbook of Psychology* was prepared to educate and inform readers about the present state of psychological knowledge and about anticipated advances in behavioral science research and practice. To this end, the *Handbook* volumes address the needs and interests of three groups. First, for graduate students in behavioral science, the volumes provide advanced instruction in the basic concepts and methods that define the fields they cover, together with a review of current knowledge, core literature, and likely future directions. Second, in addition to serving as graduate textbooks, the volumes offer professional psychologists an opportunity to read and contemplate the views of distinguished colleagues concerning the central thrusts of research and the leading edges of practice in their respective fields. Third, for psychologists seeking to become conversant with fields outside their own specialty and for persons outside of psychology seeking information about psychological matters, the *Handbook* volumes serve as a reference source for expanding their knowledge and directing them to additional sources in the literature.

The preparation of this *Handbook* was made possible by the diligence and scholarly sophistication of 24 volume editors and co-editors who constituted the Editorial Board. As Editor-in-Chief, I want to thank each of these colleagues for the pleasure of their collaboration in this project. I compliment them for having recruited an outstanding cast of contributors to their volumes and then working closely with these authors to achieve chapters that will stand each in their own right as valuable contributions to the literature. Finally, I would like to thank Brittany White for her exemplary work as my administrator for our manuscript management system, and the editorial staff of John Wiley & Sons for encouraging and helping bring to fruition this second edition of the *Handbook*, particularly Patricia Rossi, Executive Editor, and Kara Borbely, Editorial Program Coordinator.

Irving B. Weiner
Tampa, Florida

Volume Preface

The topic of this volume represents a perspective that can be traced to the founding of psychology as a scientific discipline. Since the late 19th century, biological psychologists have used the methods of the natural sciences to study relationships between biological and psychological processes. Today, a natural science perspective and the investigation of biological processes have increasingly penetrated all areas of psychology. For instance, social and personality psychologists have become conversant with evolutionary concepts in their studies of traits, prejudice, and even physical attraction. Many cognitive psychologists have forsaken black boxes in favor of functional magnetic resonance imaging brain scans, and clinical psychologists, as participants in the mental health care of their clients, have become more familiar with the basis for the action of pharmacological therapeutics on the brain. Indeed, the reliance of neuroscience in psychology has provoked us to change the name of this volume from *Biological Psychology* to *Behavioral Neuroscience*.

The scientific revolution in molecular biology and genetics will continue to fuel the biological psychology perspective. Indeed, it can be anticipated that some of the most significant scientific discoveries of the 21st century will come from understanding the biological basis of psychological functions. The contributors to this volume provide the reader with a highly accessible view of the contemporary field of behavioral neuroscience. The chapters span content areas from basic sensory systems to memory and language and include a perspective on different levels of scientific analysis from molecules to computational models of biological systems. We have assembled this material with a view toward engaging the field and our readership in an appreciation of the accomplishments and special role of behavioral neuroscience in our understanding of behavior. Notwithstanding the trend for a greater influence of biological studies in the field of psychology in general, behavioral neuroscience represents a distinctive fusion of biology and psychology in its theory and methods. For example, evolution as a fundamental tenet in the field of biology has long permeated the work of behavioral neuroscientists. The rapid growth in publications in the area of evolutionary psychology over the past two decades suggests a growing acceptance of the importance of evolutionary ideas in the behavioral sciences. In addition to this influence, the contribution of biology, rooted in evolutionary and ethological traditions, has sustained a broad base of comparative studies by behavioral neuroscientists, as reflected in the contents of this volume.

Research in the field of psychology using different species serves a dual purpose. Many studies using nonhuman species are motivated by the utility of information that can be gained that is relevant to humans, using a range of preparations and techniques in research that are not otherwise possible. Of equal importance, comparative research provides insights into variation among biological organisms. Studies of a variety of species can show how different solutions have been achieved for both processing input from the environment and elaborating adaptive behavioral strategies. The organization and content of this volume focus squarely on the need to recognize these dual objectives in studies of biological and psychological processes. The question of how translation is made across species is ever more central to the undertaking of behavioral neuroscience. In the not-distant past, most psychologists viewed research using nonhuman animals as irrelevant to a broad range of psychological functions in humans, including affective and cognitive processes that were considered exclusive capacities of the human mind and social lives of humans in relationships. Today, animal models are increasingly recognized as possessing at least some elements of cognitive and affective processes that are potentially informative for understanding normal functions and disorders in humans. This progress has contributed to several research areas described in the ensuing chapters, many of which include insights that have come from using new gene targeting or imaging technology. Because human studies do not provide the opportunity for rigorous experimental control and manipulation of genetic, molecular, cellular, as well as brain and behavioral system processes, the use of genetically manipulated mice has become a powerful tool in research. At the same time, the limitations and pitfalls of wholesale acceptance of such animal models are clear to behavioral neuroscientists. In addition to the fact that mouse species have faced different evolutionary pressures and adapted to different ecological niches, the use of genetically altered systems presents new challenges because these novel mice are likely to express new constraints and influences beyond their target characters. The tradition of comparative studies of different animal species makes the role of biological psychology central to the effort to use these new and powerful approaches to advance scientific understanding.

