

Avian Cognition

Edited by Carel ten Cate
and Susan D. Healy



Avian Cognition

The cognitive abilities of birds are remarkable: hummingbirds integrate spatial and temporal information about food sources, day-old chicks have a sense of numbers, parrots can make and use tools and ravens have sophisticated insights in social relationships. This volume describes the full range of avian cognitive abilities, the mechanisms behind such abilities and how they relate to the ecology of the species.

Synthesising the latest research in avian cognition, a range of experts in the field provide first-hand insights into experimental procedures, outcomes and theoretical advances, including a discussion of how the findings in birds relate to the cognitive abilities of other species, including humans. The authors cover a range of topics such as spatial cognition, social learning, tool use, perceptual categorization and concept learning, providing the broader context for students and researchers interested in the current state of avian cognition research, its key questions and appropriate experimental approaches.

Carel ten Cate is Professor of Animal Behaviour at Universiteit Leiden, the Netherlands. His research focuses on behavioural development and communication by vocal and visual signals in species ranging from birds and fish to humans. He also uses birds for comparative studies on the cognitive mechanisms relevant for speech and language processing in humans.

Susan D. Healy is a Reader in Zoology at the University of St Andrews, Scotland and Executive Editor of *Animal Behaviour*. Her work integrates theoretical and empirical data from the fields of biology and psychology to investigate the behavioural ecology and neurobiology of animal cognition, with a focus on birds.

Avian Cognition

Edited by

CAREL TEN CATE

Leiden University

SUSAN D. HEALY

University of St Andrews



CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom
One Liberty Plaza, 20th Floor, New York, NY 10006, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
4843/24, 2nd Floor, Ansari Road, Daryaganj, Delhi - 110002, India
79 Anson Road, #06-04/06, Singapore 079906

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning and research at the highest international levels of excellence.

www.cambridge.org

Information on this title: www.cambridge.org/9781107092389

DOI: [10.1017/9781316135976](https://doi.org/10.1017/9781316135976)

© Cambridge University Press 2017

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.

First published 2017

Printed in the United Kingdom by TJ International Ltd. Padstow Cornwall in May 2017.

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

Library of Congress Cataloging-in-Publication data

Names: Cate, Carel ten, editor. | Healy, Sue, editor.

Title: Avian cognition / [edited by] Carel ten Cate, Universiteit Leiden, Sue Healy, University of St Andrews.

Description: New York, NY : Cambridge University Press, 2017.

Identifiers: LCCN 2017005184 | ISBN 9781107092389

Subjects: LCSH: Birds – Psychology. | Birds – Behavior. | Cognition in animals.

Classification: LCC QL698.3.A95 2017 | DDC 598.15 – dc23

LC record available at <https://lccn.loc.gov/2017005184>

ISBN 978-1-107-09238-9 Hardback

Cambridge University Press 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.

Contents

	<i>List of Contributors</i>	page vii
	<i>Preface</i>	x
1	Introduction: Avian Cognition – Why and What? Carel ten Cate and Susan D. Healy	1
2	Spatial Cognition in Birds James F. Reichert, Sebastian Schwarz and Debbie M. Kelly	6
3	Spatial Cognition and Ecology: Hummingbirds as a Case Study Susan D. Healy and T. Andrew Hurly	30
4	Food Storing and Memory David F. Sherry	52
5	Avian Cognition and the Evolution of Warning Signals Candy Rowe, John Skelhorn and Christina G. Halpin	75
6	Social Learning and Innovation Louis Lefebvre and Lucy M. Aplin	93
7	Solving Foraging Problems: Top-down and Bottom-up Perspectives on the Role of Cognition Andrea S. Griffin and David Guez	119
8	Objects and Space in an Avian Brain Giorgio Vallortigara and Cinzia Chiandetti	141
9	Physical Cognition and Tool Use in Birds Alice Auersperg, Irmgard Teschke and Sabine Tebbich	163
10	Avian Numerical Cognition: A Review and Brief Comparisons to Non-Avian Species Irene M. Pepperberg	184

11	Mechanisms of Perceptual Categorization in Birds	208
	Ludwig Huber and Ulrike Aust	
12	Relational Concept Learning in Birds	229
	Leyre Castro and Edward A. Wasserman	
13	The Linguistic Abilities of Birds	249
	Carel ten Cate	
14	Avian Vocal Perception: Bioacoustics and Perceptual Mechanisms	270
	Neil McMillan, Marc T. Avey, Laurie L. Bloomfield, Lauren M. Guillette, Allison H. Hahn, Marisa Hoeschele and Christopher B. Sturdy	
15	Sing Me Something Smart: Does Song Signal Cognition?	296
	Neeltje J. Boogert	
16	Avian Social Relations, Social Cognition and Cooperation	314
	Thomas Bugnyar and Jorg J. M. Massen	
	<i>Index</i>	337

Contributors

Lucy M. Aplin

Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, UK

Alice Auersperg

Messerli Research Institute, University of Veterinary Medicine, Medical University of Vienna, University of Vienna, Vienna, Austria

Ulrike Aust

Messerli Research Institute, University of Veterinary Medicine, Medical University of Vienna, University of Vienna, Vienna, Austria

Marc T. Avey

Ottawa Hospital Research Institute, Ottawa Hospital, Ottawa, Canada

Laurie L. Bloomfield

Department of Psychology, Algoma University, Sault Ste. Marie, Canada

Neeltje J. Boogert

Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, UK

Thomas Bugnyar

Department of Cognitive Biology, University of Vienna, Vienna, Austria

Leyre Castro

Department of Psychology, University of Iowa, Iowa City, Iowa, USA

Cinzia Chiandetti

Department of Life Sciences, University of Trieste, Trieste, Italy

Andrea S. Griffin

School of Psychology, University of Newcastle, Callaghan, Australia

David Guez

School of Psychology, University of Newcastle, Callaghan, Australia

Lauren M. Guillette

School of Biology, University of St Andrews, St Andrews, UK

Allison Hahn

Department of Psychology, University of Alberta, Edmonton, Canada

Christina G. Halpin

Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Newcastle, UK

Susan D. Healy

School of Biology, University of St Andrews, St Andrews, UK

Marisa Hoeschele

Department of Cognitive Biology, University of Vienna, Vienna, Austria

Ludwig Huber

Messerli Research Institute, University of Veterinary Medicine, Medical University of Vienna, University of Vienna, Vienna, Austria

T. Andrew Hurly

Department of Biological Sciences, University of Lethbridge, Lethbridge, Canada

Debbie M. Kelly

University of Manitoba, Winnipeg, Canada

Louis Lefebvre

Department of Biology, McGill University, Montreal, Canada

Jorg J.M. Massen

Department of Cognitive Biology, University of Vienna, Vienna, Austria

Neil McMillan

Department of Psychology, University of Alberta, Edmonton, Canada

Irene M. Pepperberg

Department of Psychology, Harvard University, Cambridge, Massachusetts, USA

James F. Reichert

University of Manitoba, Winnipeg, Canada

Candy Rowe

Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Newcastle, UK

Sebastian Schwarz

University of Manitoba, Winnipeg, Canada

David F. Sherry

Department of Psychology, Western University, London, Ontario, Canada

John Skelhorn

Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Newcastle, UK

Christopher B. Sturdy

Department of Psychology, Neuroscience and Mental Health Institute, University of Alberta, Edmonton, Canada

Sabine Tebbich

Department of Cognitive Biology, University of Vienna, Vienna, Austria

Carel ten Cate

Institute of Biology Leiden, Leiden Institute for Brain and Cognition, Leiden University, Leiden, the Netherlands

Irmgard Teschke

Department of Cognitive Biology, University of Vienna, Vienna, Austria

Giorgio Vallortigara

Centre for Mind-Brain Sciences, University of Trento, Rovereto, Italy

Edward E. Wasserman

Department of Psychology, University of Iowa, Iowa City, Iowa, USA

Preface

In the 1980s the emergence of behavioural ecology significantly changed the study of animal behaviour. It shifted the focus of many researchers from studying causal mechanisms to addressing the adaptive significance and costs and benefits of the way in which animals behaved. We are currently witnessing a similar shift in focus, one in which researchers are asking and addressing questions about the cognitive processes that underlie animal behaviour. This shift is visible in the rapidly expanding field of animal cognition where the focus is on analysing the nature and development of the ‘knowledge’ that enables animals to respond to the challenges they face in their daily life: going to the right place at the right moment, getting the food they need, dealing with conspecifics, and so on. These are intriguing questions and their answers not only tell us something about how animals ‘think’, but may also provide a window on the origin of our own thinking. Although primates, apes in particular, have long been the main group to which these questions have been addressed, more recently birds have emerged as the focus of attention. Birds show a diverse range of mental abilities, which are proving accessible to systematic research. Against this background, we organised an ‘Avian Cognition’ symposium at the International Ethological Congress in Newcastle, UK in 2013. It attracted a lot of interest and when we organised another one at the next meeting in Cairns, Australia in 2015, it was even more popular.

