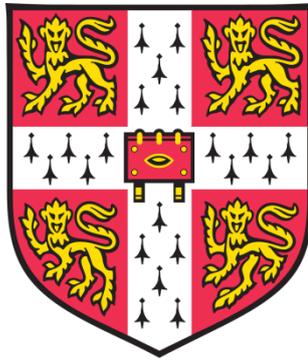


A multi-faceted approach to investigating theory of mind in corvids



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Preface

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Declaration and specified in the text. No part of this thesis has been submitted, or is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution.

This thesis does not exceed the prescribed word limit.

Declaration

The work in this thesis was carried out under the supervision of Professor Nicola S. Clayton and Ljerka Ostojić at the Department of Psychology and the Sub-Department of Animal Behaviour at the University of Cambridge.

In all studies reported here, I openly and truthfully describe how I determined sample size, all data exclusions, all manipulations, and all measures.

In Chapter 2, the experiments were designed by Edward Legg. Natalie Williams was involved in data collection. Edward Legg coded the videos. The analysis and interpretation of the data are my own.

In Chapter 3, Ljerka Ostojić and Rachel Crosby were involved in data collection, experimental design, and interpretation of results. Michael Mendl (University of Bristol) contributed to discussions about the experimental design. Piero Amodio and Rachel Crosby served as second raters for the interrater-reliability analysis.

In Chapter 4, Ljerka Ostojić was involved in experimental design and Corina Logan and Rachel Crosby served as second raters for the interrater-reliability analysis.

In Chapter 5, Ljerka Ostojić and Edward Legg were involved in designing the study and data analysis. Marta Halina and Greg Davis commented on earlier drafts.

In Chapter 6, Andreas Nieder (University of Tübingen) and Ljerka Ostojić contributed to experimental design. Lysann Wagener (University of Tübingen) was involved in programming experiments and helped with training. She collected data for Experiment 6.2.

Summary

Theory of mind refers to the ability to attribute mental states to others and to predict their behaviour based on inferences about their mental states, for example their perception, desires, or beliefs. Forty years ago, research on theory of mind originated from the question of whether or not chimpanzees (*Pan troglodytes*) have a theory of mind, a question that – after all this time – is still debated. In the present thesis, I investigate theory of mind and its precursors in birds of the crow family, specifically Eurasian jays (*Garrulus glandarius*), California scrub-jays (*Aphelocoma californica*), and carrion crows (*Corvus corone corone*).

Corvids have been reported to possess theory of mind-like abilities. This qualification reflects the fact that most research on theory of mind in these birds has revolved around the ability to respond to perceptual and desire states of conspecifics, and so far has not produced evidence for or against an ability to also respond to others' beliefs. Further, it is unclear which mechanisms could be the basis of corvids' abilities. Thus, there are two open questions in regard to corvid theory of mind my thesis aims to address.

To address these questions, first, I investigated the ability of Eurasian jays to respond to the false belief of a conspecific in a caching paradigm, where the knowledge of a conspecific observer about the accessibility of two caching sites was manipulated (Chapter 2). In Chapter 3 I explore which behavioural cues might present the basis of the jays' ability to respond to the desire of a conspecific in a caching context. In Chapter 4, I report a study on biological motion perception in scrub-jays, a phenomenon suggested to be crucial for the detection of social agents. In Chapter 5, I assess scrub-jays' sensitivity to gaze of a human and a conspecific. Finally, in Chapter 6, I report a study investigating the face inversion effect in carrion crows, an effect that is indicative of a 'special' relevance of faces. I conclude by discussing how the presented studies could help us inform our understanding of corvid theory of mind-like abilities.

Publications

Chapter 4 includes content from:

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Content

Chapter 1: Introduction.....	1
Defining and Assessing Theory of Mind	2
Theory of Mind in Infants	4
Theory of Mind-Like Abilities in Non-Human Animals.....	5
Theory of Mind-Like Abilities in Corvids	7
Why corvids?	8
Understanding ‘seeing’ and ‘hearing’.....	8
Understanding desire states.....	10
False belief understanding.....	11
Alternatives to Theory of Mind in Animals.....	11
A Basis for Corvids’ Social Cognitive Abilities?	13
Overview of Thesis	14
Chapter 2: False belief understanding in Eurasian jays.....	19
Introduction.....	20
Overview of Procedure	22
Experience with (In-) accessibility (Step I and II).....	23
Method	24
Results and Discussion.....	29
Experience of the Removability of the Lid (Step III)	31
Method	31
Experiment 2.1: False and True Belief Task	32
Method	33
Results and Discussion.....	35
General Discussion	38
Conclusion.....	42
Chapter 3: Changes in behaviour as a function of changes in desire states	43
Introduction.....	44
Taking Desire States into Account in a Caching Context.....	45
Behaviour Reading Accounts of Theory of Mind Experiments.....	48
Experiment 3.1: Attention of Observer	49
Method	50
Results	53
Experiment 3.2: Behaviour of the Observer	55
Method	55
Results	60
General Discussion	63
Conclusion.....	65
Chapter 4: Biological motion perception in California scrub-jays.....	66
Introduction.....	67
Experiment 4.1	70
Methods.....	70
Results and Discussion.....	75
Experiment 4.2.....	77
Method	77
Results and Discussion.....	79
General Discussion	80
Chapter 5: Assessing the sensitivity to direction of gaze in California scrub-jays	83

Summary	83
Introduction	84
Experiment 5.1	86
Method.....	86
Results and Discussion	88
Experiment 5.2	89
Method.....	91
Results and Discussion	94
Experiment 5.3	96
Method.....	97
Results and Discussion	98
General Discussion.....	99
Chapter 6: Face Inversion Effect in Carrion Crows.....	103
Introduction	104
Experiment 6.1	107
Method.....	107
Results	111
Experiment 6.2	115
Method.....	115
Results	116
General Discussion.....	117
Chapter 7: Discussion and Conclusion	121
What are the limits of theory of mind in corvids?.....	125
What mechanisms could be the basis of corvids' theory of mind-like abilities?	130
Concluding remarks	133
References.....	135
Appendix A: Subjects, Set-up & Supplementary Material	151
Appendix B: Supplementary Raw Data	154
Appendix C: Supplementary Data analysis	162
Chapter 4, Experiment 4.2.....	162
Analysis	162
Results	162

Chapter 1

Introduction

A human adult readily “imputes mental states to himself and others” (Premack & Woodruff, 1978, p. 515). In other words, humans consider other peoples’ mental states, such as their perceptions, bodily feelings, beliefs, and desires (Goldman, 2012) and therefore possess a ‘theory of mind’ (Apperly, 2011; U. Frith, Morton, & Leslie, 1991). The term ‘theory of mind’ reflects the fact that, firstly, the states that are of interest are internal to others’ minds – hence mental states – and cannot be directly observed. Instead, mental states have to be inferred, using information about one’s own experience and perspective (Penn & Povinelli, 2007). Secondly, it reflects the fact that we use these inferences drawn about others’ mental states to predict their behaviour. Thus, having a *theory* of mind allows its holder to predict behaviour and possibly manipulate it (Frith & Frith, 1999).

Research on theory of mind has its origin in comparative psychology. It began almost 40 years ago when Premack and Woodruff (1978) asked whether the chimpanzee (*Pan troglodytes*) has a theory of mind. Since then, the question of whether individuals possess theory of mind has inspired a broad range of studies, focussing mainly on infant and animal theory of mind in an attempt to understand the development and evolution of this somewhat extraordinary ability. So far, it is however debated whether the animals’ behaviour is based on a theory of mind (e.g., Lurz, 2011). I hence use the term ‘theory of mind-like’ when referring to animal abilities. The qualification ‘-like’ acknowledges the fact that their abilities allow them to behave *as if* they have a theory of mind while it is not clear whether they actually do attribute mental states. However, note that it is equally unclear whether they are *not* able to attribute mental states.

Recent work has also extended to taxa other than mammals, most prominently to birds of the crow family (Emery, 2005). A plethora of studies on corvids suggest that these birds might be able to attribute auditory and visual perspective as well as knowledge and desires to others (reviewed in Clayton et al., 2007; Grodzinski & Clayton, 2010a; Keefner, 2016). In my thesis I put forward a line of studies that further investigate theory of mind abilities in corvids, with the aim of 1) exploring the boundaries of corvid theory of mind, and 2) elucidating which mechanisms could be the basis of corvids’ ‘theory of mind-like’ abilities.

Defining and Assessing Theory of Mind

Premack and Woodruff (1978) coined the term ‘theory of mind’ to refer to the ability to attribute mental states to others. Mental states share the feature that they are intentional in that they capture how an agent relates to things (Crane, 1998), for example, whether she believes something to be true, whether she desires a certain object, or whether she sees and knows about a certain object. In line with the empirical literature (Apperly, 2011), I shall distinguish between attributing perceptual states, knowledge states, desire states, and belief states¹ – theory of mind concerns the ability to attribute these different mental states².

