

CONTENTS

Contributors.....	vii
Preface.....	ix
<i>Gregory R. Samanez-Larkin</i>	
Introduction.....	3
<i>Gregory R. Samanez-Larkin</i>	
Chapter 1. Structure and Function of the Aging Brain	9
<i>R. Nathan Spreng and Gary R. Turner</i>	
Chapter 2. Neural Mechanisms Underlying Age-Related	
Changes in Attentional Selectivity	45
<i>Briana L. Kennedy and Mara Mather</i>	
Chapter 3. Learning and Memory in the Aging Brain:	
The Function of Declarative and Nondeclarative	
Memory Over the Lifespan	73
<i>Nichole R. Lighthall, Lindsay B. Conner, and</i>	
<i>Kelly S. Giovanello</i>	

Copyright American Psychological Association

Chapter 4.	Age-Related Changes in Episodic Memory	111
	<i>Audrey Duarte and Elizabeth Kensinger</i>	
Chapter 5.	Motivated Memory, Learning, and Decision-Making in Older Age: Shifts in Priorities and Goals	135
	<i>Mary B. Hargis, Alexander L. M. Siegel, and Alan D. Castel</i>	
Chapter 6.	Social Function and Motivation in the Aging Brain	165
	<i>Angela Gutches and Gregory R. Samanez-Larkin</i>	
Chapter 7.	Compensation and Brain Aging: A Review and Analysis of Evidence	185
	<i>Laura B. Zahodne and Patricia A. Reuter-Lorenz</i>	
Chapter 8.	Risk and Protective Factors in Cognitive Aging: Advances in Assessment, Prevention, and Promotion of Alternative Pathways.....	217
	<i>Roger A. Dixon and Margie E. Lachman</i>	
Index		265
About the Editor		273

CONTRIBUTORS

- Alan D. Castel, PhD**, Department of Psychology, University of California, Los Angeles
- Lindsay B. Conner, MS**, Department of Psychology, University of Central Florida, Orlando
- Roger A. Dixon, PhD**, Department of Psychology, University of Alberta, Edmonton, Canada
- Audrey Duarte, PhD**, School of Psychology, Georgia Institute of Technology, Atlanta
- Kelly S. Giovanello, PhD**, Department of Psychology and Neuroscience, Biomedical Research Imaging Center, The University of North Carolina at Chapel Hill
- Angela Gutchess, PhD**, Department of Psychology, Brandeis University, Waltham, MA
- Briana L. Kennedy, PhD**, Leonard Davis School of Gerontology, University of Southern California, Los Angeles
- Mary B. Hargis, MA**, Department of Psychology, University of California, Los Angeles
- Elizabeth Kensinger, PhD**, Department of Psychology, Boston College, Chestnut Hill, MA

- Margie E. Lachman, PhD**, Department of Psychology, Brandeis University, Waltham, MA
- Nichole R. Lighthall, PhD**, Department of Psychology, University of Central Florida, Orlando
- Mara Mather, PhD**, Leonard Davis School of Gerontology, University of Southern California, Los Angeles
- Patricia A. Reuter-Lorenz, PhD**, Department of Psychology, University of Michigan, Ann Arbor
- Gregory R. Samanez-Larkin, PhD**, Department of Psychology and Neuroscience, Duke University, Durham, NC
- Alexander L. M. Siegel, MA**, Department of Psychology, University of California, Los Angeles
- R. Nathan Spreng, PhD**, Montreal Neurological Institute, Department of Neurology and Neurosurgery, McGill University, Montreal, Canada
- Gary R. Turner, PhD**, Department of Psychology, York University, Toronto, Canada
- Laura B. Zahodne, PhD**, Department of Psychology, University of Michigan, Ann Arbor

PREFACE

GREGORY R. SAMANEZ-LARKIN

Many years ago as a first-year PhD student, I was sitting among about a dozen senior faculty members at the Stanford Center on Longevity, along with Jane Fonda. Ms. Fonda was at Stanford to talk to scientists doing aging research while working on an upcoming book. My advisor, Laura Carstensen, had invited me to the meeting to share my own emerging research on aging and decision making. In several studies, we had found a perhaps surprising lack of age differences in affective and motivational brain signals and decision-making behavior across adulthood. At one point in the discussion, Ms. Fonda turned to me and said, “What about you, young person, why are *you* interested in aging?”

Just a few years earlier, as a college student, I *hadn't* been interested in aging at all. When I first learned about the psychology and neuroscience of aging, it was fairly depressing. I learned about the steep and relatively linear declines in many aspects of memory and other fluid cognitive abilities. I learned about the similarly steep losses in gray matter and dopamine receptors in the brain. And I wondered how, with all of this consistently documented deterioration, does the aging brain function so well while making decisions?