This volume arose out of the interest shown for these symposia. It became clear that many people would like to know more about the questions and progress of the field. It inspired us to invite colleagues working at the forefront of avian cognition to contribute to a book on the topic. We got enthusiastic responses, as well as stimulating support for the idea from Cambridge University Press, resulting in what has become this book. Right from the start we wanted it to be a book that would be of interest to those working in the field, reviewing the current state of knowledge, while at the same time being accessible for a broader audience consisting of interested researchers from other areas as well as suitable for (graduate) student seminars. We challenged our contributors to review relevant work beyond their own studies, to draw comparisons both among bird species as well as between birds and other species, including humans, and to keep their writing understandable. We thank all our authors for their great contributions (and for their patience with dealing with our comments). It has been a very rewarding exercise to collect all the wonderful work presented in this book. We hope it will be similarly rewarding to those reading it and that it will contribute to advancing the topic!

Carel ten Cate and Susan D. Healy
November 2016

1 Introduction: Avian Cognition – Why and What?

Carel ten Cate and Susan D. Healy

We, humans, are amazing animals. We devise and use tools to do things we would not be able to do otherwise; we can remember how we solved a problem in the past and use this knowledge to solve a current problem; we can plan ahead; we can distinguish and categorise objects on abstract as well as on functional properties; we can communicate about events in the past, present or the future; we form complex social networks, and so on. Not only do we take these abilities for granted, many people assume they demonstrate our cognitive superiority over other animal species. However, many non-human animals also do amazing things: New Caledonian crows can manufacture tools to extract food from wood logs, chimpanzees tell each other what kind of predator is in the vicinity, honey bees tell their sisters where to find food, racing pigeons return to their home loft from hundreds of miles away and bottlenose dolphins coordinate their hunting. These are just a very few of the examples that give rise to questions about how these animals are able to do what they do: Do they have an ‘understanding’ of the situation? What characterises this ‘understanding’? And how do the mechanisms involved relate to those of humans? Such questions are core to the study of animal cognition.

Animal Cognition

Analogous to the study of human cognition, the study of animal cognition examines how animals perceive, process, learn, store and use information (Shettleworth, 2010). It asks for the kind of knowledge and the mechanisms that enable animals to behave as described above, how the relevant knowledge has been acquired and how that knowledge is used to produce the behaviour observed. The focus in this field is on observing behaviour followed by experimental manipulations to test how the behaviour is brought about. Animals may or may not have private experiences like consciousness or feelings related to their behaviour, but because these experiences are private it is difficult to access them. Animals may behave *as if* they have ‘thought’ about how to solve a problem, and their behaviour may suggest forward planning or causal reasoning, but we can measure only their behavioural solutions to the problem and how and what kind of previous experiences and contextual information affect that solution. Fortunately, as demonstrated by the chapters in this book, this approach to the study of animal cognition is very successful.

Research Questions

The wonder about the remarkable abilities that animals display in their daily lives is what drives many researchers to study animal cognition. These animal abilities give rise to different types of questions similar to those formulated by Tinbergen (1963) for the study of animal behaviour: what are the underlying mechanisms (how is it done?), how does the ability develop (what experiences affect its emergence?), how did it evolve (what was its origin, what are the selection pressures?) and is it adaptive (i.e. do the animals that have the cognitive ability leave more offspring?). While many researchers find their inspiration for research questions in the natural abilities of animals, others find their inspiration in the cognitive abilities of humans and wonder where they come from and how they relate to those of non-human animal species: to what extent do other species and humans solve the problem at hand by the same mechanisms? Are there general principles that apply to humans and non-human animals alike? In the past, the distinction between these two types of researchers was related to differences in the research traditions that gave rise to them: behavioural ecology and the study of animal behaviour versus comparative psychology. Both approaches have a lot to offer and it is therefore encouraging to see that there has been a merger of these approaches over the years. This is also reflected in the contents of this book, with contributions by people from a wide range of backgrounds.

Why Birds?

If examples of remarkable cognitive abilities can be found among many species, ranging from insects to mammals, why then single out birds? One trivial reason is that the field of animal cognition is flourishing and broad. Rather than attempting to capture everything, a focus on a single clade enables a more comprehensive and coherent treatment of the main topics addressed for that clade. Birds form a very interesting group for such a focus. With over 10,000 species, birds are a species-rich and without doubt the most conspicuous, vertebrate clade. They are present on every continent and in all environments, whether it is the center of a busy city, a remote oceanic island or a pristine rain forest, and their presence is usually well visible and audible. It is thus no wonder that they have always drawn the interest of researchers of animal behaviour. Both Niko Tinbergen and Konrad Lorenz, two of the three men awarded the Nobel Prize for founding the study of animal behaviour, derived many of their ideas from studying birds. Later researchers have followed in their footsteps with the result being an extensive knowledge about bird behaviour and a wealth of examples of apparently sophisticated abilities like tool use, spatial orientation, concept formation, episodic-like memory and others. Across the chapters in this book, we aim to present an overview of what is known about the cognitive processes underlying such abilities.

We focus on birds also because studies on their cognitive abilities are increasingly demonstrating that many birds appear able to match some or all of the abilities of the primates, often considered the most 'intelligent' of animals (e.g. Emery & Clayton, 2004). These cognitive similarities are intriguing as there is an extensive phylogenetic

gap that separates birds from mammals. The current-day insights are that the ancestor of modern birds arose from theropod dinosaurs during the Cretaceous period, around 100 million years ago, and lived alongside the earliest mammals. Dinosaurs and mammals, in turn, are assumed to have evolved from a common reptile-like stem amniote ancestor that lived over 310 million years ago. Although it is possible that cognitive abilities that are shared between some, but not all, mammals and birds might originate from this common ancestor, it is more likely that such similar abilities arose by independent, but convergent evolution. This will certainly hold for similarities in more specialised abilities. Comparing birds with other taxa thus provides the opportunity to examine which selection pressures might have been at work to shape particular cognitive abilities, to determine whether functionally similar behaviours in different taxa result from similar cognitive mechanisms, and to compare their neural instantiation. Take, for example, vocal learning. Humans acquire speech and language by being exposed to spoken language. Although such vocal learning occurs in a few other mammal groups, like cetaceans and bats, humans are the only primate species that learn their vocalisations. Among non-mammalian vertebrates, vocal learning is known only from birds, where it occurs in hummingbirds, parrots, songbirds and some suboscines. Investigation of vocal learning by songbirds has revealed striking similarities with vocal learning in humans: the learning proceeds without instruction, there is a sensitive phase for learning early in life, the learning process is canalised with respect to the sounds that are most readily learned, social interactions affect the model chosen for copying, perceptual learning of the relevant sounds precedes the production, and the development is characterised by a babbling phase in which the output is gradually shaped into the adult form by auditory feedback (e.g. Doupe & Kuhl, 1999). Comparing such commonalities between birds and distant taxa can provide insights into the essential or inevitable components of cognitive abilities or on the selection pressures giving rise to them.

Cognition and the Bird Brain

Cognitive similarities at the behavioural level also raise questions about the underlying neural mechanisms. And here is another reason why birds are of interest. In their gross anatomy, the bird and mammal brain share a general vertebrate brain structure, consisting of a hindbrain, midbrain, cerebellum, thalamus and telencephalon. Of these regions, the vertebrate telencephalon is the most variable. Mammals show a strong proliferation of the outer areas of the telencephalon, which includes a layered neocortex. This neocortex is involved in many cognitive processes and for a long time, the bird brain was considered to be more ‘primitive’ with relatively large basal ganglia but no neocortex. In 2004, however, based on detailed studies of nervous connectivity plus neuromolecular and developmental evidence, a large consortium of avian neuroscientists concluded that a large part of the avian telencephalon should be considered similar in its neurobiological characteristics as well as its functionality to the mammalian neocortex (Jarvis et al., 2005). So, although superficially different, the brains of birds and mammals may be homologous. This has been confirmed for vocal learning, as discussed above, for which known functionally convergent neural circuits in songbirds and humans also show

convergent molecular changes and expression of multiple genes. These similarities are both striking and intriguing as they suggest that brain circuits for complex traits may be constrained in how they evolved from a common ancestor (Pfenning et al., 2014), despite millions of years of evolutionary separation. It makes birds a group that is all the more interesting for examining whether other behavioural similarities between birds and mammals are also based on neuromolecular similarities or whether functionally similar behaviour results from different underlying mechanisms.

This Book

The breadth of research in avian cognition is reflected in the contents of this book, which aims to provide an overview of the current state of the field. Its emphasis is on the behavioural rather than the neural analysis of cognitive processes.

