



ROUTLEDGE
INTERNATIONAL
HANDBOOKS



The Routledge International Handbook of Comparative Psychology

Edited by Todd M. Freeberg, Amanda R. Ridley and
Patrizia d'Ettorre

THE ROUTLEDGE INTERNATIONAL HANDBOOK OF COMPARATIVE PSYCHOLOGY

*Edited by Todd M. Freeberg, Amanda R. Ridley
and Patrizia d'Ettorre*

Cover image: Getty

First published 2023

by Routledge

605 Third Avenue, New York, NY 10158

and by Routledge

4 Park Square, Milton Park, Abingdon, Oxon, OX14 4RN

Routledge is an imprint of the Taylor & Francis Group, an informa business

© 2023 selection and editorial matter, Todd M. Freeberg, Amanda R. Ridley and Patrizia d’Ettorre; individual chapters, the contributors

The right of Todd M. Freeberg, Amanda R. Ridley and Patrizia d’Ettorre to be identified as the authors of the editorial material, and of the authors for their individual chapters, has been asserted in accordance with sections 77 and 78 of the Copyright, Designs and Patents Act 1988.

All rights reserved. No part of this book may be reprinted or reproduced or utilised in any form or by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying and recording, or in any information storage or retrieval system, without permission in writing from the publishers.

Trademark notice: Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

Library of Congress Cataloging-in-Publication Data

A catalog record for this book has been requested

ISBN: 978-0-367-54604-5 (hbk)

ISBN: 978-1-003-09186-8 (ebk)

ISBN: 978-1-032-31653-6 (pbk)

DOI: 10.4324/9781003091868

Typeset in Bembo

by Apex CoVantage, LLC

CONTENTS

<i>List of Contributors</i>	<i>x</i>
PART 1	
Foundations	1
Introduction to Handbook	3
1 Historical Perspectives on Comparative Psychology and Related Fields <i>Gordon M. Burghardt and Lee C. Drickamer</i>	11
2 Behaviourism: Past and present <i>Gonzalo P. Urcelay and Joaquín M. Alfei</i>	23
3 On Strengths and Limitations of Field, Semi-natural Captive, and Laboratory Study Settings <i>George W. Uetz, David L. Clark and Brent Stoffer</i>	34
4 Ontogeny of Behaviour <i>Sébastien Derégnaucourt and Patrizia d’Ettorre</i>	48
5 Sensation, Perception, and Attention <i>Jessica L. Yorzinski and Will Whitham</i>	61
6 Motivation and Emotion <i>Jerry A. Hogan</i>	71
7 Comparative Cognition <i>Mary C. Olmstead and Valerie A. Kuhlmeier</i>	84

8	Cognitive Ecology <i>Julie Morand-Ferron</i>	96
PART 2		
	Behavioural Systems	109
9	Habitat Selection and Its Importance in Conservation Biology <i>Yamil E. Di Blanco and Mario S. Di Bitetti</i>	111
10	Where, What and With Whom to Eat: Towards an Integrative Study of Foraging Behaviour <i>Mathieu Lihoreau and Tamara Gómez-Moracho</i>	124
11	Causal Factors in the Study of Vigilance <i>Guy Beauchamp</i>	136
12	Communication <i>Eleanor Caves, Patrick Green and Melissa Hughes</i>	147
13	Intraspecific Aggression and Social Dominance <i>Christine M. Drea and Nicholas M. Grebe</i>	160
14	Mating Behaviour <i>Patricia A. Gowaty</i>	175
15	Parental Behaviour <i>Juana Luis and Luis O. Romero-Morales</i>	188
16	Play Behaviour: A Comparative Perspective <i>Elisabetta Palagi and Sergio Pellis</i>	202
PART 3		
	Complexities and Interactions	213
17	What is Cooperation, and Why Does It Happen? <i>Amanda R. Ridley</i>	215
18	Cultural Behaviour in Cetaceans <i>Alex South, Ellen C. Garland and Luke Rendell</i>	227
19	Tool Use <i>Akane Nagano</i>	240
20	Bridging the Gap Between Human Language and Animal Vocal Communication <i>Sabrina Engesser and Simon William Townsend</i>	251

Contents

21	Reasoning <i>Valérie Dufour</i>	263
22	Deception in Animal Communication <i>Tom Flower</i>	274
23	Evolutionary Behavioural Ecology Perspectives on Personality in Non-human Animals <i>Niels J. Dingemanse and Denis Réale</i>	289
24	Social Contextual Influences on Behaviour <i>Todd M. Freeberg and Brittany A. Coppinger</i>	302
25	Network Approaches to Understanding Social Organization and Complexity <i>Elizabeth A. Hobson and Gerald G. Carter</i>	315
26	Changing Ideas About Mating Systems <i>Nancy G. Solomon and Brian Keane</i>	326
27	Human Mate Choice <i>Jan Havlíček, Zuzana Štěrbová and Zsófia Csajbók</i>	338
28	Bridging the Gap: Human-animal Comparisons <i>Katherine McAuliffe and Paul Deutchman</i>	355
	<i>Index</i>	370

COMPARATIVE COGNITION

Mary C. Olmstead and Valerie A. Kuhlmeier

1. Historical Background

Comparative cognition investigates how information is represented, organized, and processed in different animals with the goal of understanding the function, phylogeny, ontogeny, and mechanisms of mental activity. Interest in this topic can be traced back, at least, to Aristotle (c. 384–322 B.C.E.) who compared behavioural tendencies and intellectual characteristics of different species (Leroi 2014). As with physical attributes, psychological traits that distinguished species, particularly those separating humans from animals, were considered immutable, a belief that permeated Western thinking for centuries. The idea that an entire species may change or adapt over time was put forward by Muslim scholars in the middle ages (Malik et al. 2017). This included Al-Jahiz (776–868), a zoologist in Iraq, who classified animals based on physiology and behaviour, proposing that environmental conditions drove adaptations that were advantageous for survival (Bayrakdar 1983). Darwin's theory of natural selection (1859) introduced these ideas to a Western audience, although the extent to which he and his contemporaries were influenced by the earlier Muslim writings is unclear (Guessoum 2011).