Empirically assessing whether or not an organism has a theory of mind poses two difficulties. Firstly, how can we, as outside observers, determine whether a participant or an animal actually attributes mental states and is not simply using learned rules about associations between certain object and events? To elucidate, consider the following situation: Peter is standing in front of his closed office door. An onlooker, Sarah, could attribute to Peter the desire to open the door and a belief that his key must be in his bag, and thus predict that he will search his bag. However, Sarah could also predict that Peter will look in his bag because she sees him in front of his office door, where she previously saw him use his key, and because Sarah knows where his keys usually are (in his bag). His gaze towards his bag could also serve as a cue for Sarah allowing her to predict his behaviour. In all of these scenarios, Sarah associates Peter standing in front of the door with him retrieving his keys from his bag. Thus, in order to predict Peter’s behaviour, Sarah does not need to attribute a mental state to him. She can simply use the situational cues together with a behavioural rule that she has learned prior to this specific situation. Hence, in order to demonstrate that Sarah is able to attribute mental states, it is crucial to show that Sarah can acknowledge Peter’s mental state without just relying on situational and behavioural cues (‘behaviour reading’).

Secondly, how can we be sure that Sarah can reason about Peter’s mental states and is not simply using her own beliefs to predict his behaviour? Take the case that Peter believes the world to be in state X – that is, his keys are in his bag. Here, if Sarah reports Peter to believe that his keys are in his bag, $P_B(X)$, we cannot be sure that Sarah indeed attributes a belief to Peter. Sarah could simply be using her own belief that X to predict what Peter will do. That is, Sarah does not have to infer anything about the underlying belief to predict what

¹ In the literature, it is customary to distinguish between knowledge or ignorance on the one hand and belief on the other hand (e.g., Martcorena, Ruiz, & Mukerji, 2011; Perner et al., 1987). Knowledge amounts to being aware that something is the case, while being ignorant is simply to lack this awareness. To have a false belief, by contrast, is to positively believe that this state of the world does not obtain. Attributing knowledge and attributing true beliefs are however often used interchangeably.

² There are also other mental states, such as bodily feelings (e.g., a pain in the shoulder), emotional states etc. (Goldman, 2012).

Peter will do. By contrast, in the case that Peter has a *false* belief about the state of the world – that the keys are in his bag while they are in fact at home ($P_B(Y)$) – Sarah is only able to predict his behaviour by understanding his false belief. She cannot use her own belief that X to correctly predict his behaviour. Consequently, the understanding of another's false belief is thought to be the litmus test of theory of mind (Dennett, 1978). In what follows, I will thus use the term full-blown theory of mind to refer to such a mature understanding of mental states, which involves a demonstration of an understanding of other's false beliefs.

Typically, false belief understanding is assessed with some form of 'unexpected transfer' or 'unexpected location' task (Perner, Leekam, & Wimmer, 1987), often called 'Sally-Anne' task in the English literature (e.g., Baron-Cohen, Leslie, & Frith, 1985). In these tasks, the participant observes that individual A puts an object in location x and leaves the scene. Then, individual B arrives and moves the object to location y. If the participant understands false belief, she should predict that when A comes back, she will search for the object in x and not y. This accomplishment would then indicate that the participant possesses a full-blown theory of mind. Such tasks have been summarised under the term 'explicit' or 'elicited-response' (De Bruin & Newen, 2012) theory of mind tasks because they require the participant to give an explicit response in the form of a prediction regarding A's actions.

Adult humans are in general thought to possess such full-blown theory of mind abilities. However, in recent years, this general notion has been questioned. First, commentators have pointed out that humans, in their day to day life, might not really ascribe mental states (Heyes, 2014c), especially when predicting behaviour (Andrews, 2015). In the Sarah-Peter example, Sarah might as well be relying on a heuristic to predict Peter's behaviour, such as 'Peter carries his keys in his bag', because Peter has a history of doing so, rather than attributing knowledge about the whereabouts of his keys. According to this argument, only if the prediction fails, if Peter is going back to his car, Sarah would need to use theory of mind to explain his behaviour. Second, and related to the first point, the idea that human adults are proficient mind-readers has been challenged by research uncovering the limits to adults' ability to attribute perspectives (Apperly, 2011). For example, it seems that adult takes longer to answer questions about mental states compared to other representations (Apperly, Back, Samson, & France, 2008, but see Cohen, Sasaki, & German, 2015). Furthermore, adults have an egocentric bias in that they are biased by their own knowledge when interpreting instructions from others (Epley, Keysar, Van Boven, & Gilovich, 2004; Keysar, Lin, & Barr, 2003).

Theory of Mind in Infants

Research on animal theory of mind has influenced infant studies, and vice versa. For instance, Premack and Woodruff's (1978) first inquiry into chimpanzee theory of mind and the ensuing debate (e.g., Dennett, 1978; Savage-Rumbaugh, Duane, & Boysen, 1978) inspired Wimmer and Perner's (1983) design of a task to investigate false belief understanding in children. Hence, in what follows, I shall give a brief overview of work that has been conducted with children before turning to the animal literature.

Children younger than four years of age typically fail false belief tasks (meta-analysis by Wellman, Cross, & Watson, 2001). Their mistakes follow a systematic pattern across the different tasks used: they respond with what they know to be true without acknowledging what others believe. In an unexpected transfer task, for example, many children (incorrectly) predict that protagonist A will look for an object in location y, while A has no way of knowing that the object is there, given that she was not present when the object was transferred from x to y. Before children develop a full-blown theory of mind that would allow them to pass this test, however, they can attribute other mental states. At 24 months of age, they can acknowledge what others can see (Moll & Tomasello, 2006). Subsequently, aged three years, they understand how others see objects and that not-seeing leads to ignorance (Moll & Metzloff, 2011). Empirically, it thus seems that, for children, it is easier to attribute knowledge (and ignorance) than beliefs because attributing beliefs requires the representation of an alternative model of the world (Hogrefe, Wimmer, & Perner, 1986).

Consequently, understanding perceptual states and knowledge is thought to emerge prior to the development of a full-blown theory of mind. Similarly, the ability to attribute desires has been reported to develop earlier than the understanding of beliefs (Repacholi & Gopnik, 1997; Wellman & Woolley, 1990) and thus has been suggested to be less cognitively demanding than the attribution of beliefs (Wellman & Woolley, 1990). Hence, both visual perspective taking and desire state attribution are thought to be part of theory of mind abilities, but do not constitute a full-blown theory of mind.

In the last one and a half decades, however, the notion that a false belief understanding only emerges after the fourth birthday has been challenged. It has been argued that difficulties with explicit theory of mind tasks need not result from a lack of theory of mind but could be associated with demands on executive functions and verbal understanding, or with the difficulty of thinking about representations in general (e.g., Bloom & German, 2000). For example, a theory of mind task typically requires the participant to remember a series of events and to inhibit the pre-potent response that is based on her own mental state. Thus,

individual differences in executive functioning have been reported to correlate with performance in a false belief task (for a review see Perner, Lang, & Kloo, 2002). Consequently, it is possible that task demands prevent young children from passing a false belief task.

Instead, therefore, theory of mind has been assessed with more ‘implicit’ measures, typically with violation of expectation paradigms or anticipatory looking paradigms, which were designed to reduce the cognitive demands needed in the explicit tasks. These studies suggest that false-belief understanding emerges noticeably earlier than at the age of four (e.g., Kovács, Téglás, & Endress, 2010; Onishi & Baillargeon, 2005; Southgate, Senju, & Csibra, 2007). For example, Onishi and Baillargeon (2005) used a non-verbal violation-of-expectation version of an unexpected transfer task with 15-month-old infants. The children looked longer when an agent was reaching towards a location that, unbeknown to the agent, contained a toy they saw the agent reach towards before.

In summary, infants even below the age of four seem to display an understanding of beliefs in that they seem to correctly predict the actions of an agent that has a false belief. However, it is not yet clear whether their performance cannot be explained by other mechanisms. For example, Heyes (2014b) argues that what seems like false belief understanding in infants is in fact an increased attention to ‘low-level’ novelty, such as the presentation of novel relations between objects and agents. Similarly, Perner and Ruffman (2005) argue that infants might know about rules regarding certain behaviours and events, but need not attribute mental states.

Theory of Mind-Like Abilities in Non-Human Animals

Since Premack and Woodruff’s (1978) seminal study first asked about the existence of theory of mind in chimpanzees, a range of different experiments investigating animals have been reported, primarily focusing on great apes (for a review see Call & Tomasello, 2008). Empirical data by and large suggest that great apes can take into account what their conspecific has seen and knows (Hare, Call, & Tomasello, 2001; Melis, Call, & Tomasello, 2006). For example, Call and Tomasello (1999) tested great apes on a cooperative task, where they had to take into account the false belief of an experimenter: here, the experimenter helped the participating animals to find a reward. Great apes failed to ignore the help from the mis-informed helper while children aged six could solve this task. Subsequently, this use of a cooperative task to test theory of mind in apes has been criticised because it requires a form of communication not part of the natural repertoire of chimpanzees (O’Connell & Dunbar, 2003).

Consequently, other authors have developed competitive theory of mind tasks (Hare et al., 2001; Kaminski, Call, & Tomasello, 2008).

In Hare and colleagues' (2001) study for example, a subordinate and a dominant chimpanzee saw from opposite sides into an enclosure containing two obstacles. A human experimenter placed food behind one of the obstacles in a way that only the subordinate could see the food. Crucially, the dominant could sometimes see the baiting, and sometimes not. Then, both animals were allowed access to the enclosure, with the subordinate being given a head start. In trials where the dominant did not observe the baiting process, the subordinate approached the food much faster compared to when the dominant could see where the food was hidden by the experimenter. The subordinate chimpanzees indeed differentiated between their competitor being uninformed and knowledgeable: they had a preference for food the dominant competitor would have been unaware of, suggesting that they were sensitive to what the dominant did or did not see. However, chimpanzees did not differentiate between a misinformed and a knowledgeable competitor. In the condition with a misinformed competitor, the experimenter placed the food behind barrier A, while being watched by both the subordinate and the dominant, but then, without the dominant present, moved the food to barrier B, mirroring the unexpected transfer task described above. Subordinate chimpanzees did not approach the food behind the barrier more often when the dominant was misinformed compared to when the dominant had correct information about the change of location of the food (Hare et al., 2001), indicating that they failed to account for the competitor's false belief.