The first chapters that follow this one concern spatial orientation and food storing. In [Chapter 2](#), Reichert et al. deal with the ways in which birds orient themselves in space: what environmental features do they use and how are various types of information (the use of landmarks and geometry) weighted against each other? While this chapter covers a lot of laboratory experiments on the issue, in [Chapter 3](#), Healy and Hurly show that spatial cognition can be studied in the field and address how spatial and temporal information about food sources is integrated. In [Chapter 4](#), Sherry describes what food-storing birds remember about caches and discusses the neural basis and processes underlying the spatial learning and memory consolidation involved in food storing. In [Chapter 5](#), Rowe et al. discuss how aversive experience with insect prey, combined with specific perceptual and learning biases of their avian predators, may affect the evolution of warning colours in those prey, thereby demonstrating how cognitive processes may shape evolutionary outcomes. In the two chapters that follow, the authors deal with the relationship between innovation in the context of acquiring novel feeding behaviours and the cognitive processes involved: in [Chapter 6](#), Lefebvre and Aplin focus in particular on how innovations may spread within populations via social learning, while in [Chapter 7](#), Griffin and Guez discuss the relationship between innovation and cognition. Vallortigara and Chiandetti, in [Chapter 8](#), examine the extent to which several basic cognitive abilities that relate to physical cognition, space and numbers are already present in day-old chicks and whether this indicates their universal nature. Physical cognition is also the topic of [Chapter 9](#), in which Auersperg et al. discuss the processes underlying tool use by birds. Pepperberg reviews numerical cognition in birds in [Chapter 10](#). Numerical cognition also deals with the question as to whether birds can form abstract number concepts. Abstract concepts are also needed to deal with objects and their relationships, such as being the same or different. The three chapters that follow cover the cognitive processes of concept formation and categorisation: in [Chapter 11](#), Huber and Aust describe whether and how birds can form perceptual categories at different levels of abstraction and in [Chapter 12](#), Castro and Wasserman cover relational concept learning. While these chapters concentrate on the processing of visual input, in [Chapter 13](#) ten Cate concentrates on the processing of auditory input by birds and the

extent to which birds can detect abstract regularities in auditory input. In [Chapter 14](#), Avey et al. also deal with auditory processing, but with emphasis on the bioacoustics and perceptual mechanisms involved in processing natural vocalisations. Boogert in [Chapter 15](#) examines the relationship between song and other cognitive abilities especially with regard to mate choice. Finally, in [Chapter 16](#), Bugnyar and Massen review what is known about the cognitive abilities that birds display in their social relationships.

What's Next?

The contents of this book reflect the insights obtained in many domains of avian cognition as well as the ways in which studies of avian cognition contribute to insights in cognitive processes in general. The contents also reflect a number of questions that are still unanswered and topics that have only just begun to be explored. They show that the field is dynamic and also that views of different researchers are sometimes divergent. There are thus ample topics for future research. Apart from specific abilities of (some) birds there are also general questions waiting to be resolved, such as whether and how various cognitive abilities are related to each other; what socioecological factors drive the evolution of cognitive abilities; and what is the relationship between variation in personalities and cognitive abilities. Of course, many more topics lend themselves for further study and are worthwhile pursuing. The presence of many bird species that can be studied both in the laboratory and in the field and under a wide range of conditions make them very well suited to address such questions. Their study will enable comparison with similar studies in other animal taxa, thereby shedding light on how universal certain abilities are and how they might have evolved. They may also provide ideas on the origin and evolution of human cognitive abilities. We hope this book will provide a useful and inspiring basis for such studies.

References

- Doupe, A. J. and Kuhl, P. K. (1999). Birdsong and human speech: Common themes and mechanisms. *Annual Review of Neuroscience*, **22**, 567–631. DOI:10.1146/annurev.neuro.22.1.567
- Emery, N. J. and Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*, **306**, 1903–1907.
- Jarvis, E. D., Güntürkün, O., Bruce, L., et al. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience*, **6**, 151–159. DOI:10.1038/nrn1606
- Pfennig, A. R., Hara, E., Whitney, O., et al. (2014). Convergent transcriptional specializations in the brains of humans and song-learning birds. *Science*, **346**, 1256846. DOI:10.1126/science.1256846
- Shettleworth, S. J. (2010). *Cognition, Evolution and Behavior*, 2nd edn. Oxford: Oxford University Press.
- Tinbergen, N. (1963). On aims and methods of Ethology. *Zeitschrift für Tierpsychologie*, **20**, 410–433.

2 Spatial Cognition in Birds

James F. Reichert, Sebastian Schwarz and Debbie M. Kelly

Feats of avian spatial cognition rank as some of the most impressive in the animal world. Homing pigeons (*Columbia livia*) are able to travel hundreds of kilometers from distant locations, over varying types of landscape and weather conditions, eventually arriving at their home loft. Migratory birds are able to cover substantial distances and travel seasonally between breeding and wintering sites. These journeys require the ability to combine spatial information from earth-based cues (olfactory cues: Ioalè et al., 1990; Gagliardo et al., 2011; magnetic cues: Wiltschko & Wiltschko, 1978, 1996), visual landmarks (Biro et al., 2004; Lipp et al., 2004) or sky-based cues (position of the sun: Schmidt-Koenig, 1958; skylight polarization patterns: Kreithen & Keeton, 1974; Able, 1982). Sensitivity to such a range of cues provides birds with an impressive array of navigational tools to maintain their bearings and reach their destination. Indeed, as one of the several avian long-distance travellers, pigeons are capable of *true navigation* – as witnessed by their ability to find their way home even when displaced far off a known route (Bingman & Cheng, 2005). Food-storing birds face a similarly important challenge of spatial cognition: these birds create food stores during times of resource abundance for later retrieval during times of scarcity. The birds must encode the location of these food stores in a manner that will allow them to recover the caches within a landscape that undergoes seasonal changes between autumn and winter. Yet despite this seemingly insurmountable demand on their spatial memory skills, long-term food-storing birds routinely locate thousands of previously hidden food caches with a high degree of precision, and do so year after year (Tomback, 1980; Vander Wall, 1982). How different avian species are able to accomplish these kinds of tasks hinges on their ability to efficiently process the spatial relationships within their environment.

In this chapter we examine the different cues birds use to encode spatial information as well as the factors that influence this process. Firstly, we describe how birds use featural and geometric information for orientation, specifically how near (proximal) and far (distal) landmarks are relied upon. Secondly, we examine how spatial information is extracted from landmark arrays and continuous surfaces. Thirdly, we discuss the extent to which birds use geometric and featural cues, and how those cues interact with each other. Finally, we discuss the use of panoramic views and view-matching as an additional strategy for understanding the spatial abilities of birds.

Using Landmarks for Orientation

Before a bird can navigate it must first be able to orient itself to its surroundings, which is the initial stage of any type of navigational endeavor. It does so by remembering specific landmarks such as trees, rocks or flat surfaces such as those formed by mountain sides. The distinctive qualities of these individual landmarks, such as color, pattern and texture, are referred to as *featural cues*. In addition to featural cues, a bird may also use *geometric cues*, which comprise the geometric relations between landmarks and surfaces such as distance and directional information. By successfully encoding the identity of individual landmarks (features) within its environment, as well as the spatial location of those landmarks relative to other landmarks and surfaces (geometry), birds have many potential sources of information at their disposal when trying to stay oriented.

Cheng (1988, 1989) showed that pigeons could rely on the positions of both nearby and distant landmarks to pinpoint the location of a hidden goal. Positional estimates include both a distance component and a direction component, which together form a vector. The Vector Sum Model (Cheng, 1989, 1994) proposes that birds can code distance and direction coordinates independently from individual landmarks to a specific location. According to the model, the more landmarks that a bird has available, the more accurate its estimation is likely to be. For this reason, the encoding of the locations of multiple landmarks allows a bird more flexibility when it is trying to pinpoint a precise location such as a food source (Kamil & Cheng, 2001).

Although birds can make use of multiple landmarks, both near and far from a goal location, it appears that landmarks closer to a goal carry the greatest weight. Cheng (1989) demonstrated this point by training pigeons to find food hidden between two equal-sized landmarks, with one landmark located west and closer (10 cm) to the hidden food and the second landmark located east and farther away (40 cm). During test trials each landmark was shifted from its original position an equal distance away from the hidden goal (i.e., the closer landmark was shifted farther to the west and the more distant landmark shifted farther to the east). The result of this landmark shift was that the birds' search location shifted as a consequence, with a bias toward the landmark that had been closer to the hidden goal during training. Furthermore, Gould-Beierle and Kamil (1999) showed that search accuracy by food-storing Clark's nutcrackers (*Nucifraga columbiana*) was much better when the birds could use a nearby landmark as a reference as opposed to one that was farther away. Cheng (1992) provided a psychophysical explanation for such findings by showing that the amount of error involved when an animal estimates a vector from a landmark to a goal location increases proportionally as the distance between the two locations increases.