A related overriding theme in biological psychology is the significance of translating across levels of analysis. Biological descriptions of psychological processes are viewed by many, particularly outside the field, as a reductionist endeavor. As such, reductionism might represent merely a descent to a level of description in which psychological functions are translated into the physical and chemical lexicon of molecular events. It is increasingly evident that research directed across levels of analysis serves yet another purpose. In addition to determining biological substrates, such investigations can work in the other direction, to test between competing hypotheses and models of psychological functions. It is also the case that molecular biologists who study the brain are increasingly seeking contact with investigators who work at a systems level. More genes are expressed in the brain than in all other organs of the body combined. Gene expression is controlled by intricate information-processing networks within a neuron and is inextricably tied to the activity of neurons as elements in larger information-processing systems. Studies of psychological functions (e.g., the conditions that are sufficient to produce long-term memory or the environmental inputs that are necessary to elicit maternal behavior) will aid in understanding the functional significance of complex molecular systems at the cellular level. Scientific advances are rapidly shifting the biological psychology paradigm from one of reductionism to an appreciation that vertical integration across levels of analysis is essential to understand the properties of biological organisms. The use of high-energy imaging technology has helped to bridge brain function with behavioral, cognitive, and affective questions.

As mentioned, within the past 20 years a novel intellectual bridge has been formed between psychology and molecular biology. Molecular biologists have mapped large segments of the mouse genome as part of the ambitious Human Genome Project. As genes have been identified and sequenced, molecular biologists have begun the difficult task of identifying the functions of these genes. An increasingly common genetic engineering technique used to discover the function of genes is targeted disruption (*knockout*) of a single gene. By selectively disrupting the expression of a single gene, molecular biologists reason that the function of that targeted gene can be determined. In other cases, a specific gene is added (*knockin*). In many cases, the phenotypic description of knockout and knockin mice includes alterations in behavior. In Chapter 1 Stephen C. Maxson explores behavioral genetics, generally, and describes the implications of molecular genetics for psychology, specifically. He describes classic studies on the heritability of behavior (*viz*., selective breeding) as well as twin and adoption studies. Maxson adroitly documents gene mapping and genome projects in relation to behavioral studies. After presenting an introduction to molecular and developmental genetics, he emphasizes the importance of population genetics in studies of the evolution of behavior. Finally, Maxson explores the ethical and legal manifestations of behavioral genetics in the context of academics and society as a whole. He uses new examples and provides a thoroughly updated version of his previous chapter.

In Chapter 2 Russil Durrant and Bruce J. Ellis introduce some of the core ideas and assumptions in the field of evolutionary psychology. Although they focus on reproductive behaviors, Durrant and Ellis also illustrate how the ideas of evolutionary psychology can be employed in the development of specific, testable hypotheses, about human mind and behavior. Their ideas go far past the usual mating behaviors, and they even provide an adaptive scenario for self-esteem studies. Durrant and Ellis note that one of the most crucial tasks for evolutionary psychologists in the coming decades will be the identification and elucidation of psychological adaptations. Although most of the obvious and plausible psychological adaptations have already been cataloged, many more remain undiscovered or inadequately characterized. Because adaptations are the product of natural selection operating in ancestral environments, and because psychological traits such as jealousy, language, and self-esteem are not easily reconstructed from material evidence such as fossils and artifacts, direct evidence for behavioral adaptations may be difficult to obtain. One of the challenges for evolutionary psychology, according to Durrant and Ellis, is to develop increasingly more rigorous and systematic methods for inferring the evolutionary history of psychological characteristics, as well as to determine how best to characterize psychological adaptations.

Using the comparative method has been particularly successful for understanding the sensory and perceptual machinery in animals. In Chapter 3 Gerald H. Jacobs describes the great success that he and others have had using the comparative approach to elucidate the mechanisms and processes underlying vision. Most studies of nonhuman vision are likely motivated to understand human vision. The remaining studies of vision in nonhuman animals are aimed at understanding comparative features of vision in their own right, often from an evolutionary perspective with the intent to discover common and different solutions for seeing. Jacobs considers both approaches in his review of comparative vision. After a description of the fundamental features of photic environments, he presents basic design features and discusses the evolution of eyes. Jacobs then focuses on photosensitivity as a model of the comparative approach. He details photopigments, ocular filtering, and the role of the nervous system in photosensitivity. Three important issues in comparative vision—detection of change, resolution of spatial structure, and use of chromatic cues—are also addressed. Finally, Jacobs includes a section on the difficulty of measuring animal vision, as well as his perspective of where this field is likely to evolve.

Chris I. Baker reviews in Chapter 4 the latest knowledge about cellular to brain system mechanisms of the primate visual system. He draws on multiple levels of analysis to describe the parallel nature of visual processing from the retina to the thalamus, and how their input to the cortex begins a journey of complex analyses that result in, for example, stimulus recognition and a visual spatial understanding of the world around us. Information within the parallel pathways is integrated at all levels of processing. In this way, the culmination of visual information processing at all stages allows individuals to have unified percepts of their world.

