## **Comparative Cognition**

Integrating developments from psychology, ethology, and neuroscience, this is an undergraduate introduction to cognitive processes across species. The authors merge classic studies and contemporary research to give students the full picture of the evolving field of comparative cognition.

Engaging students in the discipline from its roots in animal learning and evolutionary biology through to current research, the chapters cover both controlled laboratory and comparative cross-species studies in the natural environment. This approach provides students with complementary ethological and neurobiological perspectives on cognition. Feature boxes encourage engaged learning, giving a deeper understanding of topics discussed in the main text. These are supported by end-of-chapter questions to help check understanding of key theories and concepts.

Online resources include links to sites of interest, further reading, PowerPoint lecture slides and additional questions, all available at www.cambridge.org/cognition.

**Mary C. Olmstead** is Professor of Psychology and Neuroscience at Queen's University, Ontario. Her research is directed towards understanding the neural and psychological interface between motivation and cognition, or how rewarding stimuli influence learning.

**Valerie A. Kuhlmeier** is Associate Professor of Psychology and Canada Research Chair in Cognitive Development at Queen's University, Ontario. Her research program explores cognition from a developmental and evolutionary perspective.

Both the authors are research psychologists who have been teaching at Canadian, US, and European institutions for the last 15–20 years.

# Comparative Cognition

MARY C. OLMSTEAD

AND

VALERIE A. KUHLMEIER

Queen's University, Ontario, Canada



Cambridge University Press & Assessment 978-1-107-01116-8 — Comparative Cognition Mary C. Olmstead, Valerie A. Kuhlmeier Copyright information <u>More Information</u>



Shaftesbury Road, Cambridge CB2 8EA, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314-321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi - 110025, India

103 Penang Road, #05-06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of Cambridge University Press & Assessment, a department of the University of Cambridge.

We share the University's mission to contribute to society through the pursuit of education, learning and research at the highest international levels of excellence.

www.cambridge.org Information on this title: www.cambridge.org/9781107011168

© M.C. Olmstead and V.A. Kuhlmeier 2015

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press & Assessment.

First published 2015 Reprinted 2017

A catalogue record for this publication is available from the British Library

Library of Congress Cataloging-in-Publication data
Olmstead, Mary C.
Comparative cognition / Mary C. Olmstead, Valerie A. Kuhlmeier. pages cm
ISBN 978-1-107-01116-8 (Hardback) – ISBN 978-1-107-64831-9 (Paperback) 1. Psychology, Comparative.
2. Cognition. I. Kuhlmeier, Valerie A. II. Title.
BF671.046 2014
156'.3-dc23 2014021238
ISBN 978-1-107-01116-8 Hardback

ISBN 978-1-107-01116-8 Hardback ISBN 978-1-107-64831-9 Paperback

Additional resources for this publication at www.cambridge.org/cognition

Cambridge University Press & Assessment has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.

## **TABLE OF CONTENTS**

	Preface	page ix
1	<ul> <li>History of comparative cognition</li> <li>1.1 Hallmarks of comparative cognition</li> <li>1.2 Influence: theory of evolution by natural selection</li> <li>1.3 Influence: experimental psychology and behaviorism</li> <li>1.4 Influence: ethology and behavioral ecology</li> <li>1.5 Emergence of comparative cognition</li> <li>1.6 An interdisciplinary approach</li> <li>Chapter summary</li> <li>Questions</li> <li>Further reading</li> </ul>	1 2 5 11 14 18 25 29 29 29 30
2	Sensory systems 2.1 Evolution of sensory systems 2.2 Development of sensory systems 2.3 Sensory system function 2.4 Perception 2.5 Attention Chapter summary Questions Further reading	32 33 42 44 50 59 66 66 66
3	Memory 3.1 Preliminary issues 3.2 Stages of memory processing 3.3 Working memory 3.4 Reference memory 3.5 Neuroscience of memory Chapter summary Questions Further reading	69 70 74 81 88 99 104 104
4	<ul> <li>Associative processes</li> <li>4.1 Terminology</li> <li>4.2 Experimental paradigms</li> <li>4.3 Associative processes as adaptations</li> <li>4.4 Mechanisms</li> <li>4.5 Theories</li> <li>4.6 Neuroscience of associative processes</li> </ul>	107 108 111 118 123 128 137

