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

Pfenning, 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
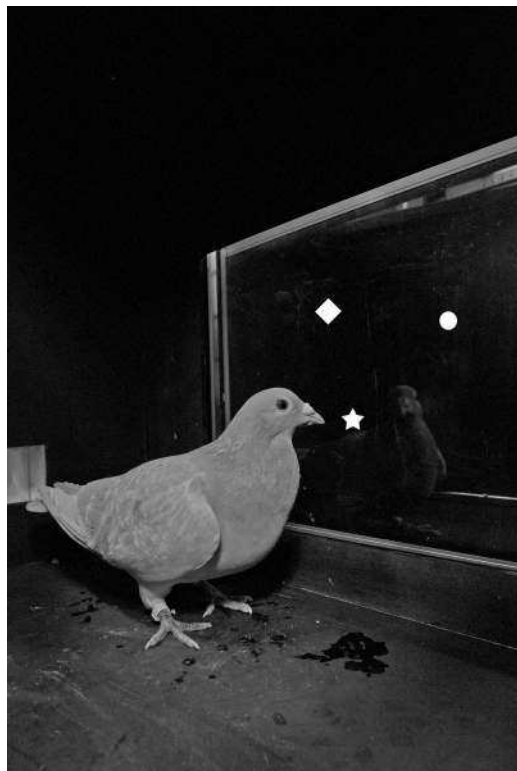
Figure 2.1 Rendition of a training trial for a landmark array task presented to pigeons using a computer monitor equipped with a touch-screen. Pecks directed at a precise location defined by the landmark array results in food presented in a nearby grain hopper (modified after Spetch, 1995; photo credit: 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
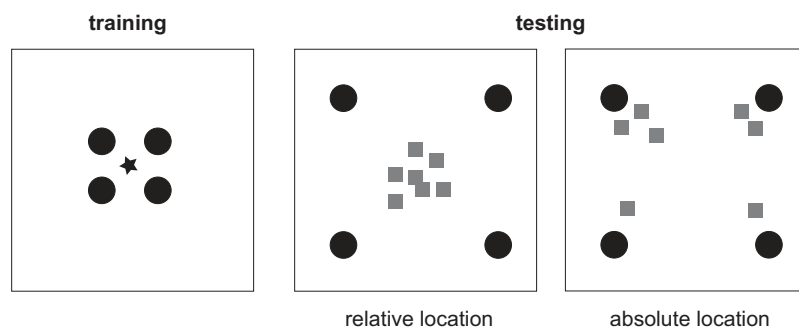
Figure 2.2 Schematic illustration of training and testing arrays in expansion tests. During training, the food location (black star) was centered in the landmark array. In expansion tests, birds could either use the "middle rule" and search for the now absent food in the relative center of the expanded 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