Darwin did not use the term cognition, but his proposal that mental faculties, such as memory, language, and emotion, were similar across species (Darwin 1871) laid the foundation for the later emergence of comparative cognition. His ideas challenged the Cartesian perspective, prevalent in Europe at the time, that only humans displayed complex thought, such as reasoning, or understood abstract concepts, such as time (King et al. 2016). Darwin's rejection of human uniqueness in intellectual abilities was consistent with ideas that were prevalent in some non-Western cultures (Malik et al. 2017). As an example, indigenous peoples of the Americas often attributed human-like psychological traits and cognitive abilities to other animals, noting that each species possessed specific knowledge and skills that allowed them to function effectively in their environment (Pierotti 2015). Humans, being the most recent species to inhabit the earth, were tasked with learning these skills from their animal cohabitants in order to survive in the same environments (Bruchac 1992). Regardless of whether he encountered these non-Western belief systems, Darwin made a unique contribution to the field of comparative cognition by articulating a process (i.e., natural selection) that explained the connection between environmental constraints and species-specific abilities. Even Alfred Russell Wallace, often considered a co-founder of Darwin's evolutionary theory, did not believe that psychological traits were shaped by the same forces that govern physiological adaptations (Wallace 1869).

By the late 19th century, proponents of Darwin's continuity theory undertook a series of studies purporting to demonstrate animal-human continuity in mental faculties: differences in degree, not kind. One of the most prominent, George Romanes (1892), collected circumstantial reports, often

vivid and anthropomorphic descriptions of behaviour, as evidence for animal prowess in problem solving, empathy, and reasoning. Critics easily identified flaws in these anecdotal observations, noting that the existing experimental evidence provided no support for insight, intelligence, or other complex thought in nonhuman animals (Morgan 1894; Thorndike 1911). These advocates of the rising school of Behaviourism promoted an experimental analysis of behaviour using quantifiable measures of both stimuli and responses (Watson 1913), a perspective that dominated North American psychology in the first half of the 20th century.

Discussions of mental processes, as mediators of behavioural change, were minimized during the height of behaviourism, although not completely absent (Maier and Schnierla 1935). Tolman (1932) is often recognized for his foresight in suggesting that mental representations control responding in laboratory rats, and Kohler (1925) proposed that insight, not stimulus-response (S-R) learning, explained problem solving in chimpanzees. Less well known is the contribution of Charles Henry Turner (1867–1923), a biologist of African-American heritage, who openly challenged associative theories of the time by discussing mentalistic concepts in animals (e.g., intentionality, awareness, consciousness) while conducting controlled experiments with quantifiable measures (Abramson 2003; Lee 2020). Close to the same time, Margaret Floy Washburn (1871–1939) argued for a rigorous methodology in behavioural experiments, but advocated a more balanced approach in discussing the findings from these studies (Burghardt 2020). Over several editions of her text, *The Animal Mind* (first published in 1908), Washburn rejected a strict behaviourist focus on stimulus-response learning, discussing higher mental processes, including consciousness, in a variety of species (Washburn 2010). Thus, North American Psychologists in the early 20th century generally agreed that animal behaviour should be measured in controlled, laboratory experiments, but disagreed on whether the outcome of these experiments could be explained without reference to non-observable thought processes.

Complementing these lab-based studies, research examining species-typical behaviours in the natural environment was advancing in central Europe. Specifically, champions of the emerging field of ethology (Lorenz, Tinbergen, and von Frisch) systematically examined causal determinants of responses that were part of an organism's behavioural repertoire (Dugatkin 2014). Like their behaviourist counterparts, ethologists devoted little time to discussing mentalistic concepts, although Lorenz (1950) proposed that fixed action patterns were initiated by central mechanisms ('action-specific energy'), and Tinbergen (1951) postulated that motivational impulses were generated in a central nervous system 'top centre'. In other words, a recognition that behaviour is controlled, or at least modified, by internal processes was overshadowed by a focus on detailed descriptions of observable phenomena, such as sign stimuli or fixed action patterns (Beer 2020).

Within the next decade, ethologists turned their attention to functional explanations, describing behaviour in terms of survival and reproductive advantage. From this, a subdiscipline of behavioural ecology arose, centered on topics such as inclusive fitness, kin selection, and foraging. Primary to the endeavour was the development of mathematical models of optimality: cost-benefit analyses of behaviour that maximized the reproductive and survival advantage of an organism (Dugatkin 2014). Although there was no expectation that individual animals consciously perform specific calculations to reach the best (i.e., most adaptive) solution in a given situation, the assumption was that natural selection had shaped biological mechanisms supporting computational processes of optimality.

As the influence of behavioural ecology spread, psychologists began to acknowledge that animal behaviour must be studied within the context of a species' evolutionary history. The point was epitomized in an experiment showing that rats easily associate a specific taste with nausea or a light-sound cue with shock, but failed to learn the alternate relationships (i.e., taste paired with shock or light-sound paired with nausea) (Garcia and Koelling 1966). This demonstration of differential sensitivity to specific cue-outcome associations fundamentally changed 'how we think about animal learning and its relationship to the rest of biology' (Shettleworth 2010b, pg. R910). Initial descriptions of this phenomenon as a 'constraint on learning' (Shettleworth 1972) emphasized the challenge it posed

to behaviourist theories, specifically the idea that principles of stimulus-response learning could be generalized across stimuli and organisms. Evidence that evolutionary history determines the ease at which a species will acquire a particular association mounted rapidly, with ‘selective associations’ becoming the more commonly employed term (Shapiro et al. 1980). Eventually, many researchers adopted the term ‘adaptive specializations’ (Shettleworth 2010a), highlighting the belief that behaviour is tied to a biological system that evolved to meet the functional needs of a particular species (Hulse 2006).

2. A Focus on Cognition

The idea that evolutionary factors shape psychological processes, at least in humans, was exemplified in Chomsky’s theory of universal grammar (Chomsky 1968). His scathing rejection of a behaviourist explanation of language acquisition (Chomsky 1959) coincided with Simon and Newell’s infamous proposal (1959) that mental activity is analogous to computational processing in computers (Lachmann et al. 1979). Theories and methodologies from both linguistics and computer science soon infiltrated other fields, most notably psychology, with terms such as storage, retrieval, and symbolic representation entering the lexicon of this discipline (Ashcraft and Klein 2010). Animal researchers soon adopted a similar perspective, using principles of information processing to explain complex abilities such as spatial navigation, decision making, and tool use in nonhumans (Shettleworth 2010a).