Over the years, the view of brain aging as a period of deterioration and decline has been replaced with a more complex characterization of changes

in brain structure and function. Not all cognitive processes decline with age; many remain stable, and some improve over adulthood. In my own area of research on decision making, this has been relatively well documented over the past several years. Younger and older adults often make similar decisions, but for different reasons or by using different strategies. As you will read throughout this volume, these sorts of findings are not limited to decision making. In nearly every chapter, there is discussion of how cognitive performance varies across different contexts, how different strategies are used at different ages, or how reorganization and plasticity of the brain supports behavioral function. Although there are undeniable losses in structure and function, the aging brain is more flexible and compensatory than research might have initially suggested.

A few years after the meeting with Jane Fonda, I was running a 92-year-old adult through a neuroimaging study and was shocked by the first whole-brain images we collected. I'd never seen so much atrophy in the striatum and sulci so expanded in the cortex. During the scan, I looked at the participant's neuropsychological test results, and they were normal. A few days later, I processed the neuroimaging data, and in that thin strip of caudate gray matter, there was fairly strong activation during our task. I was puzzled, and to some extent I still am. The aging brain continuously amazes me and is, in part, why I've dedicated my own career to studying adult development and aging. There are many unsolved mysteries of the aging brain, but as a field, we're making progress. You'll read about some of that progress throughout the chapters of this book.

The reason my interest in aging as a (formerly) young person was questioned so many years ago is likely because young people don't often learn about the complexities of aging. The hope is that this volume will provide a more comprehensive picture and, in doing so, inspire more emerging scientists to pursue aging research as well.

The. Aging. Brain

INTRODUCTION

GREGORY R. SAMANEZ-LARKIN

Historically, the scientific study of aging was focused heavily on deterioration and decline. Within psychology departments, for example, researchers studying aging were in clinical areas where their colleagues were focused on disease and disorder. Over the past 25 years, the historical view of brain aging as a decades-long period of deterioration and decline has been slowly replaced with a more complex characterization of changes—growth, decline, adaptation, selectivity, and reorganization—in brain structure and function across adulthood. This shifting view has been driven by research in both the behavioral and brain sciences. The research of psychologists and neuroscientists has revealed that not at all cognitive processes decline with age; some improve over adulthood, and often those that improve compensate for those that decline.

Being happy, healthy, and financially stable in old age depends on a wide range of psychological functions and behaviors across the life span. In response to recent demographic shifts (resulting from increased longevity

<http://dx.doi.org/10.1037/0000143-001>

The Aging Brain: Functional Adaptation Across Adulthood, G. R. Samanez-Larkin (Editor)
Copyright © 2019 by the American Psychological Association. All rights reserved.

and low fertility rates), policymakers and private industry leaders across the globe are looking to psychologists and neuroscientists for advice on how best to promote and protect health and well-being in old age. Unfortunately, psychological research on aging is often too far removed from informing policy. A major reason for this is that aging research is not sufficiently integrative or translational, which significantly limits the potential for broader impact. The current within-area approach impedes cross-talk between disciplines and contributes to a fragmented understanding of aging. The recent rise in interdisciplinary research programs has potential for increasing translation of aging science for real-world impact. In the spirit of these recent developments in the field, this volume aims to combine multiple perspectives on aging from previously disconnected but complementary lines of research. Within most chapters of the volume, we invited contributors working in complementary areas but who had never worked together to coauthor a review of the literature. The hope was that this activity would not only provide a unique resource to the field in the near term but would also inspire new lines of interdisciplinary research that have greater potential for enhancing well-being in old age in the long term.

The primary goal of this volume is to present a more complete, nuanced, and modern view of brain aging by reviewing emerging behavioral and brain research from a broad range of areas across psychology and neuroscience. Although previous books have focused on what is known about cognitive losses with age, less attention has been paid to the broad range of psychological and neural functions (e.g., affective, socioemotional, motivational, cognitive, and decision-related processes) that decline, remain stable, or improve with age. The collection of chapters here aims to provide a more balanced perspective on our current understanding of normal human brain aging.

The book begins with a broad overview of regional and network-level brain structure and function (Chapter 1) to lay the foundation for the remaining chapters. A series of process-focused chapters follow (Chapters 2–6) that discuss attention, learning, memory, motivation, cognition in everyday life, and social function. The final two chapters (Chapters 7 and 8) are once again more general and deal with broader theoretical issues that are critical to our understanding of both the processes discussed in the focused chapters throughout the middle of the book and our understanding of the function of the aging brain overall. The majority of chapters begin by reviewing the brain functions being discussed, the brain structures involved, the current state of empirical research, and the topic's significance within the broader realm of brain-aging studies, then conclude by outlining future avenues of research.

Chapter 1 by Spreng and Turner provides a broad summary of age-related changes in the structure and function of the brain based mostly on

evidence from in vivo human neuroimaging. Across studies, there is relatively consistent evidence that structurally, anterior cortical regions, including the prefrontal cortex, decline in early older adulthood, whereas posterior sensory–motor regions decline in later older adulthood. Functionally, older adults tend to display less network specialization, with greater recruitment of frontal and contralateral regions during cognitively demanding tasks. The chapter introduces a number of larger scale brain networks and individual brain regions that are discussed throughout the book.