Analogous to these open-field type tasks during which active locomotion is possible, Spetch (1995) used a two-dimensional computer-based touch-screen task to show that pigeons also relied on visual landmarks when searching for a hidden goal on the screen. The pigeons were required to peck on the screen of a computer monitor at a particular point at a consistent vector from an array of landmarks, with the landmark array

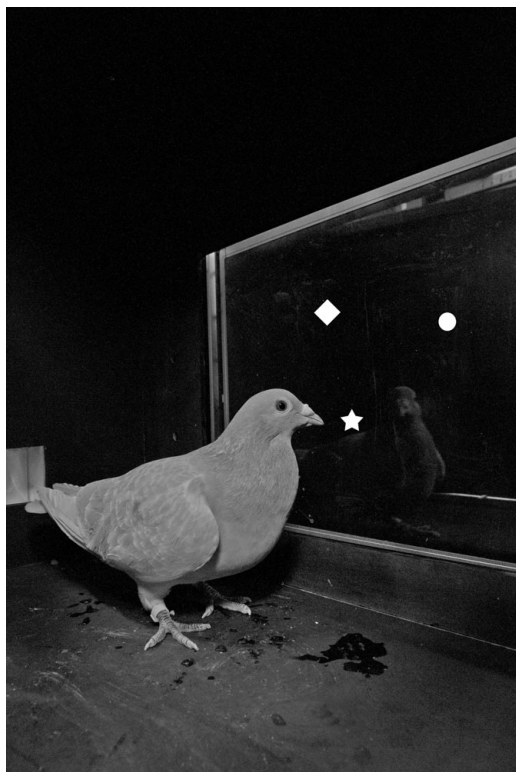


Figure 2.1 Rendition of a training trial for a landmark array task presented to pigeons using a computer monitor equipped with a touch-screen. Pecks directed at a precise location defined by the landmark array results in food presented in a nearby grain hopper (modified after Spetch, 1995; photo credit: H. Hobson).

appearing at different screen locations across trials (see [Figure 2.1](#) for a photographic illustration). Therefore, although the absolute location of the goal relative to the screen changed from trial to trial, the location relative to the landmark array remained constant. Test trials consisted of select exposure to only certain landmarks within the array to determine how much control individual landmarks had acquired over the pigeons' search strategies. The pigeons not only relied more on near rather than farther landmarks, but the learning of the nearer landmarks overshadowed learning of landmarks that were more distant from the goal.

Pigeons are excellent navigators, able to travel hundreds of kilometers using a variety of earth-based (i.e., magnetic and olfactory) and landmark cues, to arrive at a single, consistent location, which is typically their home loft. For food-storing birds such as the Clark's nutcracker, the spatial challenge is quite different as they need to remember and update a series of changing food locations. Pine seeds are the main food source for Clark's nutcrackers, which they store in individual caches during the fall when availability is high and then retrieve during the winter when food sources are scarce (Tomback, 1978). This type of behavior requires that the birds form a memory based on a spatial

representation that is flexible enough to withstand changes to the visual environment that occur between summer and winter. It is for this reason that the encoding and use of spatial cues by food-storing birds may differ from that of non-storing birds. Using an open-field paradigm similar to the computer touch-screen paradigm used by Spetch (1995), Goodyear and Kamil (2004) examined how Clark's nutcrackers use landmarks when searching for food hidden at a location relative to an array of landmarks. Similar to pigeons, during testing in which individual landmarks were presented in isolation to the nutcrackers, search accuracy decreased as landmark-goal distance increased, thus showing that the closer landmarks exerted more control over nutcrackers' search behavior than did the more distant landmarks. Taken together, the research using pigeons and nutcrackers has shown that by using bearings from multiple landmarks to a specific goal location, birds are more able to make a precise estimation of that location. However, some landmarks have an advantage over others in drawing a bird's attention, with the nearby landmark(s) often exerting the most control given that they are naturally better predictors of both distance and direction to a given position.

Landmark Arrays and Surface Geometry

When a prominent object, such as a tree or a rock, is positioned very close to a goal location (e.g., a hidden food source), it can serve as a beacon for that location, in which case a bird would simply need to fly directly to the landmark in order to reach the goal. But when an object is far enough from a goal that a beaconing strategy is no longer feasible, a bird must accurately estimate the metric coordinates from that object to the goal location in order to make effective use of it as a landmark. These types of distance and direction estimates can be accomplished by using either *absolute* or *relative* metrics. For example, assume that a bird hides a food cache midway between two trees. If it has encoded the food location using an absolute metric, it will attempt to remember the location of the food as being an exact distance from either of the trees. However, if the bird has encoded the food location using a relative metric, it will attempt to remember the food location as being approximately midway between the two trees. At first glance this second, relational strategy may seem the simpler of the two strategies, but it is actually considered to be a more sophisticated and flexible form of learning (Kelly and Spetch, 2001), specifically because it represents the formation of an abstract rule (i.e., the "middle rule") that can be applied across similar situations. It should be noted that a hallmark of human cognition is our ability to quickly adopt relational rules, and adult humans have been shown to preferentially default to a relational strategy during spatial tasks (e.g., Spetch et al., 1997; also see Gouteux et al., 2001 for a study with rhesus monkeys [*Macaca mulatta*]).

Kamil and Jones (1997) were the first to show that birds could use a relational rule to solve a spatial learning problem. Clark's nutcrackers were trained to search for food hidden at the midway point between two colored PVC pipes, which served as landmarks. During training, the inter-landmark distance was randomly varied in 20-cm increments from a minimum distance of 20 cm to a maximum distance of 120 cm. During test

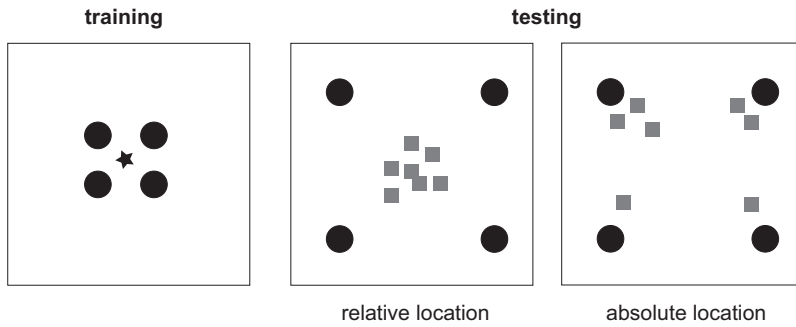


Figure 2.2 Schematic illustration of training and testing arrays in expansion tests. During training, the food location (black star) was centered in the landmark array. In expansion tests, birds could either use the “middle rule” and search for the now absent food in the relative center of the expanded array or they could search at the absolute location indicated by one single landmark. Grey squares represent hypothetical search peaks of tested birds (modified after Spetch et al., 1997).

trials when the birds were presented with novel inter-landmark distances (both shorter and longer compared to training), they continued to search at the midpoint between the two landmarks, thus establishing that the birds had applied a relational rule to remember the location of the food during training. Jones et al. (2002) went on to show that pigeons could similarly apply a middle rule when searching for food hidden between two landmarks, albeit not as accurately as nutcrackers. These studies confirmed that birds could learn the distance between two landmarks when directional information remained unchanged (i.e., the goal was always situated between the two landmarks). Researchers have also examined the use of directional cues by birds, as shown when Clark’s nutcrackers and pigeons learned to search for food located at either a constant bearing or a constant distance relative to two landmarks such that the relationship between the three points formed a triangle (Kamil & Jones, 2000; Spetch et al., 2003). These studies found that both pigeons and nutcrackers could solve these tasks using either directional or distance cues, although again, nutcrackers searched more accurately than did the pigeons.

Although birds are capable of applying relational rules when encoding landmark arrays, laboratory experiments have established that a relational strategy is usually not a default preference and that some species rely more on absolute vectors. For example, pigeons were trained to search for food hidden in the center of a four-landmark array in the overall shape of a square (Spetch et al., 1997). During expansion tests the distance between the landmarks was doubled, resulting in an array twice the size as compared to training. If the pigeons used a relational rule (i.e., the “middle rule”) to encode the landmark array, then they would be expected to search in the center of the expanded array, just as they had during training since the relative center of a square does not change as a function of size. But instead of searching in the center, the pigeons directed their searches to a location that maintained an absolute vector from a single landmark that was consistent with a landmark-to-center vector experienced during training (see Figure 2.2). A similar use of absolute geometric properties was shown

by Clark's nutcrackers when encoding a square-shaped array of four landmarks (Kelly et al., 2008). However, given that the birds in these studies were provided with only a single array size (i.e., a single exemplar) during training, an absolute strategy was sufficient to solve the task and there was no requirement to form a relational rule as there had been when multiple exemplars were provided (e.g., Kamil & Jones, 1997, 2000).

When encoding geometric properties of landmark arrays, birds seem fully capable of applying relational rules to solve spatial problems, but may rely on simpler absolute strategies when they can. For birds to use a relational strategy appears to require that they experience different exemplars (e.g., inter-landmark distances) during training, thereby allowing them multiple opportunities to learn the appropriate relational rule. Once this training is provided, birds will apply relational rules when encoding the geometry of landmark arrays. Of course, when operating in a natural environment outside of the laboratory, birds may receive ample experience in applying relational geometric learning to a variety of navigational situations, or be faced with situations in which a simple absolute encoding strategy would not suffice. To our knowledge the examination of geometric-based strategies (i.e., absolute vs. relational rules) by birds in the wild has yet to be studied, although this avenue of research would be quite enlightening. Still, the control afforded by laboratory-based research has been essential in establishing that birds are indeed capable of abstract rule learning as it relates to geometric properties.