By the early 1980s, cognitive psychology was firmly established as one of the dominant trends in academic research. Cognition, defined more than 500 years ago as the action or faculty of knowing (Chaney 2013), became an umbrella term for a collection of mental processes ranging from perception to language. The notion that cognition included all processes by which sensory input is transformed, reduced, elaborated, stored, recovered, and used (Neisser 1967) implied that cognitive research included anything *not* studied by behaviourists. More explicitly, cognition was assumed to involve emergent, untrained responses rather than learned S-R associations (Wasserman and Zentall 2006). The distinction was particularly apparent in discussions of learning and memory, the former studied in animals by behavioural psychologists, and the latter in humans by cognitive psychologists.¹ Over time, this ‘old and misplaced’ dichotomy (Emery 2017) was difficult to justify in that ‘reflex and reinforcement-based explanations suggest one type of representation, not alternatives to the concept of representation’ (Roitblatt 1987, page 19).

There are three categories of opinion regarding the difference between comparative cognition and comparative psychology.

1. Difference in kind. Comparative cognition and comparative psychology share some features but are fundamentally distinct fields (e.g., Abramson 2015).
2. Difference in level. Comparative cognition is a subfield of comparative psychology. This view is exemplified by textbooks such as Greenberg and Haraway’s *Principles of Comparative Psychology* (2002), in which animal cognition is covered in a separate chapter. This *Handbook of Comparative Psychology* adopts the same perspective.
3. Difference in degree. Comparative cognition and comparative psychology are sister fields; to carry the metaphor further, cognitive ecology (Chapter 8) is the monozygotic twin of comparative cognition. For some, comparative cognition and comparative psychology are so closely related as to be almost indistinguishable, with the terms sometimes being used interchangeably (e.g., McMillan and Sturdy 2015; Shettleworth 2010a).

Which of these three opinions one holds is related to how one defines *cognition*, which can range from more conservative to more liberal (Heyes, in Bayne et al. 2019). Liberal definitions are broad enough to include such phenomena as perception, memory, categorization, and associative learning,

What is the difference between Comparative Cognition and Comparative Psychology?

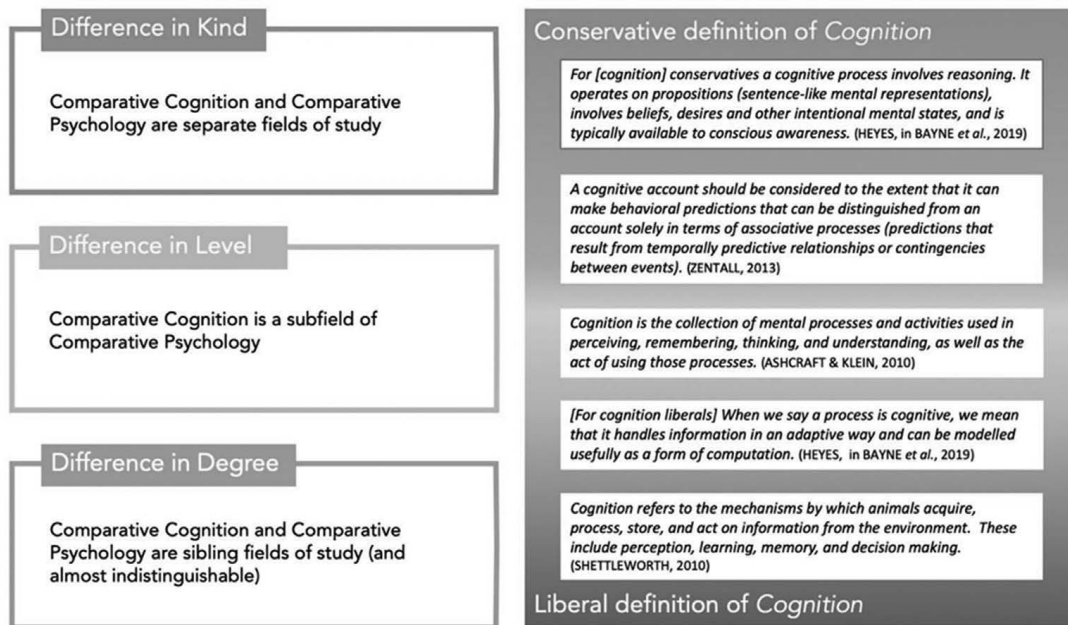


Figure 7.1 The relationship between definitions of cognition and how these relate to comparative psychology versus comparative cognition.

as well as the formation of representations that allow for flexible problem solving across contexts. More conservative definitions of *cognition* exclude processes such as associative learning, instead emphasizing reasoning and inference.

Although cognitive psychologists continue to debate which processes are to be included in their field of study, there is general agreement that cognition involves the representation, organization, and processing of mental information. This occurs through computational mechanisms linking sensory input to behavioural output. Hebb (1949) formulated one of the earliest accounts of this process, proposing physiological underpinnings of mental activities, such as memory. Technological advances over the subsequent 70 years dramatically enhanced the ability to investigate biological structures and function, leading to a consensus that cognition is an emergent property of brain activity (Wasserman and Zentall 2006). A natural outcome of this idea was the recognition that cognition is a set of adaptive traits, which evolved to solve fitness-related problems (Shettleworth 2010a).

In this chapter, we adopt a multi-faceted view of cognition that encompasses mental activities supporting attention, learning, memory, concept formation, decision making, reasoning, and communication, among others. Researchers may disagree with the specific categories of cognitive processes (as well as how these are organized), but there is growing consensus that processes can be characterized by distinct rules of operation. Domain-general processes, such as perception, attention, and memory, are ubiquitous across many species; they are also building blocks of domain-specific processes (Shettleworth 2010a). At a conceptual level, domain-specific processes can be divided, further, into two categories: those that allow a species to interact adaptively with the physical environment (e.g., navigation, timing, and physical causality) and those that allow a species to interact adaptively with the social environment (e.g., social competence, prosocial behaviour, and communication). A primary challenge in the field is to understand the relationship between these different processes, as well as how they interact with other systems and functions (e.g., motivation, temperament, and motor patterns) to produce flexible and adaptive behaviour (Burghardt 2019).