Cynthia F. Moss and Catherine E. Carr review some of the benefits and problems associated with a comparative approach to studies of hearing in Chapter 5. Comparative audition also has a primary goal of understanding human audition, but a larger proportion of this field is dedicated to understanding the relationship between the sensory system of the animal and its biologically relevant stimuli as compared to comparative vision. The ability to detect and process acoustic signals evolved many times throughout the animal kingdom, from insects and fish to birds and mammals (homoplasies). Even within some animal groups, there is evidence that hearing evolved independently several times. Ears appear not only on opposite sides of the head, but also on a variety of body parts. Out of this diversity, many fascinating, specific auditory adaptations have been discovered. A surprising number of general principles of organization and function have emerged from studies of diverse solutions to a common problem. Comparative studies of audition attempt to bring order to the variation and to deepen our understanding of sound processing and perception. Moss and Carr review many common measures of auditory function, anatomy, and physiology in selective species in order to emphasize general principles and noteworthy specializations. They cover much phylogenetic ground, reviewing insects, fishes, frogs, reptiles, birds, and mammals. The chapter begins with a brief introduction to acoustic stimuli, followed by a review of ears and auditory systems in a large sample of species, and concludes with a comparative presentation of auditory function in behavioral tasks. Behavioral studies of auditory systems reveal several common patterns across species. For example, hearing occurs over a restricted frequency range, often spanning several octaves. Absolute hearing sensitivity is best over a limited frequency band, typically of high biological importance to the animal, and this low-threshold region is commonly flanked by regions of reduced sensitivity at adjacent frequencies. Absolute frequency discrimination and frequency selectivity generally decrease with an increase in sound frequency. Some animals, however, display specializations in hearing sensitivity and frequency selectivity for biologically relevant sounds, with two regions of high sensitivity or frequency selectivity corresponding with information, for example, about mates *and* predators. One important goal of comparative audition is to trace adaptations in the auditory periphery and merge those adaptations with central adaptations and behavior.

A detailed description of the neural mechanism of auditory processing in the primate brain is presented by Jon H. Kaas, Barbara M. J. O'Brien, and Troy A. Hackett in Chapter 6. Beginning with the transduction of sound pressure waves into neural signals of auditory receptor hair cells in the basilar membrane, an intricate sequence of processing occurs at multiple steps all the way up to the cortex. Early in the process, auditory signals are distinguished according to the location of the sound source and the quality of the sound wave (e.g., frequency, amplitude, etc.). At the level of auditory cortex, sound-relevant neural signals are distributed to different cortical regions for the analysis of the meaning of the sound, the location of the sound, and sound processing relevant to voices and communication. Of great theoretical and clinical significance are findings that other sensory modalities may be processed in previously designated auditory regions of brain, and auditory information can reach other sensory cortical areas such as visual cortex. Such sensory integration has important implications for our understanding of language and speech.

The history and state of the art of, as well as future studies in, comparative motor systems are presented in this updated Chapter 7 by Karim Fouad, David Bennett, Hanno Fischer, and Ansgar Büschges. The authors carefully construct an argument for a concept of central control of locomotion and the principles of pattern-generating networks for locomotion. In common with sensory systems to understand locomotor activity, the authors argue that a multilevel approach is needed and present data ranging from the molecular and cellular level (i.e., identification of the neurons involved, their intrinsic properties, the properties of their synaptic connections, and the role of specific transmitters and neuromodulators) to the system level (i.e., functional integration of these networks in complete motor programs). They emphasize that both invertebrate and vertebrate locomotor systems have been studied on multiple levels, ranging from the interactions between identifiable neurons in identified circuits to the analysis of gait. The review focuses on (a) the principles of cellular and synaptic construction of central pattern-generating networks for locomotion, (b) their location and coordination, (c) the role of sensory signals in generating a functional network output, (d) the main mechanisms underlying their ability to adapt through modifications, and (e) basic features in modulating the network function.

Each human sensory system provides an internal neural representation of the world, transforming energy in the environment into the cellular coding machinery of vast networks of neurons. In studies of sensory information processing in nonhuman primates, particularly in the Old World monkeys, we encounter research that brings us close to understanding functions of the human brain. Tactile perception becomes a key modality in primates' ability to identify and manipulate objects within arm's reach. In Chapter 8 Steven S. Hsiao and Manuel Gomez-Romirez focus on tactile perception, a system that begins with the transduction of information by mechanoreceptor afferents that innervate our skin, muscles, tendons, and joints. The authors review evidence that information from each of these receptor types serves a distinctive role in tactile perception. This chapter then discusses how such distinct tactile input becomes combined in cortex to provide multidimensional spatial form analysis, and an understanding of texture, vibration, and tactile motion. These and other mechanoreceptors share virtually identical properties in humans and in nonhuman primates. It appears that similar mechanisms exist for tactile and visual spatial feature analysis. However object identification mechanisms differ since cutaneous and proprioceptive inputs are needed for three-dimensional tactile-based object identification. Further, tactile perception is strongly modulated by attention and experience, and this effect is reflected in alterations in the temporal cohesiveness of neural firing.