How birds encode the geometry of a walled enclosure is different from the way in which they encode the geometry of a landmark array. Whereas walls allow the overall geometric shape of a space to be clearly delineated, the overall shape of a landmark configuration requires a degree of perceptual completion – extracting an overall shape from a collection of individual components. This difference can be measured by examining birds' search behavior when presented with walled enclosures versus landmark arrays. As noted previously, when pigeons were trained to search in the center of a four-landmark array in the overall shape of a square, they did not encode the relative center but rather the center as an absolute vector from individual landmarks (Spetch et al., 1997). During testing when the landmark array was expanded outward to form a square configuration twice as large as the size of the training array, pigeons uniformly relied on this absolute vector to determine where they searched. Using a similar paradigm, Gray and colleagues (2004) trained pigeons to search for food hidden at the center of a walled square-shaped arena and subsequently tested the birds inside an expanded square arena that was twice the size of the original. The pigeons divided their search strategy between using either absolute or relative coordinates: in some cases the birds maintained an absolute vector based on the distance and direction from the center to an individual corner learned during training, whereas in other cases the birds searched in the center of the arena, a strategy indicative of the use of a relational rule. Similar evidence of dual encoding strategies for geometry in a walled arena has also been reported for chicks (Tommasi & Vallortigara, 2000).

How might birds extract information from a walled environment that allows them to more readily use relative metrics over absolute metrics? It has been suggested that animals automatically encode the shape of a walled space based on its *principal axes*, of which there are two: the major principal axis which divides the space vertically and is

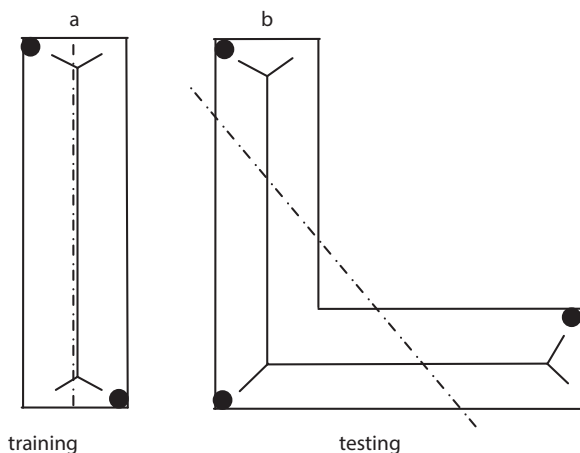


Figure 2.3 Schematic illustrations of (a) a rectangular training enclosure and (b) L-shaped testing enclosure for studies examining the use of local geometry, medial axes and principal axes. Dashed lines represent principal axes and solid line medial axis. Black circles in (a) can be defined by local geometry, medial or principal axes. Black circles in (b) define corners defined by local geometry or medial axis but not by principal axis. (modified after Kelly et al., 2011).

bisected horizontally by the minor principal axis at the center point of the space. Theoretically, any space – regardless of its size or shape – can be defined by its principal axes, with perhaps the simplest examples being either a rectangular or square-shaped environment (see dashed lines in Figure 2.3). Contrary to the principal axes, the medial axes are a more localized shape parameter that resembles a hypothetical trunk and branch structure, with a central trunk positioned down the length of a space with branches radiating to corners (solid lines in Figure 2.3). But what informational value would global (principal axis) or local (medial axis) shape encoding serve to an animal when trying to stay oriented?

(i) Local and Global Cues from Walled Environments

Kelly et al. (2011) specifically examined local and global shape encoding of geometry in both pigeons and chicks (*Gallus gallus*) by disorienting the birds and subsequently placing them inside a featureless rectangular arena to search for a hidden food reward (note that the construction of these arenas considered the relative body size differences of the two species). During training, birds had learned to find the food consistently located at one corner of the arena. During subsequent testing, the birds were disoriented and placed inside an L-shaped arena (the shape of the arena permitting the dissociation between the possible encoding strategies). Their search pattern was analyzed to determine how they had encoded the location of the hidden food source during training (no food was available during testing). Since inertial cues would have been disabled by the disorientation procedure, and no distinctive featural cues were present at any time, the birds could rely only on a geometric strategy for guidance, of which there were three:

(1) local geometry – recognition that the rewarded corner was defined by distinctive wall length and sense properties (e.g., a long wall either to the left or right of a short wall). Note this strategy would yield two “correct” corners, although only one was ever baited during training (see black circles in [Figure 2.3a](#)); (2) medial axes – recognition of the geometric shape of the rewarded corner as defined by local axes of symmetry (see solid line and black circles in [Figure 2.3a](#) and [b](#)); and (3) principal axes – recognition of the overall shape of the space as defined globally by the axis of symmetry (see dashed line in [Figure 2.3a](#) and [b](#)). Of these three possibilities, chicks showed a primary reliance on the local geometry (i.e., differential wall lengths and left-right sense), and a secondary reliance on medial axes to remember their rewarded corner, whereas pigeons relied on medial axes, which suggests differences in how species use geometric cues to orient. Importantly, Kelly et al. (2011) showed that neither the chicks nor pigeons used the global shape of the rectangular training arena to locate the correct corner, but instead they relied on more local geometric information to guide orientation.

(ii) Local and Global Cues from Landmark Arrays

Birds may have a variety of spatial cues available for remembering important locations, with some spatial cues being relatively close to a location (local) and others being more distant (global). Local cues have the advantage of being more closely associated with a specific location (e.g., a rock or configuration of rocks), whereas global cues are more associated with permanence and thus may be more reliable (e.g., a distant mountain range). By encoding both types of cues, a bird would theoretically be able to increase its level of certainty when remembering a location. If given a choice between local and global cues, which type of cue will a bird rely on most? Spetch and Edwards (1986) tested pigeons on their preference for using either local or global geometric cues during a laboratory search task. Three cardboard cartons were placed equidistant against a wall of a small experimental room and the middle carton was baited with food; the position of the carton relative to the other two cartons served as a local geometric cue (it was always in the middle of the other two cartons). Against the opposite wall of the otherwise empty room was a box in which the pigeons could enter or exit the room on select trials; the box also served as a global cue in that the middle (baited) carton was always directly across from it, albeit at a distance. Test trials revealed that the pigeons could use either local or global cues in isolation, thus establishing that they had encoded both types of cues. To determine which cue they preferred, test trials were conducted in which the local and global cues were placed in conflict. This was accomplished by shifting the three-carton array such that the middle carton was no longer directly across from the entry/exit box but a carton at the end of the array was instead. This test presented the pigeons with a clear choice: if they were going to rely on either the local or global cues they would do so at the expense of the other cue. During this experiment, the pigeons preferred the carton in the correct local position within the array even though it was in the incorrect position relative to the global cue.

One might conclude from these results that birds prefer local geometric cues over more distant global cues. However, given that pigeons are opportunistic feeders, local

cues may naturally hold more relevance for them over the short term compared to species that store food over longer time periods during which local features may become unreliable. Brodbeck (1994; Experiment 4) used a similar paradigm to investigate cue reliance of black-capped chickadees (*Poecile atricapillus*), a food-storing bird. Similar to Spetch and Edwards (1986), a single wooden feeder was baited and included within an array of other feeders (a total of four) and both local and global geometric cues were available to the birds. But unlike the previous study there were three types of cues that could be used to distinguish the correct feeder: (1) its spatial position within the four-feeder array (local geometry), (2) its spatial position within the larger experimental room (global geometry), and (3) its distinct color pattern relative to the other feeders (featural). During testing, the different cues were placed in conflict and the birds were able to select the cue on which they relied most. For black-capped chickadees it was the global spatial position within the experimental room, rather than local spatial position within the array or distinct features, which was the cue they preferred. In a follow-up experiment (Brodbeck, 1994; Experiment 5), a non-storing bird species (dark-eyed juncos [*Junco hyemalis*]) did not exhibit this same preference for global geometry, but instead weighed each type of information equally.

Hummingbirds, as foragers, also need to make use of the local and global properties of an environment in order to remember the location of nectar-producing flowers. To be efficient, hummingbirds must refrain from visiting those flowers that are either empty of nectar or close to being empty, and instead visit only those flowers that are more likely to contain nectar, a spatial memory requirement not unlike that experienced by food-storing birds. Hurly and Healy (1996, see also Chapter 3, Healy and Hurly) tested whether hummingbirds (*Selasphorus rufus*) rely more on local featural cues associated with flowers, such as color or color pattern, or whether they rely more on the global spatial position of the flower relative to other naturally positioned landmarks within the environment. The experiment was conducted in a field using free-living hummingbirds as subjects. Four featurally distinct flowers were positioned in the shape of a square and only one of the flowers was baited with a sucrose solution. Hummingbirds were freely able to approach the array and discover the baited flower which contained enough sucrose that the hummingbirds would require more than a single visit to consume it. Between visits the experimenters drained and washed the flower of sucrose and switched its position with that of another flower within the array. Upon its return, the hummingbird could choose the flower that was either featurally correct (same color or color pattern) or spatially correct (position in the array relative to other natural landmarks); results showed that it was the spatial position of the flower that the hummingbirds relied upon most, a finding that has been replicated since by the same authors (e.g., Healy & Hurly, 1998). Indeed, encoding spatial position is so vital to a hummingbird's foraging strategy that it will return to a rewarded flower's previous location even when the flower has been removed from the site, a behavior that can be prompted by just a single previous experience of feeding from the rewarded flower (Flores-Abreu et al., 2012).