Thus, it is generally acknowledged that non-human primates do not have a full-blown, human-like theory of mind (Call & Tomasello, 2008) or explicit theory of mind (C. D. Frith & Frith, 2012), because they do not seem able to respond to the false belief of a conspecific (Kaminski et al., 2008; Krachun, Carpenter, Call, & Tomasello, 2009). Recent research however might paint a different picture. First, in a looking time paradigm designed to minimise task demands, great apes looked longer at a location they expected a human experimenter to search based on his false belief (Krupenye, Kano, Hirata, Call, & Tomasello, 2016). Therefore great apes might, similar to human infants, have a form of implicit false belief understanding, an ability other non-human primates, for example rhesus macaques (*Macaca mulatta*) (Martin & Santos, 2014), do not seem to share.

In a second study, a subject either observed a human experimenter witnessing an assistant transferring a toy from box A to box B (true belief) or not (false belief) (Buttelmann, Buttelmann, Carpenter, Call, & Tomasello, 2017). Then, the human experimenter attempted to open box A (the now empty box). In the case of a false belief, when humans were trying to

open the empty box in which they expected the toy, great apes helped them by opening the other box, which actually contained the toy. The authors suggest that the subjects understood the intention of the experimenter to retrieve the toy, taking into account her false belief. In doing so, subjects performed similarly to children in the false belief task. However, they ‘failed’ the true belief task in that they chose randomly whereas children choose the empty box, seemingly inferring that here the intention of the experimenter was to open the box, not to retrieve the toy (Buttelmann et al., 2017). This result is surprising for two reasons. First, false belief tasks are usually considered to be more difficult than true belief tasks because the former requires representing an alternative model of the world (Hogrefe et al., 1986). Second, as mentioned earlier, previous research on theory of mind in chimpanzees has largely focussed on competitive tasks (Hare et al., 2001; Hare, Call, & Tomasello, 2006; Kaminski et al., 2008; O’Connell & Dunbar, 2005). Furthermore, it is possible that the participating great apes simply opened the box they last saw the object in. This was difficult for them to do in the true belief task because they had to simultaneously track the experimenter observing the switch and the assistant transferring the object (for a similar argument c.f., Heyes, 2014b). This could explain the subjects’ performance at chance level. In contrast, in the false belief task, only one person was in the room (the assistant) and thus, the transfer could be tracked, leading them to choose the correct box. Therefore, caution is warranted when drawing conclusions about explicit false belief understanding in great apes.

Theory of Mind-Like Abilities in Corvids

Primates are no longer the only non-human animals considered to possess a theory of mind (Keefner, 2016). Birds of the crow family have been subject to extensive investigation and have been suggested to possess flexible social cognitive abilities parallel to those of primates (reviewed in Clayton, Dally, & Emery, 2007a). In what follows, I shall present the most influential studies demonstrating corvids’ theory of mind-like abilities.

Why corvids? Corvidae is a family of passerine birds occurring in most climatic zones, containing for example ravens, jackdaws, crows, jays, and magpies (Clayton & Emery, 2005). Certain corvid species have been shown to be skilled tool users and makers (Bird & Emery, 2009; Hunt, 1996; Weir, Chappell, & Kacelnik, 2002; Weir & Kacelnik, 2006). Furthermore, they have an understanding of certain physical causalities (Bird & Emery, 2009, 2010; Cheke, Bird, & Clayton, 2011; Jacobs, Von Bayern, Martin-Ordas, Rat-Fischer, & Osvath, 2015) and can plan for the future (Raby, Alexis, Dickinson, & Clayton, 2007). Thus, corvids show similar levels of cognitive flexibility as great apes (reviewed in Clayton & Emery, 2004). However, the last common ancestor of primates and birds lived around 300 million years ago (Jarvis et al., 2005). This long period of parallel evolution and thus phylogenetic distance becomes apparent in the vastly different brain organization. Yet, corvids and primates seem to have developed very similar cognitive skills and complex behaviour, suggesting cognitive convergence (Güntürkün, 2012; Güntürkün & Bugnyar, 2016; Horik, Clayton, & Emery, 2012; Seed, Emery, & Clayton, 2009).

Therefore, investigating theory of mind in corvids can aid us in understanding the evolutionary precursors of human mindreading as well – namely in understanding which mechanisms are confined to primates, and which ones can be found in different taxa and thus might be an adaptation to environmental pressures that primates share with other animals (Heyes, 2014a).

Understanding ‘seeing’ and ‘hearing’. Theory of mind-like abilities in corvids have been primarily studied in the food-caching paradigm. Most corvids are food hoarders, that is, they store food for later consumption (Vander Wall, 1990). The retrieval of these caches relies on spatial memory (Clayton & Krebs, 1994). Importantly, however, some corvids such as for example California scrub-jays (*Aphelocoma californica*) are also equipped with extensive observational-spatial memory (Bugnyar & Kotrschal, 2002a; Watanabe & Clayton, 2007). That is, individuals are proficient in remembering caches made by their conspecifics, and thus are able to steal them. As a response, food hoarding birds employ a number of strategies to protect their food from pilfering conspecifics (Heinrich, 1999). Experimental studies show that these protection strategies are flexibly adjusted to an observer’s ability to see the actual caching of the food (e.g., Dally, Emery, & Clayton, 2010). When observed by a conspecific that is not their partner, scrub-jays will prefer to cache in places that are not visually accessible to an observer, for example behind an occluding barrier (Dally, Emery, & Clayton, 2004, 2006). They will also attempt to conceal their caches as best as possible, for example by hiding them further away from an observer or avoiding well-lit areas. Furthermore, they will

1: Introduction

prefer to cache in quiet compared to noisy substrate when a present conspecific can hear but not see them (Stulp, Emery, Verhulst, & Clayton, 2009). However visual access cannot always be limited or reduced at the time of caching: once they are alone, scrub-jays will thus return to a caching site and move caches made previously (i.e. while they were being observed) to new locations that are now unknown to a potential thief (Emery & Clayton, 2001). Similar protection strategies have been reported in Eurasian jays and raven (*Corvus corax*) (Bugnyar, 2011; Bugnyar & Heinrich, 2005, 2006; Bugnyar, Reber, & Buckner, 2016; Heinrich, 1999) Heinrich, 1999). Eurasian jays (*Garrulus glandarius*) for example prefer caching behind a barrier (Legg & Clayton, 2014) and re-cache (Shaw & Clayton, 2012). Cache-protection behaviour has further been shown to depend on the birds' individual experience with stealing (Emery & Clayton, 2001): birds that have previously stolen themselves, that is, that have had the experience of being a thief, are more likely to show cache protection strategies. This result suggests that birds with pilfering experience project their own experience onto others.

A more recent example that shows that corvids do not simply respond to the presence or the behavioural cues of a conspecific but understand what they can see comes from studies by Bugnyar and colleagues (2016). Here, ravens were familiarised with peepholes that allowed visual access to a human cacher. Then, in the test, they themselves were cachers and had the possibility to cache a number of food items. This was conducted either a) in an observed condition where a big window in the partition to the next compartment allowed competing conspecifics to observe them, b) in a non-observed condition where the window was closed or c) in a peephole condition with a small peephole in the partition. Crucially, in c) there were no conspecifics on the other side of the partition, but only a loud-speaker playing back sounds of a conspecific. Bugnyar and colleagues (2016) show that the ravens treat the peephole condition similarly to the observed condition in that they quickly cached the food items available to them and did not return to their caches, possibly in order to avoid drawing attention to them. Importantly, the use of a peephole made it impossible to rely on visual cues emitted by an observer, such as her line of gaze. This result thus suggests that ravens take into account that their conspecifics can observe their caches³ even if there are no cues from the observer, using their own experience about peepholes from the familiarisation.

³ Note however, that it is not clear what the cacher could infer in this experiment; for example, they might have been able to see through the peepholes that no bird was present in the next compartment. Furthermore, the cache protection strategies shown by the ravens seemed to have been inferred post-hoc and do not mirror strategies found in other experiments with corvids (Emery & Clayton, 2017).

Understanding knowledge states. There is some evidence that scrub-jays seem to attribute knowledge states to others (Dally, Emery, et al., 2006) in that they appreciate that an observer who has observed a caching event should know about the caches, whereas an observer who has not seen the caching is ignorant about the caches. In Dally and colleagues' (2006) study, birds were observed during caching once by conspecific A and once by conspecific B. When being observed by A, they could only cache in tray A, while a second tray B was present but covered with plastic strip, while the opposite pattern was the case when they were observed by B. Later, when they had the chance to recover food items to safety in the presence of either one of the competitors (A or B), they preferred to recover and remove food previously cached in the presence of this competitor, disregarding caches made in the presence of the other competitor. For example, if observed by A during recovery, they recovered food that they have previously cached in the presence of A and disregarded caches made in the presence of B. Here, competitor A posed a threat only to the caches she knew about – that is, the one that had been cached in her presence. Re-caching caches from tray B would have provided A with information about caches she had previously been ignorant about, and would thus have allowed her to pilfer them.