We all learned and accepted that there are five primary senses—that is, until we stubbed our toes and recalled our "sixth sense." A critical sensory system that alerts us to real or potential tissue damage is pain. In Chapter 9 Magali Millecamps, David A. Seminowicz, Catherine Bushnell, and Terence Coderre explore the mechanisms underlying pain. They note that pain can be considered as two separate sensory entities: (1) physiological pain and (2) pathological pain. Physiological pain reflects a typical reaction of the somatosensory system to noxious stimulation. Physiological pain is adaptive. Rare individuals who cannot process physiological pain information frequently injure themselves and are unaware of internal damage that is normally signaled by pain. Predictably, such individuals often become disfigured and have a significantly shortened life span. Pathological pain reflects the development of abnormal sensitivity in the somatosensory system, usually precipitated by inflammatory injury or nerve damage. The most common features of pathological pain are pain in the absence of a noxious stimulus, increased duration of response to brief-stimulation stimuli, or perception of pain in response to normally nonpainful stimulation. The neurological abnormalities that account for pathological pain remain unspecified and may reside in any of the numerous sites along the neuronal pathways that both relay and modulate somatosensory inputs.

Chapter 9 provides a comprehensive review of the current knowledge concerning the anatomical, physiological, and neurochemical substrates that underlie both physiological and pathological pain. Thus, Millecamps and colleagues have described in detail the pathways that underlie the transmission of inputs from the periphery to the central nervous system (CNS), the physiological properties of the neurons activated by painful stimuli, and the neurochemicals that mediate or modulate synaptic transmission in somatosensory pathways. The review is organized by neuroanatomy into separate sections: (a) the peripheral nervous system and (b) the CNS, which is further divided into (a) the spinal cord dorsal horn and (b) the brain. The authors made a special effort to identify critical advances in the field of pain research, especially the processes by which pathological pain develops following tissue or nerve injury, as well as how pain is modulated by various brain mechanisms. The multidimensional nature of pain processing in the brain emphasizes the multidimensional nature of pain, using anatomical connectivity, physiological function, and brain imaging techniques. Finally, the authors provide some insights into future pain sensitivity and expression research, with a focus on molecular biology and behavioral genetics.

The ability to detect chemicals in the environment likely represents the most primitive sensory faculty and remains critical for survival and reproductive success in modern prokaryotes, protists, and animals. Chemicals in solution are detected by the taste sensory system; chemical sensation has a central role in the detection of what is edible and where it is found. It is well known, for example, that the flavor of food (i.e., the combination of its taste and smell) is a major determinant of ingestion. Humans are able to detect volatile chemicals in air with our olfactory sensory system. Individuals may use chemical senses to protect themselves from ingesting or inhaling toxins that can cause harm. The chemical senses, olfaction and taste, are reviewed in Chapter 10 by Patricia M. Di Lorenzo and Steven L. Youngentob. Until recently, the study of taste and olfaction has progressed at a relatively slow pace when compared to the study of the other sensory modalities such as vision or audition. This reflects, in part, the difficulty in defining the physical dimensions of chemosensory stimuli. We can use human devices to deliver exactly 0.5-m candles of 484 μm of light energy to the eye and then conduct appropriate psychophysics studies consistently across laboratories and across participants. Until recently, however, it has been impossible to present, for example, 4 units of rose smells to an experimental participant. In the absence of confidence that any given array of stimuli would span the limits of chemical sensibility, investigators have been slow to agree on schemes with which taste and olfactory stimuli are encoded by the nervous system. As Di Lorenzo and Youngentob reveal, technological advances, particularly in the realm of molecular neuroscience, are providing the tools for unraveling some of the longstanding mysteries of the chemical senses.

Some of the surprising findings that have resulted from this increasingly molecular approach to chemosensation are the discovery of a fifth basic taste quality (i.e., umami) and the discovery that the differential activation of different subsets of sensory neurons, to various degrees, forms the basis for neural coding and further processing by higher centers in the olfactory pathway. For both olfaction and taste, the careful combination of molecular approaches with precise psychophysics promise to yield insights into the processing of chemical signals.

Next, we move from input to output. To fuel the brain and locomotor activities, we need energy. Because most bacteria and all animals are heterotrophs, they must eat to obtain energy. What and how much we eat depends on many factors, including factors related to palatability or taste, learning, social and cultural influences, environmental factors, and physiological controls. The relative contribution of these many factors to the regulation of feeding varies across species and testing situations. In Chapter 11 Timothy H. Moran and Randall R. Sakai detail the behavioral neuroscience of food and fluid intake. They focus on three interacting systems important in the regulation of feeding: (1) signals related to metabolic state, especially to the degree adiposity; (2) affective signals related to taste and nutritional consequences that serve to reinforce aspects of ingestive behavior; and (3) signals that arise within an individual meal that produce satiety. Moran and Sakai also identify the important interactions among these systems that permit the overall regulation of energy balance. Individuals are motivated to maintain an optimal level of water, sodium, and other nutrients in the body. Claude Bernard, the 19th-century French physiologist, was the first to describe animals' ability to maintain a relatively constant internal environment, or *milieu intérieur*. Animals are watery creatures. By weight, mammals are approximately two-thirds water. The cells of animals require water for virtually all metabolic processes. Additionally, water serves as a solvent for sodium, chloride, and potassium ions, as well as sugars, amino acids, proteins, vitamins, and many other solutes, and is therefore essential for the smooth functioning of the nervous system and for other physiological processes. Because water participates in so many processes, and because it is continuously lost during perspiration, respiration, urination, and defecation, it must be replaced periodically. Unlike minerals or energy, very little extra water is stored in the body. When water use exceeds water intake, the body conserves water, mainly by reducing the amount of water excreted from the kidneys. Eventually, physiological conservation can no longer compensate for water use and incidental water loss, and the individual searches for water and drinks. Regulation of sodium intake and regulation of water intake are closely linked to one another. According to Moran and Sakai, the body relies primarily on osmotic and volumetric signals to inform the brain of body fluid status and to engage specific neurohormonal systems (e.g., the renin-angiotensin system) to restore fluid balance. As with food intake, signals that stimulate drinking, as well as those that terminate drinking, interact to ensure that the organism consumes adequate amounts of both water and electrolytes. The signals for satiety, and how satiety changes the taste and motivation for seeking food and water, remain to be specified.