In summary, the degree to which birds rely on local and global cues depends in part on their general feeding ecology. For food-storing birds, which have to remember multiple locations in which food has been hidden, global spatial properties appear to be of prime importance. This is also true of hummingbirds which similarly need to

remember multiple locations of the most promising nectar-producing flowers. For non-storing birds, it is the more local cues such as distinct features that seem to carry the greatest weight. And yet, feeding ecology alone cannot always determine how a bird will rely on different environmental cues. For example, Hodgson and Healy (2005) examined great tits (*Parus major*), a non-storing bird species, on their cue preference during a simple spatial task. A tray consisting of several evenly-spaced shallow wells was placed inside each bird's cage; one of the wells was baited with food and covered by a colored cloth which the bird learned to remove during training to obtain the food. During testing, the colored cloth associated with the rewarded well now covered a different well, whereas a novel colored cloth now covered the rewarded well. Given a choice between the correct spatial location and the correct feature, the birds preferred to search at the correct spatial location. Similarly, food-storing birds have also been shown to prioritize featural cues over geometric cues during a spatial search task (LaDage et al., 2009), as have hummingbirds (Hurly et al., 2014). So, although the food-gathering requirements of a bird clearly influence its spatial decision-making, other contextual factors also play a role, as will be addressed further in this chapter.

Interaction of Features and Geometry from Walled Environments

To test concurrent feature and geometry use in a controlled laboratory setting, Cheng (1986) devised the rectangular reorientation paradigm. Within this paradigm, the experimental apparatus consists of a rectangular walled enclosure in which all cues external to the enclosure, both visual and auditory, are masked. Inside the enclosure often a single corner is baited with hidden food for which an animal is free to search. Prior to entering the enclosure the animal is first passively disoriented by being slowly rotated inside a darkened transport box, a procedure that is used to reduce the animal's ability to use inertial information. Once inside the enclosure the animal is expected to search as efficiently as possible by locating the baited corner without visiting any of the non-baited corners first.

To examine the use of visual features using the rectangular reorientation paradigm, a featural cue is located at each corner, in the form of either a distinct wall or a distinct object; if the animal has encoded the featural information it can then use this information to search in the baited corner without having to visit any of the other corners. However, the animal can also use the geometric properties of the enclosure to identify the baited corner. In the case of a rectangular enclosure, the baited corner will be located at the juncture of one longer wall, either to the left or right of a shorter wall, depending on which side of the enclosure that the baited corner is located. Within the rectangular reorientation paradigm, the geometric cues are not deemed to be as informative as the featural cues since two corners share identical geometric properties (the baited corner and the corner diagonally opposite; see Figure 2.4 for details and an example) whereas in the traditional procedure, only one corner contains the distinct feature associated with the baited corner. Therefore, the best that an animal can ever do if it relies strictly on geometric cues is to direct its initial search to either the baited corner or its diagonal counterpart. Despite this apparent imbalance favoring featural cues, the majority

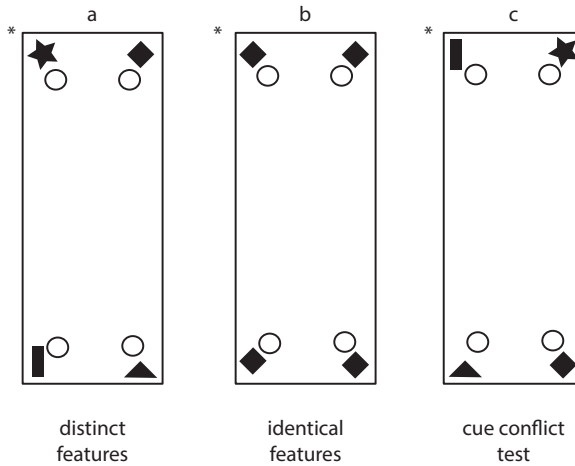


Figure 2.4 Schematic illustrations of rectangular enclosures used for the study of geometric and featural cues. Open circles represent containers from which the bird learns to search for hidden food; one corner is consistently baited with food during training (for illustrative purposes, the corner marked with “★” denotes the baited corner in this example). Individual corners can be distinguished by either (a) distinct featural cues located at the corners or (b) identical featural cues. Birds provided only with identical features must learn the location of the baited corner based on the geometric properties of the arena along with left-right sense (e.g., corner with long wall to the left and short wall to the right); since the corner diagonally opposite the baited corner contains the same geometric properties, this leads the bird to commit “rotational errors” by choosing the baited corner and its rotational equivalent at an equal rate. During cue conflict testing, (c) distinct featural and geometric cues are pitted against each other by relocating each feature to the next clockwise corner which is an incorrect geometric location relative to what the bird learned during training.

of animals studied to date show an incidental encoding of the geometric properties in addition to the featural properties of their baited corner, even though the featural information alone should be sufficient for the animal to solve the task efficiently (see Cheng & Newcombe, 2005; Cheng et al., 2013 for reviews).

(i) Factors that Affect Feature and Geometry Use: Arena Size

Studies with newborn chicks have shown that their encoding of featural and geometric cues is sensitive to the size of the environmental arena. For example, Vallortigara et al. (2005) trained chicks to search for food at one corner of a rectangular enclosure that contained a distinct featural cue in each corner. One group of chicks was trained inside a small enclosure and a second group was trained inside a large enclosure. The groups were subsequently tested inside an enclosure the same size as their training enclosure, as well as being presented with a cue conflict situation whereby the features were relocated one corner clockwise. This latter test was conducted to examine whether the chicks relied more on the geometric or featural properties of the enclosure when searching for the correct corner. Chicks that had been trained and tested in the large enclosure followed the rewarded feature to its new (geometrically incorrect) location,

thus showing a primary reliance on features; conversely, chicks that had been trained and tested in a small enclosure divided their choices between the correct geometric corner and its rotational equivalent corner (neither corner contained the correct feature), thus showing primary reliance on geometry. Taken together, these results show that geometry was more salient to the birds in the small enclosure, whereas features were more salient to birds in the large enclosure. Similar cue conflict tests using Clark's nutcrackers (Lambinet et al., 2014) have shown a similar general tendency for geometry to be the more dominant cue in smaller enclosures as opposed to larger ones. Such an effect of salience on the use of geometric information in smaller spaces has also been demonstrated in non-avian species (fish: Sovrano et al., 2005; human children and adults: Learmonth et al., 2001, 2002; Ratliff & Newcombe, 2008).

(ii) Factors that Affect Feature and Geometry Use: Rearing Experience

If an animal is reared within an environment that lacks informative spatial geometry, is it able to use geometric cues effectively to orient later in life? This question was addressed by Chiandetti and Vallortigara (2010) using newborn chicks. They reared one group of chicks within a geometrically impoverished environment (in a circular enclosure) and another group of chicks within a "normal" environment that contained a variety of geometric properties such as right corner angles and walls of different length. When later tested for their use of geometric cues, the circular enclosure-reared chicks did not differ in their cue use compared to those chicks reared in the geometrically informative environment: in small-shaped environments both groups placed higher reliance on geometry and in larger-sized environments they relied more on features (see also Chapter 8, Vallortigara and Chiandetti). Chicks are the only avian species to have been tested in this manner to date and more information is needed from other species before firm conclusions can be made about the effect that rearing environment has on spatial cognition. However, other non-avian species show that rearing environments can have a significant impact on later cue reliance. For instance, fish that have been raised in a circular environment can learn to use both geometry and features inside a rectangular-shaped tank, but they rely less on geometric cues than fish raised in a rectangular (i.e., geometrically informative) environment (Brown et al., 2007). More dramatically, mice raised in a circular environment fail to learn geometry at all (but do learn features) when trained with both features and geometry in a rectangular-shaped enclosure (Twyman et al., 2013).

(iii) Factors that Affect Feature and Geometry Use: Training Experience

Whereas rearing paradigms are designed to prevent an animal from gaining experience with specific cues prior to experimentation, another type of manipulation involves altering the type of training that an animal receives during the experiment itself. Recall that the original rectangular reorientation paradigm (Cheng, 1986) was designed such that an animal could learn to associate a specific rewarded corner based on either a distinctive featural cue located at the corner or the geometric properties that formed the corner. Although all animals tested with this paradigm will encode the featural cue, they also encode the geometric information despite it being incidental to the solution

of the task. But what if an animal received explicit geometry training whereby it was rewarded solely based on its geometrically correct choices? This was the question posed by Kelly et al. (1998) using pigeons as subjects. One group of pigeons (group Feature) was trained with distinct features at the corners whereas a second group of pigeons was trained with identical features at the corners and only later re-trained with distinct features (group Geometry-Feature). For those birds trained with identical features, geometry learning was explicitly reinforced whereas birds that were trained with distinct features only learned geometry incidentally. Following training, all birds experienced cue conflict testing in which the correct feature was relocated to an incorrect geometric corner. The group Feature birds chose the corner that contained the correct feature instead of the correct geometry. However, the choices of the group Geometry-Feature birds, which had received explicit training with geometry, were equally feature-and-geometry directed. When birds were explicitly trained to make geometry-based choices, therefore, their reliance on geometric information increased relative to their use of featural cues.