Finally, the contemporary field of comparative cognition is built on three assumptions. The first is that cognition can be studied scientifically in humans and other animals. Early work in this area included a series of studies assessing the ability of phylogenetically distant species animals to solve the same series of tasks, often with mixed conclusions (Bitterman 1975). A recognition that comparisons were compromised when animals possessed dramatically different sensory and motor capabilities helped to move the field from a focus on general intelligence to an examination of cognitive processes adapted to unique ecological niches of each species (Pearce 2008). The second assumption is that cognition, as a byproduct of biological functioning, is subject to the laws of natural selection. This explains the principle of proper mass (Jerison 1973) in which the proportion of brain area devoted to a cognitive function reflects the relative importance of that function in terms of evolutionary advantage. Evidence supporting this claim includes dramatic differences in the size of visual processing areas of diurnal and nocturnal rodents (Striedter 2005), and in hippocampal volumes of closely related bird species that experience varied environmental demands on food caching (Balda and Kamil 2006). A further corollary is that there must be heritable, within-species variability in the cognitive traits that provide an adaptive advantage (Boogert et al. 2018). Investigations in this area have not, traditionally, been a mainstay of comparative cognition research, partly because of the difficulty in assessing variability in cognitive processes (Morand-Ferron et al. 2016), although the trend is slowing changing (Griffin et al. 2015). The third assumption of comparative cognition research is that scientific questions will be addressed using two or more species. If a particular research study involves only one species, the findings will be compared to other studies using different species. A critical point, not always appreciated by those outside of the field, is that cross-species comparisons need not include *Homo sapiens*. Indeed, anthropomorphism promotes the incorrect and misleading assumption that humans are at the apex of a phylogenetic scale (Shettleworth 2010a).

3. Comparative Studies of Cognitive Structure

3.1 Architecture of Cognition

As in the broader the field of cognitive science, comparative cognition researchers continue to debate the architecture of cognition. Discussions of this topic have moved from evaluating the merits of general processing (MacPhail 1987) versus adaptive specialization (Gallistel 1998) views of cognition, to describing the relationship between domain-general and domain-specific processes (see Burkart et al. 2017 and commentary). Despite ongoing work, a number of issues are unresolved, partly because the criteria used to distinguish domain categories remains controversial. Specifically, domains are defined by functional outcomes (e.g., locating cached food items) but the operations and mechanisms that support those outcomes may be parsed in multiple ways (e.g., integration of landmark cues, reference memory, timing, etc.). In other words, there is not a one-to-one mapping from cognitive process to adaptive outcome, making it difficult to ascertain a direct relationship between the two.

Adding further complication, the term ‘domain-general’ is used in at least two different ways by comparative researchers. Shettleworth (2010a) uses it to describe basic cognitive processes with the following properties: information is processed in a relatively stereotypical manner, regardless of the specific input; each process can serve multiple functions, which may occur simultaneously; and principles of operation are preserved across species. In this schematic, domain-general processes are the foundation of domain-specific processes, which are preferentially attuned to the functional demands of an organism. As an example, the domain-specific process of inter-species communication depends on the domain-general process of perception (among others). In a different formulation (Burkhart et al. 2017), domain-general describes a higher-order process that emerges from an interaction between multiple cognitive specializations. According to this view, domain-general thinking (often equated with general intelligence) describes the mental operations that integrate domain-specific

processes. Originally formulated as a human-unique trait, it is now clear that many other animals share this cognitive ability, although the extent to which it is represented across phylogeny is still unclear (Laland and Seed 2021; Poirier et al. 2020). Importantly, the capacity for domain-general thinking does not preclude the existence of cognitive specializations; humans and many animals are capable of combining functionally distinct cognitive processes in flexible ways, allowing them to respond adaptively to changing environmental demands.

In sum, the relationship between domain-general and domain-specific processes is often represented in one of two ways. In the first, domain-general processing is a foundation for domain-specific processing. In the second, domain-general thinking emerges from domain-specific specializations. A more viable hypothesis is one in which the two frameworks are overlaid such that basic, ubiquitous operations support specialized functions, which are then integrated across domains to yield flexible and adaptive responding (Burkart et al. 2017).

3.2 A Working Model

While recognizing that disagreements on the nature of mentality (i.e., cognitive structure) are unlikely to be resolved in the near future, a model in which specialized abilities build on basic and ubiquitous operations (Shettleworth 2010a) provides a useful heuristic for studying cognition in different animals. For example, if domain-general processes are comparable across species, it should be possible to examine the operations and functions of domain-general processes using a similar set of protocols. This approach has been applied to attention, which is present in species ranging from honeybees to humans, facilitating and supporting adaptive behaviours, such as foraging and mate selection. Comparative studies of the limitations and capacities of attention helped to uncover its plausible structure, leading to the proposal that this multidimensional construct includes at least three separable factors: focusing, scanning, and sustaining attention (Washburn and Taglialetela 2006). It should go without saying that subsequent modifications to this theory must account for research findings from studies using a range of species.

In a separate line of work, comparative studies of domain-specific processes have helped to refine contemporary ideas of cognitive structure. This work often focuses on identifying links between specialized cognitive abilities and distinct environmental demands facing a species. A classic example is superior memory, specifically for spatial locations, in corvid species that rely on food caching to survive harsher winters (Balda and Kamil 1989), supporting the idea that the refinement of domain-specific processing is an adaptation to environmental constraints of a species. The parameters of a memory system that support this behaviour are likely to be functionally incompatible with those that support song learning in birds (Sherry and Schacter 1987). The idea that memory for different types of information may have distinct principles of operation helped to solidify the concept of multiple memory systems, that developed from clinical and preclinical lab studies (Squire and Zola-Morgan 1988).