We continue with a review of motivated behavior in Chapter 12. Elaine M. Hull and Juan M. Dominguez review the recent progress made in understanding sexual differentiation, as well as the hormonal and neural mechanisms that drive and direct male and female sexual behavior. They begin their chapter by considering the adaptive function of sexual behavior by asking why sexual reproduction is by far the most common means of propagating multicellular species, even though asexual reproduction is theoretically much faster and easier. The prevailing hypothesis is that sexual behavior evolved to help elude pathogens that might become so precisely adaptive to a set of genetically identical clones that future generations of the host species would never rid themselves of the pathogens. By mixing up the genomic characters of their offspring, sexually reproducing creatures could prevent the pathogens—even with their faster generational time and hence faster evolution—from too much specialization. Pathogens that preyed on one specific genome would be extinct after the single generation of gene swapping that occurs with each sexual union. Thus, sexual reproduction has selected pathogens to be generalists among individuals, although sufficiently specific to be limited to a few host species. Hull and Dominguez next provide a description of the copulatory patterns that are common across mammalian species and summarize various laboratory tests of sexual behavior.

After a thorough description of sexual behavior, the mechanisms underlying sexual behavior are presented. Because hormones are important for sex differentiation in all mammalian and avian species and because hormones also activate sexual behavior in adulthood, the chapter focuses on the endocrine mechanisms underlying sexual behavior and explores the mechanisms by which hormones modulate brain and behavior. The authors next describe the hormonal and neural control of female sexual behavior, followed by a similar treatment of the regulation of male sexual behavior. In each case, they first summarize the effects of pharmacological and endocrine treatments on sexual behavior. The pharmacological data indicate which neurotransmitter systems are involved in the various components of sexual behavior (e.g., sexual motivation vs. performance). A variety of techniques has been used to determine where in the brain sexual behavior is mediated, including lesions and stimulation, local application of drugs and hormones, and measures of neural activity. Finally, Hull and Dominguez observe that the hormonal and neural mechanisms that control sexual behavior are similar to the mechanisms that regulate other social behaviors. The authors close with a series of questions and issues that remain largely unanswered. For example, they suggest that more neuroanatomical work is necessary to track the neural circuits underlying sexual behavior in both females and males. Neurotransmitter signatures of those neurons are important pieces of the puzzle, as well as neurotransmitter receptor interactions and intracellular signal transduction activation in response to various neurotransmitter and hormonal effects. What changes in gene transcription are induced by specific hormones? How do rapid membrane effects of steroids influence sexual behavior? What changes in gene transcription mediate the effects of previous sexual experience? They close with broader questions that include the interrelationships among sexual and other social behaviors, and how species-specific differences in behavior are related to their ecological niches. All of these issues are critical for a full understanding of sexual behavior.

Life on Earth evolves in the presence of pronounced temporal fluctuations. The planet rotates daily on its axis. Light availability and temperature vary predictably throughout each day and across the seasons. The tides rise and subside in predictable ways. These fluctuations in environmental factors exert dramatic effects on living creatures. For example, daily biological adjustments occur in both plants and animals, which perform some processes only at night and others only during the day. Similarly, daily peaks in the metabolic activity of warm-blooded animals tend to coincide with the daily onset of their physical activity. Increased activity alone does not drive metabolic rates; rather, the general pattern of metabolic needs is anticipated by reference to an internal biological clock. The ability to anticipate the onset of the daily light and dark periods confers sufficient advantages that endogenous, self-sustained circadian clocks are virtually ubiquitous among extant organisms In Chapter 13 Stephanie G. Jones and Ruth M. Benca describe the importance of biological clocks and sleep on cognition and behavior. In addition to synchronizing biochemical, physiological, and behavioral activities to the external environment, biological clocks are important to multicellular organisms for synchronizing the internal environment. For instance, if a specific biochemical process is most efficiently conducted in the dark, then individuals that mobilize metabolic precursors, enzymes, and energy sources just prior to the onset of dark would presumably have a selective advantage over individuals that organized their internal processes at random times. Thus, there is a daily temporal pattern, or phase relationship, to which all biochemical, physiological, and behavioral processes are linked. Jones and Benca provide an overview of sleep, as well as the circadian system. Then, they discuss the regulation of sleep in the context of biological rhythms and show how sleep-wake homeostasis interacts with alertness and cognitive function, mood, cardiovascular, metabolic, and endocrine regulation. Their chapter closes with a description of sleep disorders in the context of circadian dysregulation.