Understanding desire states. More recent research has focussed on desire state attribution and made use of Eurasian jays' propensity to share food with their mated partner. Male Eurasian jays have been found to attend to their partner's desire when catering for her during courtship feeding (Ostojić, Shaw, Cheke, & Clayton, 2013). In these studies, Ostojić and colleagues (2013, 2014, 2016) used the fact that animals can learn that eating one type of food to satiety will lead to a decreased desire for that food, largely independent from desire for other food types (Balleine & Dickinson, 1998; Dickinson & Balleine, 1994). Thus, Ostojić et al. (2013) manipulated their subjects' desire by prefeeding them a certain type of food: the value of this food should then be decreased while other foods stay desired. When males were presented with their partner being sated on a certain type of larvae (for example larvae of the wax moth, *Galleria mellonella*), they shared more of a different type of larvae (larvae of the mealworm beetle, *Tenebrio molitor*) than when the partner was fed on larvae of the mealworm beetle.

This work was recently been extended to a caching context by investigating Eurasian and scrub-jays' desire state attribution in a cache-protection context (Ostojić et al., 2017). This approach served an additional purpose: so far desire-state attribution has only been shown in a food-sharing context. However, evidence for the attribution of desires acquired in more than one situation would support the notion that corvids can extrapolate across different

situations on the basis of attributing mental states (c.f., Heyes, 1993; Penn & Povinelli, 2013). Thus, it was of interest whether corvids would be able to attribute desires in a context other than food sharing. Ostojić and colleagues (2017) allowed cachers to watch a conspecific observer being pre-fed on different types of food, and subsequently allowed a cacher to cache both the same and a different food type. Results of this study suggest that birds take into account the desire of an observer when protecting their caches in that they prefer to cache food the observer has been pre-fed on and does not desire.

False belief understanding. So far there is no research on the question whether corvids can take into account the false belief of their conspecifics. Such an ability would suggest that corvid theory of mind-like abilities extend beyond a simpler understanding of perspective taking and desire state attribution, and comprise the understanding that others behaviour can be driven by their counterfactual mental states rather than reality.

Previous work suggests that scrub-jays are at least able to attribute knowledge: Emery and Clayton (2001) show that scrub-jays with experience in pilfering would re-cache food they previously cached when they were observed by a conspecific. Scrub-jays thus seem to use their own experience about which information is relevant to a pilferer to protect their caches – in other words, they might be able to attribute knowledge to their conspecific observer. They manipulate this knowledge by re-caching and thus vitiating the observer's knowledge about their caches. However, note that this study does not explicitly test whether the cacher assumes that the observer has a false belief or whether the cacher assumes that the observer is simply ignorant about the true location of the caches. Still, this study suggests that corvids could be a potential candidate for false belief understanding.

In summary, these results suggest that corvids respond to the visual perspective, desires and knowledge of their conspecific competitors and use their own experience in doing so (see Clayton & Emery, 2005; Clayton et al., 2007). However, as will shortly be discussed, it is still an open question whether they do so by using behavioural cues or by attributing mental states.

Alternatives to Theory of Mind in Animals

A number of critiques have been voiced, both of the explicit and implicit measures of theory of mind in animals (Heyes, 2014a, 2017; Lurz, 2011; Penn & Povinelli, 2007, 2013). Here, I shall loosely summarise them as 'behaviour reading accounts'. Such accounts share one important feature: they claim that animals rely predominantly on certain regularities in a conspecific's environment and the *effect* of the mental states of that conspecific (i.e., the behaviour) rather than on the actual mental states. Specifically, Penn and Povinelli (2007)

argue that suggesting that animals are able to attribute visual perspective and knowledge to others is not the most parsimonious explanation for their performance. Rather, they suggest, animals react to some form of behavioural and contextual cues that they have learned about in previous encounters with conspecifics (Dennett, 1983; Penn & Povinelli, 2007), similarly to the Peter-Sarah example discussed earlier.

How do behaviour reading accounts explain the results reported above? For example, Hare and colleagues' (2001) chimpanzees could use a strategy such as "Don't go after food if a dominant that is present has oriented towards it" (Penn & Povinelli, p. 735). This strategy could be based on a rule that has been learned by the subordinate about the relationship between a set of observable cues and behaviour (Heyes, 1993). Such observable cues would be "eyes of dominant orientated towards food" or "A had visual access during placement of food". Thus, in such a situation, the subordinate would have no need to infer the mental states underlying the dominant's behaviour. In the case of the caching studies, birds could have associated the items cached while an observer was present with her line of gaze. Then, they could have used a rule such as "re-cache food if a conspecific's line of gaze is associated with it" (Penn et al., 2008; Penn & Povinelli, 2007).

However, behaviour-reading accounts have been challenged. It is unclear whether or not a learned association between "conspecific observed the caching" and "conspecific was able to pilfer the caches" can explain the scrub-jays versatile cache protection strategies (for a review see Emery & Clayton, 2008). For example, scrub-jays do not protect their caches when presented with a mirror image of themselves during caching. Therefore, they do not simply respond to the sighting of a 'conspecific' (Dally et al., 2010). This implies that the behavioural rules suggested by Penn and Povinelli (2007) need great flexibility and abstraction, an issue Penn and Povinelli (2007, 2013) explicitly acknowledge. Thus, behaviour-reading animals would require a series of flexible rules that can be applied in different context and in interaction with different individuals and their potentially distinct behaviours (c.f., Emery & Clayton, 2008).

The issue with behaviour-reading accounts is that they are post-hoc in that they have not been positively tested. New behavioural rules are introduced to explain findings only after the performances in new theory of mind tasks have been reported (Fletcher & Carruthers; Halina, 2015), thus making the behaviour-reading account difficult to falsify. However, the question about which skills a behaviour-reading animal has should be subject to empirical investigation with clear predictions (Halina, 2015; Heyes, 2014a). Therefore, theory of mind research should involve clear specifications and tests of the behaviour-reading hypothesis.

A Basis for Corvids' Social Cognitive Abilities?

While there is ample research on theory of mind-like abilities in corvids, relatively little is known about the precursors of such abilities. Put differently, what is the basis of this sophisticated accomplishment? A candidate for such a basis⁴, or “substrate”, might be an increased attention towards animate agents (Heyes, 2014c, p. 140).

Agents are defined as entities that behave on the basis of their internal states (Barrett & Johnson, 2003). Events involving social agents are unpredictable and often have a larger degree of freedom than events involving physical objects (Gelman & Spelke, 1981). Agents are thus much more complex than objects (Legerstee, 1992, 2005). In humans, a special attention towards other social agents is generally thought to be a highly relevant disposition that allows humans to learn about the relevant aspects in their environment (Rakison & Poulin-Dubois, 2001). This, in turn, allows the development of more complex social cognitive abilities, for example theory of mind (Flavell, 1999). A special attention to social agents might thus also be relevant for theory of mind-like abilities in corvids. Previous studies suggest that certain corvid species prefer observing a conspecific over an object or an empty cage (Bird & Emery, 2008) and that they prefer watching a conspecific cache over simply looking at a caching tray (Grodzinski, Watanabe, & Clayton, 2012). Both studies suggest that agents are particularly interesting for corvids. It is thus conceivable that this interest for social agents forms the basis upon which corvids' complex social abilities are built. There are a range of different features that can be used to differentiate between animate agents and inanimate objects, but motion is probably the most readily observable of them (Rakison & Poulin-Dubois, 2001). There are different characteristics of motion that are relevant for differentiating animate from inanimate agents, for example the onset of motion (self-propelled vs. caused motion), the line of trajectory, and the pattern of interaction with other objects (contingent vs. non-contingent) (Rakison & Poulin-Dubois, 2001). Furthermore, agents generally possess a face and eyes (Legerstee, 2005), and therefore faces and eyes are important features to learn about (Johnson & Morton, 1991). Indeed, human infants follow gaze directions (Butterworth & Jarret, 1991; Hood, Willen, & Driver, 1998) and are sensitive to whether adults are looking at them or looking away from them (Hains & Muir, 1996). In animals, too, there is good evidence that eyes constitute crucial stimuli (reviewed in Davidson, Butler, Fernández-Juricic, Thornton, & Clayton, 2014). For example, rhesus macaques (Emery, Lorincz, Perrett, Oram, & Baker, 1997; Ferrari, Kohler, Fogassi, &

⁴ This basis need not be of a ‘social’ nature but could be domain-general. Heyes for example proposed on several occasions that there might be domain-general attention that equips the human infant to acquire social abilities (e.g., Heyes & Frith, 2014)

Gallese, 2000) and ravens (Bugnyar, Stöwe, & Heinrich, 2004) will follow the gaze of a human, and primates will also follow the gaze of a conspecific (Tomasello, Call, & Hare, 1998). Wild jackdaws (*Corvus monedula*) also tend to respond to a human's gaze with defensive behaviour (Davidson, Clayton, & Thornton, 2015). In humans, newborns also attend more closely to and track preferably face-like patterns compared to non-face patterns (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991). Consequently, it is of interest whether the motion, eyes, and faces of conspecifics are of similar interest to corvids.

Overview of Thesis

In summary, previous research suggests that corvids, similar to great apes, take into account the perceptual states, knowledge and desires of a conspecific. They seem to be sensitive to what others can see and hear, what they know and what they desire, and they seem to use their own experience to do so (reviewed in Clayton et al., 2007). However, the answers to a number of questions are still outstanding, and in my thesis I have chosen to focus on the following two in particular:

- 1) What are the limits of theory of mind in corvids?
- 2) Which mechanisms could be the basis of these abilities in corvids?