The role of comparative work in advancing our understanding of domain-specific processing can be extended to other research topics. For example, the idea that separate memory systems are characterized by different properties, constraints, and biological mechanisms was consistent with a modular theory of cognitive structure (Fodor 1983), and with the proposal that adaptations serving one function cannot effectively serve another (Cosmides and Tooby 1994). Further comparative work, however, challenged these models, revealing instead that distinct operations in separate domains need not be functionally incompatible (Jacobs and Gardenfors 2017). Similarly, although anatomical localization of functional systems is consistent with the principles of a multiple memory system model, it is not a prerequisite for domain-specific processing (Glascher et al. 2010). In other words, an organized cognitive structure can be produced by coordinated integration of brain activity across multiple anatomical regions (Duncan et al. 2020). The phenomenon is not limited to humans in that nonhuman primates show similar patterns of activation across multiple neural sites in

response to specific cognitive demands. Comparative work that incorporates contemporary neuroscience approaches can reveal the extent to which this phenomenon extends across phylogeny, possibly revealing new principles of cognitive organization and its evolution.

3.3 Domain-specific Interactions

As described in Section 2, domain-specific cognitive processes can be divided into at least two categories: those that allow a species to interact adaptively with the physical environment and those that allow a species to interact adaptively with the social environment. The first category includes cognitive processes such as spatial navigation, counting, and an understanding of physical causality whereas the second includes communication, theory of mind, and social learning, among others. As with domain-general categories, domain-specific processes are not functionally distinct: adaptive behaviours are supported by interactions within each of these categories. In terms of physical cognition, seasonal migration of many bird species relies on both spatial navigation and timing (i.e., circadian cues) (Wiltschko and Wiltschko 2003). Similarly, within the social domain, a combination of social competence (i.e., an understanding of group hierarchies) and conspecific communication facilitates reproductive success in vervet monkeys (Seyfarth and Cheney 2003).

Additionally, cognitive processes may interact across physical and social domains to produce complex behaviours, such as tool use. Flexible tool use that includes the manufacture, modification, and sequential use of tools is rare yet phylogenetically spread, with well-studied examples from birds (e.g., New Caledonian crows) and nonhuman primates (e.g., chimpanzees and capuchin monkeys). Comparative work suggests that flexible tool behaviours require domain-general processes such as inhibition of prepotent responses, but also specialized attention to relevant physical features of objects (for review, see Visalberghi et al. 2017). Crows, chimps, and capuchins, for example, show some sensitivity to the causal features of tools (e.g., shape, connectivity, rigidity) in learning the association between the tool movement and its outcome (Hoffman et al. 2016). The development of tool use occurs in a social context, though, and is supported by social learning mechanisms: novice tool users observe the behaviour – or outcomes of the behaviour – of local experts. It is thus proposed that complex tool use may only be seen in species with extended parental care or a certain degree of social tolerance which, in turn, creates social learning opportunities (van Schaik et al. 1999). Indeed, species with the greatest contextual diversity of tool use are those with increased reliance on social learning (Visalberghi et al. 2017).

4. Challenges and Next Steps

4.1 Assessing Cognition

The primary challenge in comparative cognition research was articulated more than 100 years ago: “knowledge of the animal mind, like knowledge of human minds ... must come by way of inference from behaviour” (Washburn 1908, page 4). Washburn goes on to note that a first step in this endeavour is the identification of behavioural tests that provide operational definitions of mental activity. The task has become increasingly complex over the last century as evidence accumulates that cognition is a multi-faceted construct. Researchers in this field have long advocated employing multiple tests of the same function (Beran et al. 2014; Bitterman 1975; Macphail 1987; Roitblatt 1987; Shettleworth 2009, 2010a), a triangulation approach that acknowledges the need to examine complex processes (i.e., cognition) from multiple perspectives (Heyes 1993). A goal of this approach is to identify a common set of tasks that tap into specific constructs of cognition (e.g., working memory), which are then linked to underlying biological mechanism. Dividing cognitive constructs into smaller components (e.g., working memory can be parsed into active maintenance, flexible updating, and limited capacity) makes it easier to identify those that are shared among species, under

what conditions, and why (Shettleworth, 2009). In addition, grouping individual components based on commonalities in mechanism or function may uncover relationships among cognitive processes in animals that were not otherwise apparent: a ‘forest rather than trees’ approach that encourages cross-talk among researchers studying different phenomenon (Beran et al. 2014).

Most importantly, the recognition that behavioural measures of cognition in nonhumans must be sensitive to the context in which the behaviour occurs increased the use of ecologically valid paradigms and reduced the tendency for anthropomorphic interpretations of animal behaviour (Shettleworth 2009). At the same time, research that relied on naturalistic behaviours revealed some surprising abilities in nonhumans, including evidence for cognitive faculties such as tool use, numerical competence, and social learning in insects (Chittka et al. 2019). The extent to which these processes are analogous to those in other species has yet to be determined. Finally, any behavioural measure of cognition must yield a range of scores across a population in that the adaptive value of a cognitive process cannot be assessed in the absence of individual variability in these traits (Boogert et al. 2018).

4.2 Diversity of Species Studied

Comparative cognition, like its parent discipline of comparative psychology, consistently faces the question of whether the field is truly comparative (Beran et al. 2014). In the early 20th century, Washburn (1908) summarized contemporary research on animal thought in more than four dozen species, ranging from amoebas to crayfish to cows. By the middle of the century, the number of species represented in comparative psychology publications had declined dramatically, with an increasing number of studies using a single species, most commonly the rat (Bitterman 1960). This tendency is generally attributed to the dominance of behaviourism in psychology, and the ensuing belief that principles of learning were ubiquitous across species. The trend was reversing by the late 1990s, particularly as comparative cognition became an independent field and incorporated methodologies and perspectives from ethology into the discipline (Shettleworth 2009). If the current volume is an accurate reflection, comparative psychology, itself, is broadening the range of species it studies, with different chapters covering research on a variety of invertebrate, reptilian, fish, avian, and mammalian species.

The challenge now facing comparative researchers is that access to many species is declining. Tragically, we know very little about the natural ecology and behaviour of some endangered species (e.g., pangolins), making it difficult to develop policies and practices to ensure their survival (DiPaola et al. 2020). Research in animal cognition can make a valuable contribution to conservation practices by identifying cues, mechanisms, or experiences that could improve the efficacy of behaviourally oriented manipulations (Greggor et al. 2014). As an example, collisions with manmade structures, which are directly linked to population declines of many avian species, could be reduced by practices that incorporate knowledge of attentional biases, social learning, or other cognitive processes displayed by these animals (Martin 2011). In addition, associative learning, specifically taste aversion training, is an effective means to reduce ingestion of cane toads (which are both invasive and toxic) by native Australian northern quolls (O’Donnell 2011); a similar methodology may be a non-lethal means to reduce nest predation by pied crows in South Africa (Ferguson et al. 2021). These cognitive-based approaches are particularly attractive as conservation tools in that they are generally less expensive and easier to implement than traditional methods of animal control (e.g., culling, trapping, translocation, or poisoning), that often introduce ethical concerns of their own.