Cambridge University Press & Assessment 978-1-107-01116-8 — Comparative Cognition Mary C. Olmstead, Valerie A. Kuhlmeier Copyright information <u>More Information</u>

vi

### **Table of Contents**

	Chapter summary Questions	143 143
	Further reading	144
5	Orientation and navigation	146
	5.1 Finding the way	147
	5.2 Orientation	152
	5.3 Small-scale navigation	154
	5.4 Large-scale navigation	166
	5.5 Neuroscience of spatial behaviors	175
	Chapter summary	182
	Questions	182
	Further reading	183
6	Timing and number	185
	6.1 Periodic timing	186
	6.2 Timing intervals	188
	6.3 The approximate number system	195
	6.4 Representing small numbers	202
	6.5 Operations	205
	Chapter summary	211
	Questions	211
	Further reading	212
7	Decision making	213
	7.1 Evolution of decision making	214
	7.2 Choice in the lab	225
	7.3 Choice under uncertainty	229
	7.4 Emotional decision making	239
	7.5 Neuroeconomics	240
	Chapter summary	245
	Questions	246
	Further reading	246
8	Causality and tool use	248
	8.1 Causality	249
	8.2 Object physics	254
	8.3 Tool use defined	258
	8.4 Development of tool use	262
	8.5 Causality and tool use	264
	Chapter summary	269
	Questions	269
	Further reading	270
9	Categorization and concept formation	271
	9.1 Fundamentals	272
	9.2 Perceptual categorization	277

Cambridge University Press & Assessment 978-1-107-01116-8 — Comparative Cognition Mary C. Olmstead, Valerie A. Kuhlmeier Copyright information <u>More Information</u>

		Table of Contents	vii
	9.3 Functional categorization		284
	9.4 Relational categorization		286
	9.5 Social categorization		289
	9.6 Concept formation		299
	9.7 Neural mechanisms		303
	Chapter summary		306
	Questions		307
	Further reading		307
	Turtici redding		507
10	Social competence		309
	10.1 Detection of animacy		310
	10.2 Thinking about thinking		317
	10.3 Understanding intentions		320
	10.4 Understanding seeing and knowing		323
	10.5 Social knowledge		333
	Chapter summary		337
	Questions		338
	Further reading		338
11	Prosocial behavior		339
	11.1 Evolution of prosocial behavior		340
	11.2 Types of prosocial behavior		343
	11.3 Helping		344
	11.4 Sharing		349
	11.5 Comforting		354
	11.6 Cooperation		359
	Chapter summary		364
	Questions		364
	Further reading		365
12	Communication		366
	12.1 Features of communication		367
	12.2 Evolution of communication		370
	12.3 Bee dance		372
	12.4 Alarm and food calls		376
	12.5 Communication in play behavior		381
	12.6 Teaching language to animals		383
	Chapter summary		388
	Questions		389
	Further reading		389
13	Learning from others		391
	13.1 Evolution and selectivity of social learning		392
	13.2 Types of social learning		395
	13.3 Learning food and mate preferences		400
	13.4 Social learning and communication: vocal learning		404

Cambridge University Press & Assessment 978-1-107-01116-8 — Comparative Cognition Mary C. Olmstead, Valerie A. Kuhlmeier Copyright information <u>More Information</u>

viii

### Table of Contents

13.5 Learning to use objects	407
13.6 Culture	413
Chapter summary	416
Questions	416
Further reading	417
Glossary	419
References	428
Figure credits	461
Index	467

## PREFACE

Comparative cognition is a highly interdisciplinary field that arose from a synthesis of evolutionary biology and experimental psychology. In its modern form, researchers from a variety of scientific backgrounds (e.g. neuroscience, behavioral ecology, cognitive and developmental psychology) come together with the common goal of understanding the mechanisms and functions of cognition. Over the past 10 years, we have taught both undergraduate and graduate courses that covered the subject matter of comparative cognition, although frequently in a course of another name. Like many instructors, we put together course material that included scientific articles, chapters in other textbooks, and our own writings as an attempt to represent the evolving field of comparative cognition. This was not ideal as the presentation of material from different sources is uneven, and undergraduate students often have difficulty conceptualizing the fundamentals of a discipline without the framework provided by a solid textbook. We realized that our experience was not unique when we spoke to colleagues teaching similar courses at other universities.