In this thesis, I investigated the behaviour and cognitive capacities of three species of food caching corvids: Eurasian jays, California scrub-jays, and carrion crows (*Corvus corone corone*). All three species form long-lasting relationships with their mated partner, a feature that has been related to social intelligence and cognition, such as theory of mind (Emery, 2004; Emery, Seed, von Bayern, & Clayton, 2007). Eurasian jays do not live in social groups. However, during breeding season, they will pair up and defend their territory with their mated partner (Goodwin, 1951). California scrub-jays, like Eurasian jays and unlike their closely related Florida and Mexican scrub-jays, do not breed cooperatively (Clayton & Emery, 2007). Scrub-jays are semi-territorial and flock in small groups outside of breeding season (Balda, Kamil, & Bednekoff, 1996). Carrion crows live in territorial pairs, similar to Eurasian jays as well as ravens (Clayton & Emery, 2007), and breed mostly unassisted (Richner, 1990). However, under certain environmental conditions, they have been reported to breed cooperatively with their relatives (Baglione, Marcos, & Canestrari, 2002). The social bonds of all three species require a considerable amount of coordination with their partner (Emery et al., 2007). Furthermore, it has been hypothesized that their caching and pilfering behaviour created a need to defend caches from pilferers which in turn might require theory of mind-like abilities such as being able to respond to the perspective of a conspecific (Grodzinski &

Clayton, 2010a). Both the complexity in social groups and the competition over food has been suggested to be related to complex social cognition, such as theory of mind (Clayton et al., 2007).

In **Chapter 2**, I present a paradigm to test the understanding of false belief in Eurasian jays, where the knowledge of a conspecific observer about the accessibility of a caching site was manipulated. At the beginning of the task, subjects had access to only one of two caching trays because one of the trays was covered with a Perspex lid. During caching, however, a curtain between the cacher and a conspecific observer in an adjacent cage obscured the observer's view. Unbeknown to the observer, the experimenter removed the cover, and cachers were now able to access both caching trays. Thus, the observer had a false belief about the accessibility of one of the caching trays. Prior to the false belief task it was ascertained that this manipulation worked and that the observer did have a tendency to search preferentially in the seemingly only accessible tray. If the cachers understood the false belief of the observer in regard to the accessibility of one of the two caching trays, they would be expected to preferentially cache in the tray the observer thought to be inaccessible. However, the cachers did not show a preference for the 'inaccessible' tray when an observer was present, compared to when there was no observer present. Thus, the results provide no evidence for an ability to attribute false beliefs in Eurasian jays.

While birds might not be able to reason about the beliefs of a conspecific, previous research suggests that they do respond to the desire of a conspecific (Ostojić et al., 2014, 2016, 2017, 2013). Interestingly, to protect their caches birds responded to the desire states of a conspecific observer both when they could see what food the observer has been pre-fed on prior to the caching event and when the pre-feeding was concealed from them (Ostojić et al., 2017). With this, Ostojić and colleagues' (2017) study specifically included a condition to assess whether birds could have used behavioural cues to respond to the desires of a conspecific observer. Hence, this study constitutes a starting point to investigate which exact cues corvids could use in order to respond to mental states of their conspecifics.

In **Chapter 3** I thus build on this work by Ostojić and colleagues (2017). Specifically, I focussed on observers and how their behaviour could have been altered by experiencing a decreased desire for different foods. Here, observers were pre-fed on food A and then either saw food type A or food type B being cached by a human experimenter. Using peepholes, I assessed the observers' attention towards the caching events. Additionally, in a second experiment, I allowed birds to observe a caching conspecific more freely, exploring where and how close to the cacher they would stay during the caching. In the first experiment, birds

tended to attend more to the caching when the food they desired was being cached while in the second experiment there was no clear change of the observer's behaviour as a function of her desire. This finding suggests that observers might show certain behavioural changes, which could be used by the cacher to determine what food she should cache. Thus, it is likely beneficial for a cacher to pay close attention to the behaviour of its conspecific observer to determine what she is likely to do. To do so, corvids need to be especially interested in other conspecifics. Consequently, in the subsequent chapters 4, 5 and 6, I focus on different cues that, in humans, are indicative of social agents. These cues have been suggested to guide attention to and, consequently, learning about social agents and their (inter-) actions (Rakison & Poulin-Dubois, 2001). Such cues could thus also be relevant for corvids and build a basis for their theory of mind-like abilities.

In **Chapter 4**, by using peepholes to measure looking time in scrub-jays, I first investigate whether corvids indeed show an increased interest in their conspecific. Scrub-jays were used in these experiments because previous looking time studies have shown that scrub-jays will look more at events that are of interest for them (Grodzinski et al., 2012; Watanabe, Grodzinski, & Clayton, 2014). I demonstrate that scrub-jays have a preference to observe a conspecific agent, compared to a novel object. But what is it that they use to differentiate an agent from an object? One important feature (among others) of an agent seems to be that its motion is biological (Poulin-Dubois, Crivello, & Wright, 2015). Hence, preference for biological motion as a means to distinguish inanimate from animate entities has been proposed to be crucial for social cognition. Especially intriguing is the finding that, when given only the reduced information provided by moving dots, humans readily detect the movements of an agent in these dots and have a strong preference for such biological motion patterns even from a very early age (Simion, Regolin, & Bulf, 2008). Support for a similar preference for biological over random motion in animals with higher social-cognitive abilities such as corvids could be relevant for the question whether or not corvid theory of mind rests on similar mechanisms as human theory of mind. Therefore, in two additional experiments birds were allowed to observe through peepholes random motion and two different types of biological motion patterns. The biological motion was either that of another scrub-jay or the unfamiliar motion pattern of a horse. In both experiments, birds did not prefer to observe the biological motion over the random motion patterns.

Motion is not the only relevant cue animals need to attend to. A sensitivity to the direction of gaze has long been of interest in the theory of mind literature as a precursory ability: others can see only things that are in their line-of-sight (Povinelli, Bering, &

Giambrone, 2000). Thus, ‘mind-readers’ should be sensitive to gaze. Note though that a sensitivity to gaze is also relevant for ‘behaviour-readers’: if, as suggested in Chapter 3, birds’ attention can give conspecifics cues about what they desire, and are thus likely to pilfer, it would be important to attend to these cues. In humans, understanding what others can see is associated with the perception of direction of gaze, which is generally thought to be crucial in learning about others’ intentions and beliefs (Farroni, Csibra, Simion, & Johnson, 2002; Langten, Watt, & Bruce, 2000). In the context of cache-protection strategies in corvids, however, it is so far unclear whether cachers take notice of the observer’s gaze and eyes, which might be related to the understanding that a conspecific can see the caching event (Povinelli et al., 2000), or whether cachers simply react to the presence of an observer. It was the aim of **Chapter 5** to determine whether scrub-jays take into account the direction of gaze of an interactant in two different contexts. Firstly, birds were presented with a human experimenter who was either facing towards them or away from them while they had the chance to retrieve food in front of the experimenter. Scrub-jays took longer to approach food when a human experimenter looked towards them, compared to when she was facing the other way. This is in line with prior studies showing that corvids are sensitive to the direction of gaze of a human experimenter (von Bayern & Emery, 2009). Secondly, the influence of direction of gaze on two different cache-protection strategies was assessed: cache-protection at the time of caching by caching preferentially out of the observer’s view or by re-caching once they are in private. The observer’s direction of gaze was manipulated with video playback. If scrub-jays understand the importance of the observer attending to the caching-event, they should only protect their caches when confronted with a conspecific directing its attention towards them but not when confronted with a conspecific looking the other way. However, contrary to prediction, the birds did not protect their caches from a forward facing observer presented as video playback by caching preferentially in the out-of-sight location and did not re-cache caches that the observer had had visual access to.

In **Chapter 6**, I investigated the relevance of faces. Due to their high ecological relevance for social species, it has been suggested that faces are processed differently than other stimuli (Kanwisher & Yovel, 2006; Yovel & Kanwisher, 2004). In line with this hypothesis, when compared to stimuli of other categories, recognition and memory of faces is disproportionately impaired when faces are presented upside down although both upright and inverted stimuli carry the same physical information (Yin, 1969; for reviews see Rossion and Gauthier 2002; Valentine 1988). In this chapter, I used a delayed matching-to-sample task to investigate the face inversion effect in two carrion crows. In the task, crows had to recognise

the profile of crow faces, presented upright and inverted. Furthermore, the crows were presented with upright and inverted pictures of human faces, because previous research suggested that wild American crows (*Corvus brachyrhynchos*) discriminate humans on the basis of their faces (Marzluff, Walls, Cornell, Withey, & Craig, 2010). Performance in recognising human and crow faces was compared to performance when recognising matched non-social controls.⁵ Both crows tested, however, did not show a face inversion effect, neither for crow-faces nor for human-faces.