Preceding chapters in the volume considered specific motivated behaviors, such as feeding and mating. In Chapter 14 Ryan T. LaLumiere and Peter W. Kalivas deal with neural circuitry in the brain that is relevant to many different goal-directed behaviors. Whether the goal is food or a sexual partner, common circuitry is now believed to be required for activating and guiding behavior to obtain desired outcomes. This brain system, referred to here as the *motive circuit,* involves a network of structures and their interconnections in the forebrain that control motor output systems. The authors present a scheme, based on much evidence, that the motive circuit comprises separate but interactive subsystems that integrate information from our external sensory world, internal drives, and decision mechanisms that drive behaviors. One of these subsystems provides control over goal-directed behavior under routine circumstances, where prior experience has established efficient direct control over response systems. The other subcortical-limbic circuit serves a complementary function to allow new learning about motivationally relevant stimuli. The motive circuit described in this chapter includes not only anatomically defined pathways but also definition of the neurochemical identity of neurons in the system. This information has proved vital because the motive circuit is an important target for drugs of interest for their psychological effects. Indeed, the field of psychopharmacology has converged to a remarkable degree on the brain regions described in this chapter. Substances of abuse, across many different classes of agents such as cocaine and heroin, depend on this neural system for their addictive properties. Consequently, the role of subsystems within the motive circuit in drug addiction is a topic of great current interest. Within the scheme described in the chapter, drug-seeking behavior, including the strong tendency to relapse into addiction, may reflect an inherent property of circuit function that controls routine responses or habits. Behavioral and neural plasticity underlying addiction is becoming an increasingly important topic of study in this area of behavioral neuroscience for providing an inroad to effective treatment for drug abuse.

Emotion encompasses a wide range of experience and can be studied through many variables, ranging from verbal descriptions to the measurement of covert physiological responses, such as heart rate. In Chapter 15, Paul J. Whalen, M. Justin Kim, Maital Neta, and F. Carolyn Davis consider this topic with a focus on the nature of the contribution of the human amygdala to emotional responses. In particular these authors focus on how humans respond to emotional events such as threats and rewards, and how we learn to predict such situations in the future. Results from recent human neuroimaging studies are consistent with the vast literature on the role of nonhuman amygdala in emotional regulation, the relevant parts of which are reviewed here. This chapter also discusses how these data can be used to better understand the neural roots of emotion-related disorders such as that which occurs in pathological anxiety.

Life is challenging. The pressure of survival and reproduction takes its toll on every individual living on the planet; eventually and inevitably the wear and tear of life leads to death. Mechanisms have evolved to delay death presumably because, all other things being equal, conspecific animals that live the longest tend to leave the most successful offspring. In the Darwinian game of life, individuals that leave the most successful offspring win. Although some of the variation in longevity reflects merely good fortune, a significant part of the variation in longevity among individuals of the same species reflects differences in the ability to cope with the demands of living. All living creatures are dynamic vessels of equilibria, or homeostasis. Any perturbation to homeostasis requires energy to restore the original steady-state. An individual's total energy availability is partitioned among many competing needs, such as growth, cellular maintenance, thermogenesis, reproduction, and immune function. During environmental energy shortages, nonessential processes such as growth and reproduction are suppressed. If homoeostatic perturbations require more energy than is readily available after nonessential systems have been inhibited, then survival may be compromised. All living organisms currently exist because of evolved adaptations that allow individuals to cope with energetically demanding conditions. Surprisingly, the same neuroendocrine coping mechanisms are engaged in all of these cases, as well as in many other situations. The goal of Chapter 16, written by Angela Liegey Dougall, Minhnoi C. Wroble Biglan, Jeffrey N. Swanson, and Andrew Baum, is to present the effects of stress and coping on immune function. The authors themselves worked under stressful conditions. Our friend and colleague, Andy Baum, passed away during the preparation of this revised chapter. We are grateful to his coauthors and colleagues for updating this chapter. Because description should always precede formal analyses in science, it is important to agree on what is meant by *stress*. This first descriptive step has proved to be difficult in this field; however, it remains critical in order to make clear predictions about mechanisms. To evaluate the brain regions involved in mediating stress, there must be some consensus about what the components of the stress response are. The term *stress* has often been conflated to include the stressor, the stress response, and the physiological intermediates between the stressor and stress responses. The concept of stress was borrowed from an engineering-physics term that had a very specific meaning (i.e., the forces outside the system that act against a resisting system). The engineering-physics term for the intrinsic adjustment is *strain*. For example, gravity and wind apply stress to a bridge; the bending of the metal under the pavement in response to the stress is the strain. Had we retained both terms, we would not be in the current terminological predicament. It is probably too late to return to the original engineering-physics definition of these terms in biological psychology because despite the confusing array of indefinite uses of the term *stress*, an impressive scientific literature integrating endocrinology, immunology, psychology, and neuroscience has developed around the concept of stress. What, then, does it mean to say that an individual is under stress? For the purposes of this chapter, Dougall and colleagues use some of the prevailing homeostatic notions of stress to arrive at a flexible working definition. The authors next describe coping, which is a way to counteract the forces of stress. Next, Dougall and coauthors describe the psychological and behavioral responses to stress and emphasize the effects of stress on immune function. Although stress causes many health problems for individuals, not all the news is bleak. Dougall and colleagues review the various stress management interventions. In some areas researchers are making remarkable progress at identifying the genetic and molecular mechanisms of stress with little regard for the integrative systems to which these molecular mechanisms contribute. In other areas scientists are still struggling to parse out the interactive effects of behavioral or emotional factors such as fear and anxiety on stress responsiveness. Obviously, a holistic approach is necessary to understand the brain stress system—perhaps more importantly than for other neural systems. Acute stress can actually bolster immune function, whereas chronic stress is always immunosuppressant. One important goal of future stress research, according to Dougall and coauthors, is to determine how and when acute stress becomes chronic and how to intervene to prevent this transition.