Chapter 2 by Kennedy and Mather discusses emerging research on how attentional selectivity changes across adulthood and into older age. One of the most well-characterized cognitive deficits in older age is the difficulty in inhibiting attention to irrelevant information, even though there is relative preservation of other attentional processes. In this chapter, the authors detail how age-related changes in the frontoparietal network—slowing in alpha band activity, decreased GABAergic and dopaminergic densities, and impaired frontoparietal connectivity with noradrenergic release under arousal—play a critical role in age-related changes in attentional selectivity.

Chapter 3 by Lighthall, Conner, and Giovanello begins a series of three chapters that discuss elements of memory abilities. This chapter discusses how long-term nondeclarative (priming, classical conditioning, procedural, and reinforcement learning) systems and declarative (episodic and semantic memory) systems decline or may be partially preserved with age. The authors first introduce the distinct learning and memory systems for the acquisition, retention, and subsequent retrieval of information but go on to discuss evidence that these systems are highly interactive.

Chapter 4 by Duarte and Kensinger focuses specifically on episodic memory, the ability to encode and retrieve details that allow individual events to be distinguished from one another. They discuss both the neural declines that contribute to memory impairments as well as the relative preservation of older adults' emotional memories. They also highlight how memory can be preserved with age by staying mentally and physically active across adulthood.

Chapter 5 by Hargis, Siegel, and Castel is the third in the series related to learning and memory but focuses on the critical contributions of motivation and goals. Rather than focusing on findings from neuroimaging (of which there are currently few), the authors examine how younger and older adults selectively learn information, highlighting reward salience and the importance of attentional control during encoding. They also discuss how goals and extrinsic and intrinsic motivational factors may change decision-making and lead to preservation of function across adulthood. Overall, the chapter identifies many examples of how motivation can enhance learning and memory well into old age.

Chapter 6 by Gutchess and Samanez-Larkin examines the influence of aging on social processes, including thinking about the self and others, mentalizing and empathizing, and responding to stigmatized others. In addition to discussing the types of processes that are preserved or decline with age, they consider ways in which the impact of aging on socioemotional processes may differ from the ways in which aging impacts cognitive processes. They identify multiple interacting brain networks that have subcomponents that are preserved or decline with age that may account for these behavioral effects. Functional adaptation of these brain systems may account at least partially for some of the preservation of motivational and emotional function identified in Chapters 4 and 5.

Chapter 7 by Zahodne and Reuter-Lorenz introduces and discusses the concept of neural compensation in older age. They review emerging findings from the past couple of decades that identify alterations in neural function in response to age-related neural declines that preserve cognitive function. Many of the previous chapters identify aspects of preserved functional output from brain networks that show unquestionable losses with age. This chapter describes how these compensatory processes may work in both normal and pathological aging.

Chapter 8 by Dixon and Lachman discusses risk and protective factors and their independent and interactive effects on trajectories of cognitive change across adulthood. They discuss the contributions of both nonmodifiable factors such as genetics and modifiable factors such as lifestyle interventions that may contribute to preservation of function in both normal and pathological aging. On the basis of emerging research, the chapter identifies goals to potentially reduce or delay neurodegenerative cognitive declines and potentially prevent the onset of dementia.

This book is not intended to be comprehensive in its coverage of all areas of human cognitive function. There are important areas of research that are not covered. For example, although many chapters discuss issues of cognitive control, there is not a dedicated chapter on the topic. We also do not provide a comprehensive treatment of how the processes of normal aging and age-related diseases may diverge, although there is discussion of how compensatory function and modification of risk factors may slow or prevent the onset of serious cognitive decline in Chapters 7 and 8. This book is also quite focused on systems-level neural function as revealed by human brain imaging—mostly functional magnetic resonance imaging. A limitation is that there is little discussion of the specific lower level cellular and molecular changes across adulthood that influence function. Some discussion of declines and preservation in neuromodulatory (e.g., norepinephrine, dopamine) and neurotransmitter (e.g., GABA) function is provided in Chapters 2 and 6. This book would be an ideal companion to other books that provide broader coverage of cognitive

change or lower level coverage of specific cellular and molecular mechanisms of brain aging.

The target readership for this book is primarily researchers working on the psychology and neuroscience of aging from graduate students and post-docs to faculty members. The collection of chapters could be used together in a graduate seminar on the psychology and neuroscience of aging. It also has the potential to be used in a focused, upper level, undergraduate seminar for students with a solid foundation in both psychology and human brain imaging. The individual chapters vary in their accessibility, so some of them may be used in more introductory courses at the undergraduate or graduate level. Individual chapters could also be used in a nonaging, topic-focused course that with the intent of exposing students to how these processes vary across adult development. For example, a course on attention might include Chapter 2, or a course on memory might include Chapters 3, 4, or 5.

In nearly every chapter, there is discussion of how cognitive performance varies across different contexts, how different strategies are used at different ages, or how reorganization and plasticity of the brain supports behavioral function. Although there are undeniable losses in structure and function, the aging brain is more flexible and compensatory than research might have initially suggested. The hope is that this book presents a more comprehensive picture of the functionally adaptive aging brain.