Finally, in **Chapter 7** I discuss how the studies I have conducted relate back to the questions I asked in this introduction and how they could help us inform our understanding of corvid theory of mind-like abilities. Specifically I address the following issues. First, in Chapter 2, I did not find evidence of false belief understanding in Eurasian jays in a caching context. Second, the results presented in Chapter 3 support the notion that corvids can, at least in principle and in certain situations, read the behaviour of conspecifics. Third, corvids seem to be interested in agents as such (Chapter 4) and responsive to where others are looking (Chapter 5). However, scrub-jays do not seem to be attentive to biological motion patterns (Chapter 4), and carrion crows do not show a face inversion effect (Chapter 6). Superficially, their theory of mind-like abilities suggest that corvids are ‘feathered apes’ (Emery, 2004) in possession of a similar cognitive tool-kit to that of primates (Emery & Clayton, 2004b). Parallels found in behaviour, however, need not imply comparable underlying mechanisms, especially in the case of more complex abilities (Güntürkün & Bugnyar, 2016). It is thus possible that human theory of mind and corvid theory of mind-like abilities rest on different mechanisms: humans seem to be very tuned to a range of different cues of agency, such as the perception of biological motion (e.g., Grossmann, Cross, Ticini, & Daum, 2012; Pavlova, 2012). Taken together the results of my experiments suggest that although corvids might be sensitive to conspecifics and to how conspecifics are related to and interact with objects in their world, they do not seem to be sensitive to cues that, in humans, have been associated with social cognitive abilities, such as theory of mind.

⁵ Additionally, the capacity of the stimuli and procedures used to produce a face inversion effect was validated by testing human adults on the same delayed matching-to-sample task.

Chapter 2

False belief understanding in Eurasian jays

The ability to understand false beliefs is considered to be a litmus test of a ‘full-blown’ theory of mind, because it involves the ability to understand that others’ mental states can differ from reality. So far, research investigating corvid theory of mind has mainly focussed on the ability to consider what others can see or hear, and therefore know, rather than the ability to attribute false beliefs. Here, I report a novel paradigm to investigate false belief understanding in Eurasian jays. Initially, an observer watched a cacher have access to one of two caching trays because one of the trays was covered with a transparent Perspex lid. During the subsequent caching phase, the cacher could now access both caching trays, unbeknown to the conspecific observer in an adjacent cage whose view was obscured by an opaque curtain. Critically, the acoustic cues exhibited by the cacher were concealed by using a ‘quiet’ caching substrate (sand) so that the observer could not hear whether or not the cacher was hiding food and, if so, where. Consequently, the observer should have formed a false belief about the cacher’s access to one of the caching trays, namely the one that had previously been made inaccessible by covering it with the lid. If the cacher understands that the observer has a false belief about the caching trays, then that bird should cache more in what the observer thought to be the inaccessible tray (hereafter ‘inaccessible’ tray) than in what the observer thought to be the accessible tray (hereafter ‘accessible’ tray). Prior to the false belief task, birds in the role of observers were provided with the experience that Perspex lids make caching trays inaccessible. Importantly, as observers, they had no knowledge of the removal of the lid. In addition, it was tested whether observers – when given the opportunity to search through the two caching trays after the caching event – will preferentially search in the tray they predict the cacher will have hidden food in, namely the ‘accessible’ tray. There were two key findings. The first is that the observers tended to search more in the ‘accessible’ tray than in the ‘inaccessible’ one, as predicted. However, cachers did not show a preference for caching in the ‘inaccessible’ tray contrary to prediction. In short, the experience of which tray was accessible and which one was inaccessible did influence the observer’s pilfering behaviour, but it did not influence the cacher’s behaviour. Therefore, these findings provide no evidence that they can attribute false beliefs to others.

Introduction

An individual in the possession of a theory of mind should be capable of drawing inferences about someone else's unobservable mental states. These inferences subsequently allow the individual to explain and predict others' actions (C. D. Frith & Frith, 1999). In corvids so far, most research on theory of mind has revolved around visual (e.g., Bugnyar et al., 2016; Clayton et al., 2007; Dally et al., 2004, 2010; Emery & Clayton, 2001; Shaw & Clayton, 2012) and auditory perspective taking (Shaw & Clayton, 2014; Stulp et al., 2009) as well as knowledge state (Bugnyar, 2011; Dally, Emery, et al., 2006) and desire state attribution (Ostojić et al., 2014, 2017; Ostojić, Shaw, Cheke, & Clayton, 2013). Thus, a range of different studies suggest that corvids can account for what others can and cannot see or hear, and for what they desire, and predict the likely future actions of pilferers based on their own experience of having played that role in the past (Emery & Clayton, 2001). A 'full-blown' theory of mind, however, also involves the ability to acknowledge that others can believe things that are not necessarily true. This chapter aims to demonstrate such an understanding in Eurasian jays.

More specifically, in order to demonstrate a full-fledged understanding of others in terms of their beliefs, it is crucial to show that an individual S can predict the actions of a protagonist P by attributing mental states to P, such as the belief that the world is in state Y, $P_B(Y)$, even when the world is in fact in state X (Dennett, 1978). If S predicts the actions of P based on a true belief $P_B(X)$, it is in principle possible for S to do so by simply knowing the state of the world X, that is, without having to infer P's belief about the world, $P_B(X)$. To return to the Sarah-Peter example in Chapter 1, if Sarah predicts Peter to search for his keys in their true location, his bag, Sarah could do so by simply using her own (correct) knowledge about the location of the keys. Hence, for an experimenter a situation where S predicts P's action by attributing a true belief to P, $P_B(X)$, is indistinguishable from S predicting P's actions based on her own knowledge. As argued in Chapter 1, an understanding of false belief needs to be established in order to demonstrate full-blown belief understanding. Therefore, false belief tasks are thought to be the litmus test of theory of mind (Dennett, 1978).

Understanding false beliefs in humans is typically assessed with a task where a situation changes from X to Y, unbeknown to a protagonist. Participants then have to predict the behaviour of a protagonist based on the protagonist's now false belief $P_B(Y)$ (e.g., Baron-Cohen et al., 1985; Butterworth, 1994; Wellman et al., 2001). Only older children seem to understand that others can have a belief about reality that actually contradicts the state of reality or one's own belief about reality (Wellman, Cross, & Watson, 2001). In animals, false

belief understanding has been investigated in great apes (Buttelmann et al., 2017; Call & Tomasello, 1999; Hare et al., 2001; Kaminski et al., 2008; Krupenye et al., 2016) – that is, so far, in research on false belief understanding in non-human animals great apes have been the prime subject of interest. One example of such a task has been presented by Call and Tomasello (1999), where a reward was hidden in one of two containers. The apes were given the opportunity to pick one of them. An experimenter helped the apes search for the food by marking the container she saw the food being hidden in (situation X). Initially, this helper sees the baiting while the apes themselves could not see which container was baited. Critically, in the false belief condition, the experimenter left the room, and the food reward was moved to the other container (situation Y). Upon their return, the experimenter marked the container according to her now false belief. To succeed, the animals had to ignore the marking in the false belief condition, and pick the other container; however, they failed to do so.

In corvids, research has mainly focussed on the understanding of which conspecific has knowledge about X and which conspecific is ignorant towards X (Bugnyar, 2011; Dally, Emery, et al., 2006; Emery & Clayton, 2009; Grodzinski & Clayton, 2010a), as well as the understanding of another's visual and acoustic perspective (reviewed in Clayton et al., 2007, Grodzinski & Clayton., 2010a) and desires (Ostojić et al., 2014, 2016, 2017, 2013). Specifically, corvid theory of mind-like abilities have been predominantly investigated in a caching context where corvids are reported to protect their cached food from pilfering conspecifics (e.g., Clayton et al., 2007; Dally et al., 2004; Grodzinski & Clayton, 2010a). The reason is that, in corvids, conspecifics pose a particular threat to caches (Vander Wall, 1990) because – unlike most animals that cache – corvid observers remember where food was hidden ('observational spatial memory'; Watanabe & Clayton, 2007; Kamil & Balda, 1985) and use this memory to efficiently steal this food at a later date once the cacher has left the scene (Watanabe & Clayton, 2007). To avoid this cache loss, California scrub-jays as well as Eurasian jays will try to limit an observer's visual and auditory access to their caches (Dally et al., 2004; Dally, Emery, & Clayton, 2005; Dally et al., 2010; Legg & Clayton, 2014; Shaw & Clayton, 2012, 2013, 2014; Stulp et al., 2009), suggesting that they take into account what others can perceive. If this is not possible, scrub-jays have been reported to relocate previously made caches to a new site the observer has no knowledge about once they are alone (Dally et al., 2010; Emery & Clayton, 2001) or to engage in confusion tactics of re-caching multiple times within the same area if the observers remain (Dally et al., 2006). Furthermore, scrub-jays' cache protection behaviour suggests that they keep track of which

particular observer knows what – they thus seem to attribute knowledge to conspecifics (Dally, Emery, et al., 2006). Similarly, ravens differentiate between conspecifics that know about their caches and conspecifics that can only guess where their caches are located (Bugnyar, 2011). This finding, however, does not answer the question of whether or not the cachers understand that their competitors might have a correct or false belief about the whereabouts of their caches. These previous studies do not explicitly test whether the observer did form a false belief about the caches of the conspecific, for example, where Dally and colleagues' (2006) ignorant observer will search. Furthermore, in Bugnyar's (2011) case, the observer is simply ignorant about the caches but does not necessarily have a false belief. As discussed previously, being ignorant generally amounts to not being aware of something whereas having a false belief generally amounts to positively believing that something else is the case (see Chapter 1).