Determinants of behavior have historically been discussed in terms of the influence of nature versus nurture. The more contemporary view is that behaviors are determined by interactions between one's genetic makeup and one's experiences. In Chapter 17 Laura Petrosini, Debora Cutuli, and Paola De Bartolo discuss these issues within the context of the emergence of experience-expectant and experience-dependent behaviors and cell functions through early development. Thus, this chapter begins with a review of the principles of early brain development, and this is followed by a summary of how experience alters gene-driven maturational processes. Examples of experience-expectant and experience-dependent processes are provided within the context of the development of a number of sensory systems (such as visual, auditory, and tactile systems) and the motor system, as well as the maturation of emotional regulatory systems. The notion that environmental enrichment can alter sensory, motor, affective, and cognitive functions is also reviewed. The chapter ends with the rather provocative suggestion that one may build up a "cognitive reserve" that can be used in older individuals to age gracefully.

The comparative approach to understanding cognition is probably central within behavioral neuroscience and is thoughtfully reviewed in Chapter 18 by Edward A. Wasserman and Leyre Castro. Here the focus is on a deeply historical perspective, examining age-old questions, but with a modern point of view. To what extent are our mental functions similar to those of other animals? Are nonhuman animals intelligent? What do we know about the cognitive capacities of nonhuman animals? What forms and aspects of cognition have been studied? Wasserman and Castro examine how animals respond to the passage of time, how they remember the past, how they respond effectively in the present, and how they plan for the future. They also review the literature demonstrating that animals can master abstract and numerical concepts, and even display signs of analogical reasoning as well as many of the precursors to human symbolic language. The authors place this work in an adaptive functional context and consider the possibility that animals may monitor their current state of knowledge to control their behavior. Wasserman and Castro present a variety of preparations in which a neural systems analysis has shed light on the neural circuits and mechanisms of learning. Those preparations range from research in relatively simple organisms, such as invertebrates, to several forms of learning in mammals that have closely tied research in laboratory animals to an understanding of the neural bases of learning in humans.

In Chapter 19, Jeansok Kim, Richard F. Thompson, and Joseph E. Steinmetz review the significant progress that has been made in terms of our understanding of the neurobiology of learning via targeted investigations of classical or Pavolvian networks of the brain. This chapter begins with a summary of a number of popular invertebrate conditioning models, one that describes our current understanding of the neural basis of conditioning phenomena such as sensitization and habituation. Following this is a brief discussion of spinal conditioning. These authors then turn their attention to providing an in-depth review of two well studied vertebrate models: fear conditioning and eyeblink conditioning. The reviews present both historical perspectives and contemporary analyses. The richness of the significant results from studies of both models can be attributed at least in part to the multilevel and multisystem approaches conducted by an impressive number of laboratories around the world. By knowing the specific pathways of the brain that process CS and US information, fundamentally new insights are drawn concerning the critical neurochemical cascades that are responsible for these special forms of learning. The convergent evidence that defines the properties of these models is sufficiently impressive that these models are now being used to study complex human behavioral disorders such as autism, and used as markers of lifespan changes in human learning and memory.

The study of more cognitive forms of memory is now firmly grounded in the recognition that multiple memory systems exist. In Chapter 20 Howard Eichenbaum traces the historical antecedents of this understanding. As a record of experience, habits and skills develop with practice and are enduring forms of memory. Habits and skills control routine simple activities as well as the exquisitely refined performance of the virtuoso. Historically, memory in the form of habits and skills can be seen as the focus of behaviorism in which effects of experience were studied in terms of stimulus and response topographies. Such forms of procedural memory that are exhibited in performance have been distinguished from declarative memory. Declarative memory refers to deficits encountered in amnesic syndromes where habit and skill memory (among other procedural types of memory) are entirely preserved but patients have a profound inability either to recollect episodes of experience consciously from the past or to acquire new knowledge. The distinction between forms of declarative and procedural memory has become well established in studies of human memory. Eichenbaum shows how these distinctions are addressed in research on neurobiological systems. In particular, the chapter deals with the challenge of translating declarative memory into studies with laboratory animals. The neural circuitry critical for this form of memory is similarly organized in the human brain, and in the brains of other species including laboratory rodents. Neural structures in the medial temporal lobe, including the hippocampus, are linked to information-processing systems in the cortex. Chapter 20 deals with research that shows how the organization and function of this system allows for distinctive features of cognitive memory, involving representational networks that can be flexibly accessed and used in novel situations. These properties of memory can be tested across human and nonhuman subjects alike. The animal models, in particular, are an important setting for research on the neural mechanisms of memory, including the cellular machinery that alters and maintains changes in synaptic connections.