A separate line of work builds on comparative cognition research to increase the well-being of animals in zoos, helping to improve reproductive success of endangered animals in captivity (MacDonald and Ritvo 2016). Some of these principles are being incorporated into external settings, such as ecotourism, in which high levels of stress may interfere with breeding and other naturalistic behaviours (Pichegru et al. 2016). This work will become increasingly important in the future as the rate and impact of human–animal interactions is likely to increase.

4.3 Ontogeny

Comparative cognition researchers frequently refer to Tinbergen's four questions of behaviour as guiding principles in their field, noting that a comprehensive understanding of any cognitive process requires knowledge of function, phylogeny, ontogeny, and mechanisms. Of these four, there are relatively few theories of cognitive development in animals, particularly compared to human research (Sabbagh 2020). Notable exceptions include communication in songbirds (Searcy and Nowicki 2019) and the mapping of developmental milestones in chimpanzees (Brundl et al. 2021). Admittedly, the task is not straightforward, particularly when research on animal cognition is conducted in the natural environment. One of the biggest challenges in this work is disentangling ontogeny from phylogeny, particularly as environmental experience can dramatically alter biological systems that support cognition. For example, a larger hippocampal volume in food storing birds could reflect an adaptation to ecological constraints of food shortage, increased experience with caching and recovering food, or a combination of the two (Shettleworth 2012).

Despite these difficulties, comparative cognition research would be enriched by a wider discussion of developmental processes in nonhumans, specifically how cognition emerges and adapts over a lifetime. As an example, individual differences in cognitive abilities are often exacerbated as humans age, but it is not clear whether this is a general principle of neurobiological development or a byproduct of human society and culture. In addition, the performance of very young children on many cognitive tasks (e.g., theory of mind, numerosity, physical causality) is often closer to that of animals than to human adults (Shettleworth 2012), but how these processes emerge in young animals is largely unknown. Importantly, comparative studies of cognitive development should not be limited to early life in that changes in cognition are likely to occur across the lifespan in species other than humans. The time may be ripe to undertake this work as recent technological advances in molecular biology (i.e., epigenetic) provide exciting new opportunities to understand the relationship between maturational and experiential factors in shaping cognition.

5. Conclusion

A primary goal of comparative cognition research is to further our understanding of cognitive evolution (Roitblatt 1987). As outlined in this chapter, the work may also provide insight into principles that govern these two independent subjects (i.e., cognition and evolution). Indeed, more than half a century beyond the establishment of cognitive science as an independent discipline, unified theories of mental structure, as well as descriptions of operations that may instantiate such theories, are lacking (Laird et al. 2017). Comparative studies could inform these discussions, potentially leading to novel conceptualizations of how general and specialized cognitive processes may be linked, both functionally and mechanistically (Burkart et al. 2017). In terms of understanding evolution, the use of sophisticated molecular biology tools combined with large-scale data collection across a variety of species has allowed researchers to reconstruct phylogenetic maps of animal cognition (Emery 2017). A complementary line of work employing ecologically valid paradigms revealed how similar cognitive processes emerged in distantly related species, reinforcing the tenet that evolution is not restricted to homology (Emery and Clayton 2004). Finally, the primary message of all comparative work, cognition or otherwise, is that diversity is critical for survival, both within and across species.

Note

1. As we frequently ask our students, how could learning be present without memory (and vice versa)? And if it were, how would it be measured?

Acknowledgements

This work was supported by Discovery Grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) to Mary C. Olmstead and Valerie A. Kuhlmeier.

Queen's University is situated on traditional Anishinaabe and Haudenosaunee Territory.