Specifically, in these previous studies, the observer was either knowledgeable or ignorant regarding the location of caches. In the present study, a novel modification of a caching experiment was used to investigate *false* belief understanding in corvids. To this end the knowledge of the observer about the accessibility of caching sites was manipulated. According to the observer, a cacher had access to only one of two caching trays because one of the trays was covered by a transparent Perspex lid, thereby making it completely inaccessible. However, unbeknownst to the observer, the cacher could in fact access both caching trays. Thus, the observer had a false belief about the accessibility of one of the caching trays: her belief that the seemingly inaccessible tray was inaccessible (situation X, e.g., “the left tray is inaccessible and no caches can be hidden here”) was vitiated (situation Y is the case, e.g., “both trays are equally accessible, and caches can be hidden in both trays”). Consequently, the observer would have no reason to search in the seemingly inaccessible caching tray. Therefore, if birds understand that the observers have a false belief about the accessibility of those caching trays, they should cache more in the seemingly inaccessible (henceforth ‘inaccessible’ caching tray) than the seemingly only accessible tray (henceforth ‘accessible’ caching tray).

Overview of Procedure

An initial series of tests was conducted to ensure that the necessary prerequisites and experiences to succeed in the false belief task were given. Specifically, the study involved the following steps. *Step I* provided the birds with the experience that a transparent Perspex lid renders items underneath inaccessible. *Step II* tested which tray an observer will search in when she believes that one of two trays was inaccessible to a cacher because a Perspex lid

was positioned over it. Only if the observer preferentially pilfers the accessible over the seemingly inaccessible tray would caching in the ‘inaccessible’ tray be an efficient cache-protection strategy. In addition, Step II allowed the birds to experience the perspective of the observer. Specifically, they learned that, as *observers*, a) they cannot witness the caching event, and b) they are under the impression that one of the trays is inaccessible. Subsequently in *Step III*, birds experienced that the Perspex lid can be removed. At the same time, this step ensured that they would cache in the tray after the lid has been removed. Finally, in the false belief task (*Experiment 2.1a*) it was tested whether cachers took into account that an observer had a false belief about the accessibility of a location. Lastly, birds participated in a true belief task (*Experiment 2.1b*) where the observer had a true belief about the accessibility of the caching tray because she witnessed the lid removal prior to the cacher’s caching event.

Note that Step II and the false belief task (*Experiment 2.1a*) were connected. Birds participated first as *observers*, to gain experience of the (in)accessibility of trays (*Step I* and *Step II*). Then, after familiarisation with the lid (*Step III*) they participated as *cachers* in the false belief task. Thus, *Step II* provided experience to one bird in the role of the observer and at the same time constituted *Experiment 2.1a*, a false belief task, for a different bird in the role of the cacher. Birds needed this experience of the different accessibility of the trays as observers before they could participate in the false belief task as cachers; thus birds were observers first, before they could take part as cachers in *Experiment 2.1a*. Therefore, *Step II* was conducted in private so that the cacher received no feedback about the observer’s behaviour. Furthermore, for the first observer to participate in *Step II*, a cacher was required whose data would not be included in the analysis of the false belief task.

To illustrate the order in which a bird that participated in both roles experienced the different steps of the study, I will report the methods and results of *Step I* and *Step II* before describing the experience of the removability of the lid (*Step III*) and the false and true belief task itself (*Experiment 2.1*).

Experience with (In-) accessibility (*Step I* and *II*)

In *Step I*, the Eurasian jays were presented with a Perspex lid covering a bowl of larvae of the wax moth. In *Step II*, birds saw two caching trays, one of them covered with a Perspex lid in the compartment of a conspecific. A curtain was drawn between the compartments of the observer (the focal bird) and the cacher, so the observer did not have visual access to the removal of the lids. Importantly, sand was used as substrate so the birds were not able to use acoustic cues to infer in which of the two trays the cacher was caching (e.g., Shaw & Clayton, 2014b; Stulp et al., 2009). After the caching ended, the observer had

the possibility to search for caches in both trays. Furthermore, the pilfering phase was conducted in extinction, that is, there were no nuts to be found in either tray to avoid the possibility that birds were using smell or visual cues emanating directly from the caches to guide their search. Previous studies found that when birds see food being hidden in one of two locations and later on have access to both locations that are empty, they will search longer in the location that they find more surprising to be empty (Garland & Low, 2014). Consequently, it was predicted that if birds (falsely) believe that the cacher has only access to the ‘accessible’ tray, they should approach the ‘accessible’ tray first. Furthermore, they should search more in the presumably only accessible tray.

Note that while all the Eurasian jays had received ample experience with Perspex barriers (such barriers are used to allow birds to see a conspecific but not interact with her, for example, Ostojić et al., 2013), birds from colony 1 had no experience of Perspex being used to cover caching trays. Contrary to that, the birds from colony 2 had previous experience with covered caching trays (Shaw & Clayton, 2014) because in Shaw and Clayton’s (2014) experiment, parts of a caching tray had been covered by a transparent Perspex strips.

Method

Subjects and housing. The subjects were 10 Eurasian jays (three female) from two separately housed colonies at the Sub-department of Animal Behaviour, Madingley. Birds from colony 1 were born in 2007, and birds from colony 2 in 2008, and were sourced from a registered breeder. They were hand-raised and had coloured rings for individual identification. All birds had previously participated in previous research (see Appendix A, Table A1) involving caching and pilfering (e.g., Legg & Clayton, 2014; Ostojić et al., 2017; Shaw & Clayton, 2013, 2014).

Birds were housed in outdoor aviaries (20 x 6 x 3m) constructed of wood and mesh with gravel floors (see Appendix A, Figure A.1, Panel A). A variety of perches and enrichment, in the form of small toys and other novel objects, were available in the aviaries. Outside of testing, all jays had ad libitum access to their maintenance diet consisting of a mix of dog biscuits, seeds, nuts, cheese, vegetables and fruits.

Experiments in this and Chapter 3 were conducted under the UK Home Office Project Licence PPL 80/2519. For testing, birds were brought into indoor compartments (1 x 2 x 2m) (see Appendix A, Figure A.1, Panel B). Birds were deprived of their maintenance diet for around 1h on testing days to motivate participation. During testing and at all other times, birds had ad libitum access to water. Birds from colony 1 (Caracas, Dublin, Lima, Lisbon, Quito, Jerusalem, and Washington) were tested by me, and Natalie Williams tested birds from

colony 2 (Romero, Hoy, and Pendleton). Data were collected from November 2015 to February 2016.

Set-up. Birds were tested in a compartment measuring 1 x 2 x 2m. Wooden platforms ran across the whole length of the compartment. The Perspex lid used in this and later Steps was transparent at the top, and had a wooden frame (~ 5cm high) that allowed making caching trays in later steps inaccessible in their entirety. That is, there was no possibility for the birds to peel off the lid, or to cache items on the sides of the caching tray.

In Step I, a bowl with worms was covered with a Perspex lid and placed in the middle of the compartment. The experimenter put worms on and around the Perspex lid, and left the testing room.

In Step II, two compartments were used with the set-up depicted in Figure 2.1, panel A. Two caching trays, one of which was covered with a Perspex lid at the start of the trial, were placed into the adjacent compartment (the cacher's compartment). Both compartments had small windows (~40cm x 40cm) in the compartment wall that allowed the experimenter to remove or return the lid. A middle compartment between the cacher's and the observer's compartment was left empty to allow the experimenter to access the windows. A curtain next to the observer's compartment allowed the experimenter to restrict the observer's visual access to the cacher's compartment.

Caching trays were seedling trays containing 5 x 3 small flower pots filled with sand. Figure 2.1, panel B shows an example of a tray covered with the transparent Perspex lid. Each caching tray was made perceptually distinct through different coloration.

2: False Belief task in Eurasian Jays

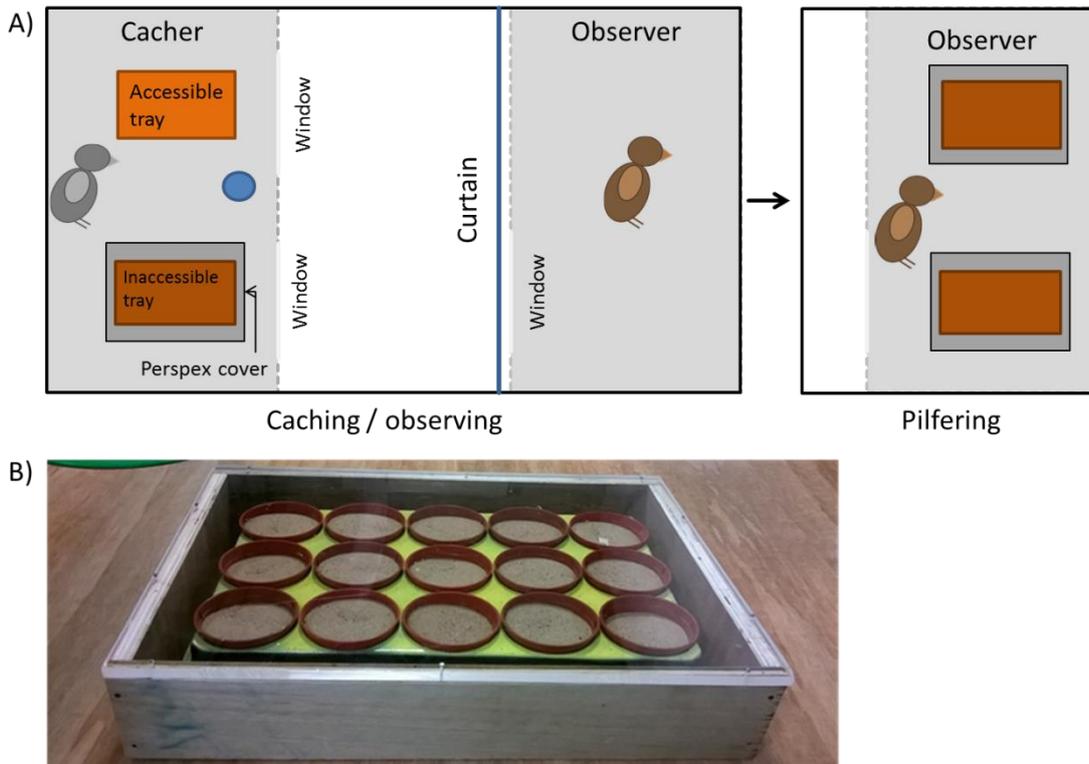


Figure 2.1. Panel A) depicts the experimental set-up over three compartments (not to scale) during caching and observing, respectively, and during the observer test. The middle compartment allowed the experimenter to access the cacher's and the observer's compartments through the windows. Location of 'accessible' and 'inaccessible' trays was randomized between birds. The grey bird signifies the cacher, the brown bird the observer, the small blue circle the food the cacher could cache. During pilfering, there was no conspecific in the next compartment. Panel B) shows a covered caching tray made trial-distinct by painting it yellow.