But what about food-storing birds, which might naturally possess a heightened preparedness to use environmental geometry given its relative stability compared to features? Reichert and Kelly (2015) tested Clark's nutcrackers in a version of the rectangular reorientation paradigm similar to that of Kelly et al. (1998). One group of nutcrackers (group Distinct) was trained in an enclosure with distinct features in the corners and rewarded for choosing the specific corner that contained the correct feature. Two other groups of nutcrackers received differential training: birds in group Distinct-Identical were trained with distinct features at the corners but, after having learned the task, were retrained with an enclosure in which the features in each corner were identical. These birds were rewarded for their geometric choices. The birds in group Identical-Distinct were trained with the same procedure as for group Distinct-Identical, only in reverse order. Just as with the pigeons in the previous experiment, the explicit training to use geometry was sufficient to shift reliance toward the use of geometry and away from features. For the birds in group Identical-Distinct this shift was even more dramatic as they weighed geometry significantly higher than features. These results are important because they highlight a distinction between the use of geometric information when it is learned incidentally and when it is learned more purposively. Experiments that have varied training experience have been critical for demonstrating that, although birds will learn about the geometry of their environment, it is only when geometry-based choices are made integral to solving a task that the weight of geometrical information can rival or even surpass that of features.

View-Matching: An Alternative Spatial Encoding Strategy

Reorientation tasks that are used to investigate the spatial processing of featural and geometric cues may seem quite abstract considering that birds live in habitats where they rarely encounter rectangular experimental arenas. Hence it is worth discussing the extent to which geometric and featural cues might be involved in ecologically-relevant navigational tasks. Using an outdoor field study, Hurly et al. (2014) investigated whether hummingbirds rely more on geometric or featural cues in their natural habitat,

which includes a surrounding panorama that contains a wealth of nearby and distant landmarks. The birds were trained to approach one of four identical flowers that were positioned in the shape of a rectangle. The rewarded flower was baited with a sucrose solution and identified by a landmark situated nearby (a red cube), and during training the hummingbirds learned to approach only the rewarded flower. During tests in which the landmark was removed the hummingbirds continued to choose the rewarded flower at a high rate and showed no evidence for using the configural geometry of the array as a guide (i.e., they did not commit rotational errors) but instead appeared to rely at least partly on the distal panorama. These results not only demonstrate the value of conducting experiments on birds in their natural habitat (to compare and contrast with laboratory research), but also show how outdoor field studies can be used to examine the extent to which birds rely on the larger panoramic views afforded by their natural environment.

In order to understand how view-matching could be used by birds during small or large-scale navigational tasks it is necessary to understand how view-matching has been studied in the past. Thus far, the vast majority of research examining view-matching ability in animals has been conducted on insects. Insects, and especially social insects (ants and bees), are known to rely predominantly on vision for their foraging and homing routes (Collett et al., 2006; Zeil, 2012). It was once assumed that ants and bees navigate by using nearby terrestrial objects as landmarks and rely on the more distal panoramic view only as a contextual reference that initiates the recall of the appropriate landmark memory when navigating through an environment (Collett & Collett, 2002; Collett et al., 2006; Cheng, 2012a). Using modern advanced image analysing techniques (Zeil, 2003) that are able to obtain a better representation of what the animal actually sees during navigation (Zollikofer et al., 1995; Schwarz et al., 2011), it appears that view-matching using the whole panorama is likely to be the main navigational strategy in insects (Philippides et al., 2011; Wystrach et al., 2011a; Wystrach et al., 2013).

View-matching can facilitate a compass orientation process by which the current perceived retinotopic view is compared to a memorized view of a familiar environment to set a heading direction (Zeil, 2003). Consequently, heading directions usually correspond to directions with the lowest mismatch between the perceived and memorized views. The use of the visual-compass does not require a distinction between discrete landmarks and the rest of the panoramic view; instead, landmarks and other terrestrial objects are naturally embedded in the current and memorized views and together serve as a reference for heading direction. Views also include the high-contrast skyline between the terrestrial landscape and the celestial sky. For instance, the mere contour and shape of the skyline provide enough information for ants to home without the information of discrete landmarks or other terrestrial objects (Graham & Cheng, 2009; Reid et al., 2011; Lent et al., 2013). Thus, according to this approach, concepts such as geometry and features do not apply to view-matching as there is no segregation between them.

View-matching has been proposed as an alternative explanation for the rotational errors committed by birds and other animals during rectangular reorientation experiments. As mentioned previously, birds that learn the geometric shape of a rectangular arena fail to distinguish between the two geometric identical corners as they provide

the same geometric information. When ants and bees were similarly tested in rectangular arenas they also displayed rotational errors as reported for vertebrates (Wystrach & Beugnon, 2009; Wystrach et al., 2011c; Sovrano et al., 2012; Sovrano et al., 2013; Dittmar et al., 2014). However, when the researchers examined the results from these insect studies using photographic image analyses, they concluded that a view-matching interpretation may also account for the data (Cheung et al., 2008; Stürzl et al., 2008). In its simplest form the photographic image analysis is based on a pixel-by-pixel comparison between an image of the goal location and the current image of the location of the animal. As the animal approaches the goal location, the two images will become more similar, and finally result in a match when the animal is at the goal position. Thus, this approach uses images as a tool to represent an animal's viewpoint as it navigates (Wystrach & Graham, 2012a). Importantly, these images are constructed to take into consideration the animal's visual capacities as well as to include visual cues such as contours and edges of the arena walls. An animal that uses view-matching will move toward the goal location (in the case of a rectangular arena this would be one of the corners) by heading to the direction with the lowest mismatch between the current and remembered view. Note that this is only an alternative explanation as to why animals might make rotational errors and does not necessarily exclude the encoding of geometric properties such as the length of the walls or the surface layout of the arena.

Although it is clear that view-matching is not the omnipotent answer for all navigational abilities in birds given that birds can detect a variety of sensory cues (Cheng et al., 2013), view-matching does represent a simple and parsimonious strategy for successful navigation through familiar terrain (Cheng, 2012b; Wystrach & Graham, 2012b). Since view-matching combines the whole panoramic view for orientation it is less prone to errors caused by changes or removal of individual landmarks. Furthermore, relying on a panoramic view instead of individual landmarks would be beneficial for food-storing birds that need to recover food after a significant period of time has elapsed between storage and retrieval, a period in which the local properties of landmarks might change considerably. Indeed, research with ants has shown that their ability to accurately navigate is robust even under conditions of extreme alterations to the panoramic view. Thus, panoramic views alone may provide a high degree of spatial information for successful homing (e.g., Wystrach et al., 2011b, Schwarz et al., 2014).

Previous results mentioned earlier in this chapter involving geometric encoding of landmark arrays and walled arenas have also been studied using a view-matching approach. During an elegant series of studies conducted by Pecchia and Vallortigara (2010, 2011, 2012) the use of a view-matching strategy was specifically tested using both pigeons and chicks. Each bird was individually trained to locate food hidden inside one of four identical cylinders that together formed a rectangular-shaped array. Each cylinder contained four openings, with only one opening granting access to the food reward during training. To examine the use of view-matching during training, birds were trained with either a variable or a stable viewpoint when accessing the food; during variable training, birds accessed the food from variable viewpoints whereas for birds trained with a stable viewpoint, the viewpoint at which they accessed the food remained consistent (see Figure 2.5). If birds relied on an allocentric (i.e., object-to-object) strategy to encode the geometry of the array they should commit rotational errors