A central problem in comparative biology and psychology is to determine the evolutionary mechanisms underlying similarity between species. As Robert M. Seyfarth and Dorothy L. Cheney emphasize in their chapter on social relationships, social cognition, and the evolution of mind in primates (Chapter 21), there has been a significant shift in how cognition has been studied during the past two decades. One path had gone molecular in the lab, whereas the second path has shifted from the laboratory to the field—from studies of animals' knowledge of objects in a lab setting to research on what they know about each other in natural contexts. Primates and many other animals live in rich, complex societies where animals form highly differentiated relationships and selection has favored the formation of enduring, long-term bonds. As a result, the social environment is characterized by predictable patterns of interaction, statistical regularities that an individual must recognize if she is to predict other animals' behavior. In nonhuman primates, social cognition has several striking properties. It involves the formation of concepts, and is computational; individuals recognize others based on discrete-value traits (rank, kinship) and classify individuals along multiple dimensions simultaneously. Social knowledge is rule-governed and open-ended. Vocalizations follow specific rules of delivery, and the classification of others by kinship and rank persists despite changes in the individuals involved. Finally, social knowledge involves the attribution of motives and implicit theories of causality. Individuals know when a vocalization is directed at them, and when calls from two individuals are heard together listeners assume that one has caused the other. As Seyfarth and Cheney point out, at present we do not know whether primate social knowledge is qualitatively different from that in other species: the comparative study of social cognition in animals remains a work in progress. For all its richness, nonhuman primate social cognition remains strikingly different from that found in humans.

Interest in systems specialized for language in the human brain has a long history, dating from the earliest descriptions of aphasia by neurologists in the 19th century. In Chapter 22 Chantel S. Prat guides the reader through this field of study from its historical roots to the contemporary era, in which new tools and approaches are advancing knowledge in unprecedented ways. The chapter deals in detail with the kinds of inferences about the fundamental properties of language that have been gleaned from the patterns of language breakdown after brain damage. This area of cognitive neuropsychology has a long tradition in the field. The author then describes how recent studies of brain activation in normal subjects using functional neuroimaging technology have confirmed many functions assigned to specific brain regions and circuits based on cases of brain damage. She also considers the discrepancies that have emerged from comparison of these different approaches. This chapter further summarizes contemporary research at the level of representations and at the level of linguistic processes, especially in regards to individual differences and bilingualism. Finally, the chapter includes a discussion of another powerful approach in research in which computational modeling has become an important adjunct to empirical investigations in the biological study of language.

A broad perspective on the use of computational models in behavioral neuroscience is the subject of Chapter 23 by Eduardo Mercado III and Cynthia M. Henderson. These authors start by explaining how quantitative modeling can be used to further our understanding of more complex relationships between brain and behavior. This is followed by a review of the basic principles of computational neuroscience that can be used in artificial neural networks that are designed to better understand the neural circuitry underlying object recognition, perceptual and episodic learning, as well as age-related changes in cognitive function. These computational analyses take into consideration not only behavioral phenomenon but they also evaluate the known properties of single neuron physiology as information-processing units within the more extensive models. In this way, computational models have revealed the nature of fundamental algorithms that allow adaptive and experience dependent processing, such as supervised and unsupervised learning, error-correction learning, or self-organization. In these and other examples discussed in the chapter, computational modeling provides an important adjunct to the empirical base of research in the field.

As illustrated in many chapters of this volume, our understanding of the behavioral relevance of different brain regions is based in large part on studies of the behavioral consequences of experimental or accidental brain damage. Further, many research programs have demonstrated a striking correlation between the natural progression of brain development and behavior. Less is known about the web of brain changes that occur in normal (i.e., non-disease-related) old age, and how age-related changes in memory and other cognitive abilities relate to the brain changes. In Chapter 24, Bonnie R. Fletcher and Peter R. Rapp provide a thoughtful review of the aging literature, describing the different research approaches and the current issues in the field. They conclude that age-related cognitive alterations occur in the absence of dramatic neural changes, and that successful cognitive aging can take place as adaptations to brain changes. Further, this chapter discusses the challenges that researchers face as they try to develop effective strategies to support successful aging.

In closing this preface, we wish to express our gratitude to the contributing authors. This new edition of Volume 3 of the *Handbook* represents the field of behavioral neuroscience with its deep roots in the history of our discipline and its vital and exciting opportunities for new discovery throughout the 21st century.

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