Our textbook provides an introduction to the field of comparative cognition. It begins with an historical view of the field, emphasizing the synergy of different disciplines, both in terms of theoretical foundations and methodological tools. This lays the groundwork for later chapters in which controlled laboratory studies are presented alongside comparative studies in the natural environment. The first half of the text covers topics that reflect the influence of behavioral psychology on comparative cognition. This material, therefore, overlaps with traditional animal learning texts. The distinguishing feature of our text is an increased emphasis on the evolutionary function and underlying neural mechanisms of cognition. In addition, issues that are central to cognitive psychology (e.g. attention, episodic memory, and cognitive maps) are interwoven throughout these chapters. The second half of the book focuses on what are often described as 'higher cognitive processes,' describing recent research on topics such as tool use and causal reasoning, imitation, and functionally referential communication.

Although different cognitive processes are discussed in separate chapters, the point is continually made that none of these functions in isolation. Even seemingly simple behaviors, like foraging for food, depend on an interaction between many cognitive processes. For example, spatial navigation is required to locate the food and then return to home base, perceptual discrimination is necessary to distinguish what is a good food source from what is not, emotional memory is used to recall dangers that were encountered in previous foraging expeditions, and decision making allows animals to make cost/benefit calculations of the energy output in searching for food versus the energy gained in food consumption. Foraging may also involve more complex processes such as communication with conspecifics about where the food is located, cooperation in hunting prey or retrieving food, as well as knowledge of social hierarchies (e.g. whether a dominant animal is likely to steal the food).

The text also reflects the fundamental importance of cross-species analyses in comparative cognition research. Each chapter includes descriptions and analyses of scientific studies conducted with humans and a variety of non-human animals. (In the interest of succinctness, from hereon we use the term 'animal' to refer to all non-human animals and 'human' to refer to *Homo sapiens*, and scientific nomenclature for species' names will be presented only the first time a species is mentioned.) The relative weighting of material drawn from research using humans versus animals

Х

Cambridge University Press & Assessment 978-1-107-01116-8 — Comparative Cognition Mary C. Olmstead, Valerie A. Kuhlmeier Copyright information <u>More Information</u>

#### Preface

(or indeed one animal species versus another) depends on the topic under discussion. For example, scientific studies reviewed in the early chapters often include multi-species comparisons because research that informs these topics (e.g. perception, long-term memory) spans the entire animal kingdom; in contrast, topics covered in the later chapters are frequently defined by a comparison to human abilities (e.g. theory of mind). In some cases, we know more about how a specific cognitive process operates in certain animals simply because it has been studied more frequently in that species (e.g. operant conditioning in rats). As research in comparative cognition progresses, both the function and mechanisms of cognition are being studied in an increasing number of species. Future editions of this text, therefore, will undoubtedly include an expanded list of cross-species comparisons.

Comparative cognition research is characterized by an ongoing dialogue between scientists with different areas of specialization. This component of the field is represented in the text by an integration of material across disciplines. Importantly, each topic includes up-to-date research on neural mechanisms of cognition and on cognitive development, two of the most fruitful areas of research that inform and complement comparative cognition research. Because each topic is covered from different perspectives, the structure of the text emphasizes how complementary empirical studies lay the groundwork for theoretical positions. Many of the chapters finish with a description of ongoing controversies in the field, with no apparent 'conclusion' to a specific topic. This is a reflection of the dynamic and productive field of comparative cognition: like many scientific endeavors, there is always more work to be done. The book is timely in that the field is advancing rapidly; a textbook that presents fundamentals of this discipline will be a foundation for further scientific and scholarly investigations.