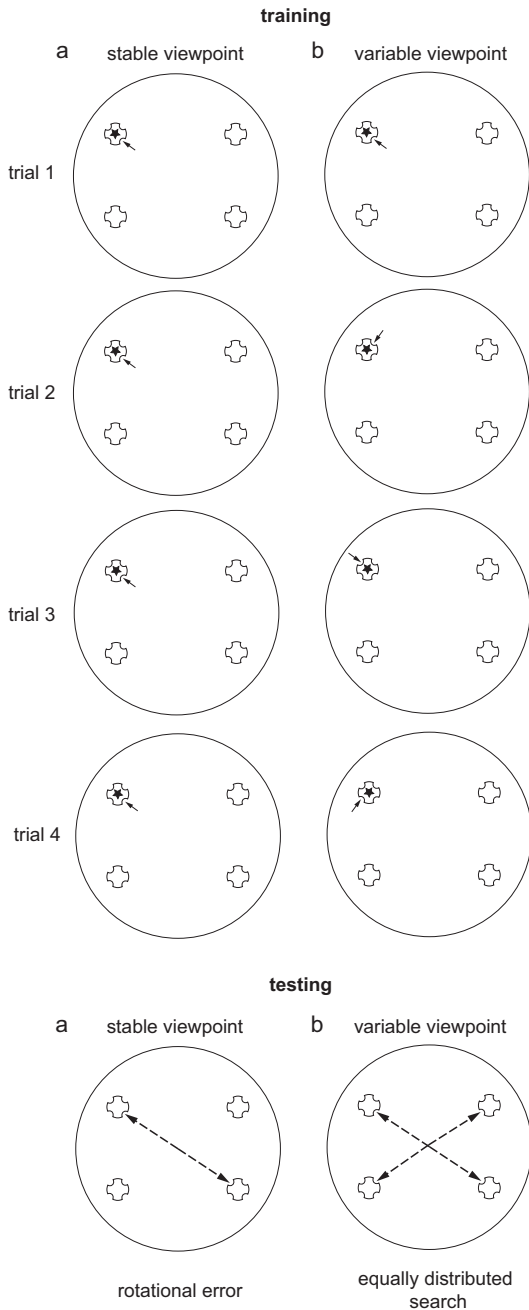


Figure 2.5 Schematic illustration of rectangular array of cylinders used for the importance of stable viewpoints during spatial cue encoding. Black stars represent hidden food locations and correct geometric corners. Small arrows indicate accessible food openings; the other three openings were blocked by a transparent film. In (a) the access to food at the correct cylinder was stable across trials (i.e., positions of the small arrows). In (b) access to food at the correct cylinder was variable across trials (i.e., positions of the small arrows). In tests when all openings were accessible, birds chose the correct and its geometrically identical corner more often than the remaining two corners (dashed arrows) after stable training (a). Birds chose equally between all four corners (dashed arrows) when tested after variable training (b) indicating that a stable viewpoint is important for spatial encoding of an environment (modified from Pecchia & Vallortigara, 2011).

(indicative of geometric encoding) regardless of the type of training they had received. However, if the birds relied on a viewpoint strategy to encode the geometry of the array they could only do so when provided with a stable viewpoint during training. Indeed, only those birds that were trained with a stable viewpoint had learned the geometry of the array as evidenced by their pattern of rotational errors. Therefore, reorientation within a rectangular arena may be accomplished by using a view-matching strategy. Yet it should be noted that further experiments are required to establish view-matching as mechanism for reorientation in birds. Future studies need to investigate the interaction of geometric cues, features and landmarks, as well as panoramic views by setting these sources of information into conflict – preferably across different behavioral contexts (e.g., caching, route following, etc.).

View-Matching as Alternative Strategy in Homing Birds

With technological advances in GPS tracking, small GPS loggers can document the flight paths of homing pigeons allowing for the investigation into the types of navigational cues the birds are using when homing. By doing so researchers have demonstrated that pigeons use visual landmarks and large visual properties of their environment to navigate (Biro et al., 2004; Lipp et al., 2004). Such landmarks can include manmade constructions such as highways and buildings. Theories about how the birds use the visual information span from “mosaic like map” or “map-and-compass” strategies to piloting. The “map-and-compass” model consists of certain waypoints along a familiar route that provide a bird with associated and memorized compass directions toward the home loft. These compass directions are based on all visible and non-visible characteristics of the waypoint and result in certain vector bearings. Piloting, however, can be independent of compass information as it involves only the use of visual landmarks along a known route. Alternatively, pigeons could use a view-matching strategy by comparing their current view with a remembered view and head in the direction of least mismatch. It should be noted that route fidelity is also common in insects (Collett, 1996; Kohler & Wehner, 2005; Wystrach et al., 2011b; Mangan & Webb, 2012) and several studies with ants demonstrate that a simple visual compass without the computation of site-specific vectors at certain waypoints along the route can account for most of the observed homing behaviors (Zeil, 2003; Wystrach et al., 2012; Wystrach et al., 2013). Piloting is based on one landmark that functions as a visual attractor whereas in view-matching the whole panoramic view is used to obtain the direction with the least mismatch. However, currently it is quite challenging to use the photographic image analysis technique to investigate view-matching in flying birds as thus far it has been specifically tailored for the study of insects.

Conclusion and Outlook

Spatial cognition in birds is influenced by a variety of factors that range from the availability and reliability of environmental cues, to ecological and evolutionary pressures,

and finally to an individual bird's previous experience. Since different bird species are confronted with a variety of spatially-based survival demands, the type of cues that they rely on most are likely to be reflective of those demands. For example, the spatial challenges that homing pigeons and migratory birds are faced with arise from the need to navigate under changing weather patterns and through unfamiliar environments and landscapes. For other birds, it is foraging for food that poses the critical spatial challenge. Non-storing birds need to locate a food source and immediately consume it whereas food-storing birds not only need to locate and collect food items, but also to relocate them to a variety of storage sites with the intention of returning to retrieve the items at a later date, a time that may be months in the future. It is these additional foraging steps that may differentially influence how storing and non-storing birds encode and rely upon spatial information within their respective environments.

In this chapter, we focused on a central aspect of avian spatial cognition, specifically how birds use featural and geometric information to stay oriented to their surroundings. We have examined how birds use nearby and distant landmarks, how geometric information is extracted from landmark arrays and surfaces, how features and geometry interact depending on arena size and prior experience, as well as how view-matching might provide birds with yet another strategy for encoding their spatial environment. Research into avian spatial cognition has provided us with a wealth of understanding to which we can only provide a limited overview. However, we have endeavored to raise many central issues regarding how featural and geometric cues can be extracted from the environment to build an accurate and reliable spatial representation.

Throughout this chapter we have attempted to provide a comparative approach to avian spatial cognition, but with a bias to raising the idea that ecological and evolutionary pressures may have shaped how different species weigh the cues within their spatial environment. A prime example is whether the spatial considerations involved in food-storing might encourage a stronger reliance on relative geometric encoding in which a general rule can be extracted from a few experiences and applied to new situations. Research in this area is still too preliminary to draw strong conclusions, and indeed the majority of the studies we have reviewed have been conducted on the pigeon and the Clark's nutcracker as representatives of non-storing and storing birds, respectively. Although this approach is clearly restricted in terms of its ability to draw firm conclusions, especially considering the number of closely related species and/or the number of species that share similar ecological pressures. However, given that an increasing number of avian species are being used to address comparative questions of spatial cognition, we are both hopeful and confident that these ecologically- and evolutionary-driven questions will be addressed in future research.

It should be noted that all of the research that has been addressed in this chapter thus far has involved spatial cognition at the behavioral level, but of parallel importance is what occurs at the neural level when an animal actively navigates its surroundings. How animals extract spatial coordinates from their environment and how this information is represented in the brain has received considerable attention over the years. One recent and noteworthy sign of the importance of this field of research is the joint awarding of the 2014 Nobel Prize in Physiology or Medicine to John O'Keefe, and May-Britt Moser and Edvard Moser for their research on the functional properties of grid cells.

Located in the mammalian entorhinal cortex, grid cells provide the framework for a metric coordinate system by which an animal can track its movements within a space (Moser et al., 2008). Grid cells in turn send their information to the nearby hippocampus where place cells are located and code for the construction of a more sophisticated neural map of an environment that serves as the foundation of spatial memory. Together with head direction cells which code for directional positioning of the animal (Knierim et al., 1995) and boundary cells which code for environmental boundaries such as walls or surfaces (Lever et al., 2009), a complete neural circuit dedicated to maintaining an animal's spatial awareness becomes evident, most of it located within the hippocampal formation.

Although knowledge of the neural components of spatial cognition has been derived chiefly from research with mammals (primarily rats), the mammalian and the avian hippocampus are considered to be homologous structures and understanding how the spatial map is represented in the avian brain is a worthy endeavor as birds are now being recognized as important models of age-related spatial decline (Wilzeck & Kelly, 2013; Coppola et al., 2014; Coppola et al., 2015), since birds rely heavily on the visual properties of their environment to navigate, just as humans do. Understanding the pressures of avian food storing has also led to a clearer understanding of neurogenesis and neural plasticity in general, most strikingly in the way that the hippocampus undergoes seasonal fluctuations in size that correlate with seasonal spatial memory demands (see Sherry & Hoshoooley, 2010).

As a whole, the study of spatial cognition in birds allows for an unprecedented breadth of knowledge given the range of different species involved and the variation in spatial demands required among those species. Homing pigeons and migratory birds often travel hundreds of kilometers to reach a destination, and with advancements in GPS data recording the cues that these birds use along their routes can be inferred with ever greater precision. Comparisons between how food-storing and non-storing birds use environmental cues provide an ideal framework from which to examine the ecological and evolutionary demands that help shape both short-term and long-term spatial strategies. Although view-matching has thus far been studied primarily in insects, the degree to which it contributes to both small-scale and large-scale navigational strategies in birds offers a promising new area of study. By studying avian behavior in the laboratory as well as in their natural environment, and correlating the results with neuronal measures, the field of avian spatial cognition offers the promise of a thorough understanding of how the brain stores, retrieves and processes spatial information.

References

- Able, K. (1982). Skylight polarization patterns at dusk influence migratory orientation in birds. *Nature*, **299**, 550–551.
- Bingman, V. P. and Cheng, K. (2005). Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethology Ecology and Evolution*, **17**, 295–318.