References

- Abramson, C.I. 2003. Charles Henry Turner: Contributions of a forgotten African American to honey bee research. *American Bee Journal*, 143:643–644.
- Abramson, C.I. 2015. A crisis in comparative psychology: Where have all the undergraduates gone? Additional comments. *Comprehensive Psychology*, 4:7.
- Ashcraft, M.H. & Klein, R. 2010. *Cognition*. Toronto: Pearson Canada.
- Balda, R.P. & Kamil, A.C. 1992. Long-term spatial memory in Clark's nutcracker, *Nucifraga Columbiana*. *Animal Behaviour*, 44:761–769.
- Balda, R.P. & Kamil, A.C. 2006. The ecology and life histories of seed caching corvids. In M.F. Brown & R.G. Cook (eds.) *Animal Spatial Cognition: Comparative, Neural, and Computational Approaches*, ed. M.F. Brown & R.G. Cook (On-line) Available at www.pigeon.psy.tufts.edu.
- Bayne, T., Brainard, D., Byrne, R.W., Chittka, L., Clayton, N., Heyes, C., Mather, J., Olveczky, B., Shadlen, M., Suddendorf, T., and Webb, B. 2019. What is cognition? *Current Biology*, 29:R603–R622.
- Bayrakdar, M. 1983. Al-Jahiz and the rise of biological evolution. *Islamic Quarterly*, 27:307–315.
- Beer, C. 2020. Niko Tinbergen and questions of instinct. *Animal Behaviour*, 164:261–265.
- Beran, M.J., Parrish, A.E., Perdue, B.M., & Washburn, D.A. 2014. Comparative cognition: past, present, and future. *International Journal of Comparative Psychology*, 27(1):3–30.
- Bitterman, M.E. 1960. Toward a comparative psychology of learning. *American Psychologist*, 15:704–712.
- Bitterman, M.E. 1975. The comparative analysis of learning. *Science*, 188:699–709.
- Boogert, N.J., Madden, J.R., Morrand-Ferron, J., & Thornton, A. 2018. Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society B*, 373:20170280.
- Bruchac, J. 1992. *Native American Animal Stories*. Minneapolis: Birchbark Books.
- Brundl, A.C., Tkaczynski, P.J., Kohou, G.N., Boesch, C., Wittig, R.M., & Cockford, C. 2021 Systematic mapping of developmental milestones in wild chimpanzees. *Developmental Science*, 24:e12988.
- Burghardt, G.M. 2019. A place for emotions in behavior systems research. *Behavioural Processes*, 166:1–7.
- Burghardt, G.M. 2020. Insights found in century-old writings on animal behaviour and some cautions for today. *Animal Behaviour*, 16:241–249.
- Burkart, J.M., Schubiger, M.N. & van Schaik, C.P. 2017. The evolution of general intelligence. *Behavioral and Brain Sciences*, e195:1–67.
- Chaney, D.W. 2013. An overview of the first use of the terms *cognition* and *behavior*. *Behavioral Sciences*, 3:143–153.
- Chittka, L., Giurfa, M. and Riffell, J.A. 2019. Editorial: The mechanisms of insect cognition. *Frontiers in Psychology*, 10:1–3.
- Chomsky, N. 1959. A review of Skinner's Verbal behavior. *Language*, 35:26–58.
- Chomsky, N. 1968. *Language and the Mind*. New York: Harcourt Brace Jovanovich.
- Cosmides, L. & Tooby, J. 1994. Origins of domain specificity: the evolution of functional organization, in *Mapping the Mind: Domain Specificity in Cognition and Culture*, ed. L. Hirschfeld & S. Gelman. Cambridge: Cambridge University Press, pp.85–116.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London UK: John Murray.
- DiPaola, J.D., Yindee, M. & Plotnik, J.M. 2020. Investigating the use of sensory information to detect and track prey by the Sunda pangolin (*Manis javanica*) with conservation in mind. *Scientific Reports*, 10(1):9787.
- Dugatkin, L.A. 2014. *Principles of Animal Behavior*. 3rd edition. New York: Norton & Company.
- Duncan, J., Assem, M., & Shashidhara S. 2020. Integrated intelligence from distributed brain activity. *Trends in Cognitive Sciences*, 24(10):838–852.
- Emery, N. 2017. Evolution of learning and cognition, in *APA Handbook of Comparative Psychology*, ed. J. Call et al. Washington: American Psychological Association: 237–256.
- Emery, N. & Clayton, N.S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306:1903–1907.
- Ferguson, A.J., Thomson, R.L., Nelson-Flower, M.J., & Flower, T.P. 2021. Conditioned food aversion reduces crow nest predation: an improved framework for CRA trials. *Journal for Natural Conservation* 60, 125970.
- Fodor, J.A. 1983. *Modularity of the Mind*. Boston: MIT Press.

- Gallistel, C.R. 1998. The replacement of general-purpose learning models with adaptively specialized learning modules, in *The Cognitive Neurosciences*, ed. M.S. Gazzaniga, 2nd edition. Cambridge: MIT Press:1179–1191.
- Garcia, J. & Koelling, R.A. 1966. Relation of cue to consequence in avoidance learning. *Psychonomic Science*, 4:123–124.
- Greenberg, G., & Haraway, M. M. 2002. *Principles of Comparative Psychology*. Boston: Allyn & Bacon.
- Giurfa, M. & de Brito Sanchez, M.G. 2020. Black lives matter: Revisiting Charles Henry Turner's experiments on honey bee color vision. *Current Biology*, 30:R1233–1255.
- Glascher, J., Rudrauf, D., Colom, R., Paul, L.K., Tranel., Damasio, H., & Adolphs, R. 2010. Distributed neural system for general intelligence revealed by lesion mapping. *Proceedings of the National Academy of Sciences*, 107(10):4705–4709.
- Greggor, A.L., Clayton, N.S., Phalan, B., & Thornton, A. 2021. Comparative cognition for conservationists. *Trends in Ecology and Evolution*, 29(9):489–495.
- Griffin A.S., Guillette, L.M. & Healy S.D. 2015. Cognition and personality: an analysis of an emerging field. *Trends in Ecology and Evolution*, 30(4):207–214.
- Guessoum, N. 2011. *Islam's Quantum Question: Reconciling Muslim Tradition and Modern Science*. London: IB Tauris.
- Hebb, D.O. 1949. *The Organization of Behavior*. New York: John Wiley.
- Heyes, C.M. 1993. Anecdotes, graining, trapping and triangulation: Do animals attribute mental states? *Animal Behaviour*, 14:443–451.
- Hoffman, M.M., Cheke, L.G. & Clayton, N.S. 2016. Western scrub jays (*Aphelocoma californica*) solve multiple-string problems by the spatial relation of string and reward. *Animal Cognition*, 19:1103–1114.
- Hulse, S.H. (2006). Postscript: An essay on the study of cognition in animals. In. *Comparative Cognition*, ed. E.A. Wasserman and T.R. Zentall, pp. 668–678. New York: Oxford University Press.
- Jacobs I. & Gardenfors, P. 2017. The false dichotomy of domain-specific versus domain-general cognition. *Behavioral and Brain Sciences*, e195:34–35.
- Jerison, H.J. 1973. *Evolution of the Brain and Intelligence*. New York: Academic Press.
- King, D.B., Winey, W. & Woody, W.D. 2013. *A History of Psychology: Ideas and Context*. 5th edition. New York: Routledge.
- Kohler, W. 1925. *The Mentality of Apes*. New York: Harcourt.
- Lachman, R., Lachman, J.L. & Butterfield, E.C. 1979. *Cognitive Psychology and Information Processing: An Introduction*. Hillsdale: Erlbaum.
- Laird, J.E., Lebiere, C. & Rosenbloom, P.S. 2017. A standard model of the mind: Toward a common computational framework across artificial intelligence, cognitive science, neuroscience, and robotics. *AI Magazine*, 38(4):13–26.
- Laland, K. & Seed, A. 2021. Understanding human cognitive uniqueness. *Annual Review of Psychology*, 72:689–716.
- Lee, D.N. 2020. Diversity and including activism in animal behaviour and the ABS: a historical view from the U.S.A. *Animal Behaviour*, 16:273–280.
- Leroi, A.M. 2014. *The Lagoon: How Aristotle Invented Science*. London: Bloomsbury.
- Lorenz, K. 1950. The comparative method in studying innate behaviour patterns. *Symposia of the Society for Experimental Biology*, 4:221–268.
- MacDonald, S.E. & Ritvo, S. 2016. Comparative cognition outside the laboratory. *Comparative Cognition and Behavior Reviews*, 11:49–61,
- Macphail, E.M. 1987. The comparative psychology of intelligence. *Behavioral and Brain Sciences*, 10:645–695.
- Maier, N.R.F. & Schneirla, T.C. 1935. *Principles of Animal Psychology*. New York: Dover.
- Malik, A.H., Ziermann, J.N. & Diogo, R. 2017. An untold story in biology: The historical continuity of evolutionary ideas of Muslim scholars from the 8th century to Darwin's time. *Journal of Biological Education*. DOI:10.1080/00219266.2016.1268190
- Martin, G.R. 2011. Understanding bird collisions with man-made objects: a sensory ecology approach. *Ibis: International Journal of Avian Science*, 153:239–254.
- McMillan, N, & Sturdy, C.B. 2015. Commentary: A crisis in comparative psychology: where have all the undergraduates gone? *Frontiers in Psychology*, 6:1589.
- Morand-Ferron, J., Cole, E.F. & Quinn, J.L. 2016. Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological Reviews*, 91(2):367–389.
- Morgan, C.L. 1894. *An Introduction to Comparative Psychology*. London: Walter Scott.
- Neisser, U. 1967. *Cognitive Psychology*. New York: Appleton-Century-Croft.
- O'Donnell, S., Webb, J.K. & Shine, R. 2011. Conditioned taste aversion enhanced the survival of an endangered predator imperiled by a toxic invader. *Journal of Applied Ecology*, 47:558–565.
- Pearce, J.M. 2008. *Animal Learning and Cognition*. 3rd edition. New York: Psychology Press.