## Using the book

This book is organized in such a way that it may be flexibly adapted to courses with different program restrictions and pedagogical requirements. One instructor may opt to cover all of the chapters in a single term, another to divide these by presenting basic (Chapters 2 through 7) and higher order (Chapters 8 through 13) cognitive processes in separate terms. We adopt the latter approach in our own teaching and assign Chapter 1 (Introduction to Comparative Cognition) to both courses. Those interested in using the text (or single text chapters) for upper level undergraduate or graduate courses can take advantage of information provided in the instructor's manual. Among other tools, this on-line resource includes a list of Supplementary Material for each chapter that presents specific topics at a more advanced level of pedagogy. For most chapters, this includes at least one 'origin of the field' paper, such as an original excerpt from one of Darwin's or Tinbergen's publications. Depending on the chapter topic, the supplementary material could also include a recent high-impact paper in the field. Each entry is accompanied by a short commentary specifying its importance and pointing out controversies that were stimulated or resolved by the publication. The section concludes with suggestions for short assignments based on this material.

Finally, the textbook includes a number of features designed to enhance student engagement. Text boxes within each chapter complement material presented in the main text by outlining extensions of comparative cognition research. Some of these discuss scientific discoveries in related disciplines such as anthropology, computer science, artificial intelligence, linguistics, or philosophy. Others present real-world applications of knowledge gained from comparative cognition studies to fields such as clinical psychology or environmental studies. Each chapter profiles one contemporary researcher in the field of comparative cognition. As interested students (not so long ago!), we often wondered how scientists began their careers, especially in a field like comparative cognition that has

Preface

xi

so many diverse influences. An overview of these biographies reveals that career and education paths vary widely, that research interests evolve, and that many different scientific perspectives converge in the field of comparative cognition. Each chapter also includes a list of 6–10 questions that cover both factual and theoretical information. Students can use these to gauge their own understanding of basic and conceptual issues related to the chapter topic. Each chapter concludes with a Further Reading section, an annotated list of 8–10 selections of supplementary readings. These include scientific articles (primarily reviews or 'classic' papers in the field), book chapters, or entire books. A description of each entry along with its relevance to the chapter material is provided such that students and instructors can select the readings based on their own interest and/or the course curriculum.

Despite teaching comparative cognition courses for close to 15 years, we never cease to be surprised (and delighted) by the insightful questions and thought-provoking comments of our students. These were the original source of inspiration for this text, for which we are eternally grateful. We were fortunate to have supportive Department Heads, Merlin Donald, Vernon Quinsey, and Richard Beninger, who encouraged and facilitated the writing of this text. In addition, many of our colleagues generously offered suggestions on individual chapters, including Hans Dringenberg, Kristen Dunfield, Barrie Frost, Megan Mahoney, Janet Menard, Niko Troje, Kristy vanMarle, and Ron Weisman, as well as the members of the Infant Cognition Group and Moticog Lab. Ruxandra Filip and the staff at CUP were invaluable during the final stages of text editing.

We are particularly indebted to the collegiality displayed by Francesco Bonadonna and his research team at the Centre d'Ecologie, Functionelle et Evolutive in Montpellier, France. Along with Anne Gorgeon, they provided a stimulating environment and ensured that nothing was lost in translation. We are grateful to a set of international reviewers who provided feedback on earlier versions of this text, and to the Natural Sciences and Engineering Research Council (NSERC) of Canada for ongoing research funding.

This text would not have materialized without the unfailing enthusiasm and support of Rodney Birch and Leslie Farquharson. We also thank Bradley, Darrell, Kermit, Digger, Bobby, Sarah, Abby, and Sheba who taught us invaluable lessons about animal communication and interspecific mutualism. Finally, Catia and Lucas opened our eyes to the wonders of the natural world and graciously put up with an absentee mother on far too many nights and weekends.

This book is dedicated to Patricia Jean Olmstead and to James and Alba Kuhlmeier.