- Pichegru, L., Edwards, T.B., Dilley, B.J., & Flower, T.P. 2016. African Penguin tolerance to humans depends on historical exposure at colony level. *Bird Conservation International*, 26(3):307–322
- Pierotti, R. 2015. Indigenous concepts of ‘living systems’: Aristotelian ‘soul’ meets constructual theory. *Ethnobiology Letters*, 6(1):80–88.
- Poirier, M.A., Kozlovsky, D.Y., Morrand-Ferron, J., & Careau, V. 2020. How general is cognitive ability in non-human animals? A meta-analytical and multi-level reanalysis approach. *Proceedings Biological Sciences*, 287(1940):20221853.
- Romanes, G.J. 1892. *Animal Intelligence*. New York: Appleton and Company.
- Roitblatt, H.L. 1987. *Introduction to Comparative Cognition*. New York: Freeman and Co.
- Sabbagh, M.A. 2020. Cognitive development: Neurobiological foundations and contemporary directions, in *Encyclopedia of Infant and Early Childhood Development*, ed. J.B. Benson. 2nd edition. Amsterdam: Elsevier, pp. 317–326.
- Searcy, W.A. & Nowicki, S. 2019. Birdsong learning, avian cognition and the evolution of language. *Animal Behaviour*, 151:271–227.
- Seyfarth, R.M. & Cheney, D.L. 2003. The structure of social knowledge in monkeys. In *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*, ed. F.B.M. de Waal & P.L. Tyak. Cambridge: Harvard University Press, pp. 207–229.
- Shapiro, K.L., Jacobs, W.J. & LoLordo, V.M. 1980. Stimulus-reinforcer interactions in Pavlovian conditioning of pigeons: Implications for selective associations. *Animal Learning and Behavior*, 8(4):586–594.
- Shettleworth, S.J. 1972. Constraints on learning. In *Advances in the Study of Behavior*, ed. D.S. Lehrman, R.A. Hinde, & E. Shaw, 4:1–68. New York: Academic Press.
- Shettleworth, S.J. 2009. The evolution of comparative cognition: Is the snark still a boojum? *Behavioural Processes*, (80):210–217.
- Shettleworth, S.J. 2010a. *Cognition, Evolution, and Behavior*. Oxford: Oxford University Press.
- Shettleworth, S.J. 2010b. Q & A: Sara J. Shettleworth. *Current Biology*, 20(21):R910–R911.
- Shettleworth, S.J. 2012. Modularity, comparative cognition and human uniqueness. *Philosophical Transactions of the Royal Society B*, 367:2794–2802.
- Sherry, D. & Schacter, D.L. 1987. The evolution of multiple memory systems. *Psychological Review*, 94:439–454.
- Squire, L.R. & Zola-Morgan, S. 1988. Memory: Brain systems and behavior. *Trends in Neuroscience*, 11:170–175.
- Striedter, G.F. (2005). *Principles of Brain Evolution*. Sunderland: Sinauer Associates.
- Thorndike, E.L. 1911. *Animal Intelligence*. New York: Macmillan.
- Tinbergen, N. 1951. *The Study of Instinct*. Oxford: Oxford University Press.
- Tolman, E.C. 1932. *Purposive Behavior in Animals and Men*. New York: Appleton Century-Crofts.
- Van Schaik, C.P., Deaner, R.O. & Merrill, M.Y. 1999. The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, 36:719–741.
- Visalberghi, E., Sabbatini, G., & Taylor, A.H. 2017. Cognitive insights from tool use in nonhuman animals. In J. Call et al., *APA Handbook of Comparative Psychology: Perception, Learning, and Cognition*, ed. J. Call et al. Washington: American Psychological Association.
- Wallace, A.R. 1869. Principles of geology (review). *Quarterly Review*, 126:359–451.
- Washburn, D.A. 2010. The animal mind at 100. *The Psychological Record*, 60:369–376.
- Washburn, D.A. & Tagliatela, L.A. 2006. Attention as it is manifest across species, in *Comparative Cognition*, ed. T.R. Zentall and E.A. Wasserman. Oxford: Oxford University Press, pp.127–142.
- Washburn, M.F. 1908. *The Animal Mind*. New York: Macmillan.
- Wasserman, E.A. & Zentall, T.R. 2006. Introduction, in *The Oxford Handbook of Comparative Cognition*, ed. T.R. Zentall and E.A. Wasserman. Oxford: Oxford University Press, pp.1–8.
- Watson, J.B. 1913. Psychology as a behaviorist views it. *Psychological Review*, 20:158–177.
- Wiltschko, R. & Wiltschko, W. 2003. Avian migration: from historical to modern concepts, *Animal Behaviour*, 65:257–272.