Procedure. In Step I, all birds were familiarised with the lid that covered a bowl of worms. After birds had unsuccessfully tried to get through the Perspex to access the worms, they were released into the main aviary. All birds from colony 1 approached the covered bowl on the first day and tried to reach for the worms beneath. In colony 2, birds were initially too frightened of the covered bowl in the compartment. Therefore, the lid had to be placed in the aviary over a bowl of food to familiarise them with it.

The observer (the focal bird) was brought into the compartment first. Two minutes after both cacher and observer entered the compartments, the experimenter returned to the testing room. This procedure allowed experimenters to keep timings constant: if birds had to be brought in from the outside, it took around 2 minutes to arrive at the inside testing compartments. This procedure also gave the observer 2 minutes to inspect the trays. The cacher was given a bowl containing 50 shelled peanut halves. This bowl was also shown to the observer before it was placed into the cacher's compartment. Then, the curtain to the

2: False Belief task in Eurasian Jays

observer's compartment was closed, preventing the observer's visual access to the cacher's compartment. Only now, the experimenter entered the empty middle compartment and removed the Perspex lid and placed it between the two trays, making both of them accessible, and left the testing room for 15 minutes.

After 15 minutes, the experimenter returned and placed the lid back on the caching tray before opening the curtain. The observer thus saw one accessible and one inaccessible tray as well as the bowl of food in the cacher's compartment. Note that the number of food items in the food bowl was always reduced compared to the beginning of the trial. Then, the second, accessible tray was covered with a lid as well. This was done to ensure that 1) for the cacher both trays were now rendered inaccessible and that 2) before the test the observer would experience both trays treated the same (with a lid covering them) to ensure that this removal did not alter their preference for one of the trays.

Both cacher and observer were released from their compartments. Both trays were placed into the observer's compartment, with a lid on both. Note that the trays were brought into the observer's compartment because not all birds were able to be moved into the cacher's compartment. The pots in the cacher's trays were replaced by empty pots with fresh sand in order to exclude the use of smell (exposure in extinction). After the observer was brought back into the testing compartment, the lids from both trays were removed. The observer then had 10 minutes to investigate the trays and was released afterwards. During that time, the cacher stayed in the aviary with the rest of the colony and thus the observer could search for the caches in private, unbeknownst to the cacher. The observer's behaviour was recorded with a camcorder mounted in front of the compartment.

Birds received one trial each. As described above, Step II served as the first social trial for the false belief task (see Table 2.1 for an overview of the birds' roles in the study). The methods and results of the cachers' behaviour will be described in Experiment 2.1.

Table 2.1. Cachers and observers in Step II.

Cacher	Observer
Wellington ^a	Washington, Jerusalem, Dublin
Washington	Lima
Jerusalem ^b	Caracas
Caracas	Lisbon
Dublin ^b	Rome
Lisbon ^b	Quito
Adlington ^a	Romero
Romero	Ainslie
Hoy	Pendleton
Pendleton	Romero

Note: ^aBirds served as cachers for the first observers and thus their data were not included in the analysis of the false belief task because they did not receive experience as observer ^bData not included in analysis of Experiment 2.1a and b because these birds stopped caching.

Analysis. All analyses were conducted in RStudio Version 1.0.136 (R Core Team, 2016). Videos were coded by Edward Legg, who was naïve regarding the location of the ‘accessible’ tray. He scored 1) which tray was approached first by each bird, 2) the number of individual pots checked in each tray by each bird (hereafter: ‘pots checked’) and 3) the number of times each bird dug in the substrate of each tray (hereafter: ‘searches’). ‘Checking’ an individual pot was defined as searching through one pot by digging into the sand, swiping through the sand with the bill or pecking into the sand. Given that the caching tray has 15 pots, this number is capped. Therefore, in addition, the number of searches was coded as the number of times a bird dug, swiped or pecked with his bill through the sand of one pot without switching to a new pot. For example, birds sometimes dug in pot A, then dug in B, and later returned to A. This was counted as 3 searches, and 2 pots checked. For inter-rater reliability, I coded 80% of all videos. Inter-rater reliability measured as intra-class correlation coefficient (Hallgren, 2012) was high ($ICC = .99$ for pots checked and $ICC = .98$ for searches).

It was predicted that if birds (falsely) believe that the cacher has only access to the ‘accessible’ tray, they should 1) approach the ‘accessible’ tray first, 2) check more individual pots in the ‘accessible’ tray and 3) make more searches in the ‘accessible’ tray. All analyses were based upon clear predictions and as such all comparisons were calculated using directional (one-sided) tests (Ruxton & Neuhäuser, 2010). First approaches were analysed using an exact one-tailed binomial test, testing whether the data differed from chance ($P = .5$). A difference score was calculated for the number of searches and the number of individual pots checked (‘Accessible’–‘Inaccessible’ tray). If birds searched more in the accessible tray, this difference should be larger than zero; thus, one-tailed one-sample Wilcoxon tests were

calculated in RStudio Version 1.0.136 (R Core Team, 2016). Alpha was set at $\alpha = .05$. P-values $< .1$ were interpreted as trends. Cohen's d s were corrected for dependence according to Morris and DeShon (2002). All descriptive averages are given as median with range in brackets.

Results and Discussion

Eight out of 10 observers approached the 'accessible' tray first. This preference to first approach the tray the observers thought the cacher had cached in was higher than expected by chance at the trend level, $p = .055$.

Of the eight observers that approached the 'accessible' tray first, there were three birds that did not search in the 'inaccessible' tray at all. The five birds that approached the 'accessible' tray first and switched to the 'inaccessible' tray or stopped searching did so after checking a median of 6 (1-15) individual pots of the 'accessible' tray. The two birds that approached the 'inaccessible' tray first switched to the 'accessible' tray after checking 15 pots and 11 pots, respectively.

Birds checked a median of 8.5 (0-15) individual pots in the 'accessible' tray, and 1.5 (0-15) pots in the 'inaccessible' tray. The difference in the number of individual pots checked in the 'accessible' tray minus the 'inaccessible' tray (median = 2.5, range: -2-11) was significantly higher than zero, $W = 4.5$, $p = .034$, Cohen's $d = 0.749$, as depicted in Figure 2.2. Birds made a median of 2 (0-39) searches in 'inaccessible' and 13 (0-45) searches in the accessible tray. The difference between searches in the 'accessible' minus the 'inaccessible' tray (median = 7.5, range: -26-16) did not differ from zero, $W = 16.5$, $p = .257$, Cohen's $d = 0.170$, which suggests that birds did make more searches in the 'accessible' than in the 'inaccessible' tray.

As stated previously, birds from colony 2 already had had experience with transparent Perspex covering caching trays from previous studies (Shaw & Clayton, 2014). Thus, the birds' performance could have been influenced by this prior experience instead or in addition to the experimental manipulations experienced in the current study. Thus, to test whether jays could use their own experience of an inaccessible tray (Step I) to anticipate that the cacher would not be able to cache in an inaccessible tray (Step II), I analysed the data from birds from colony 1 separately as these birds had not been subject to this previous experience with Perspex lids. Here, 6 out of 7 birds from colony 1 tested approached the 'accessible' tray first. This did not differ statistically from chance, $p = .125$, presumably due to the small sample size. All but one bird in this colony searched in the both trays. The birds that approached the 'accessible' tray first, switched to the 'inaccessible' tray, or stopped searching, on average

2: False Belief task in Eurasian Jays

after checking 6 (1-15) individual pots of the ‘accessible’ tray. The one bird that approached the ‘inaccessible’ tray first, switched to the ‘accessible’ tray after checking 11 pots.

In colony 1, birds checked a median of 6 (0-15) pots in the ‘accessible’ and checked 1 (0-15) pot in the ‘inaccessible’ tray. The difference of individual pots checked in the ‘accessible’ tray minus the ‘inaccessible’ tray (median = 1, range -1-11) was higher than zero at trend level, $W = 1.5$, $p = .068$, Cohen’s $d = 0.694$, again presumably due to the smaller sample size. Furthermore, birds made on average 9 (0-45) searches in the ‘accessible’ tray and 1 (0-39) search in the ‘inaccessible’ tray. The difference of searches in the ‘accessible’ minus the ‘inaccessible’ tray did not differ from zero (median = 7, range: -26-16), $W = 6$, $p = .200$, Cohen’s $d = 0.178$ (see Appendix B, Table B.1 for raw data).

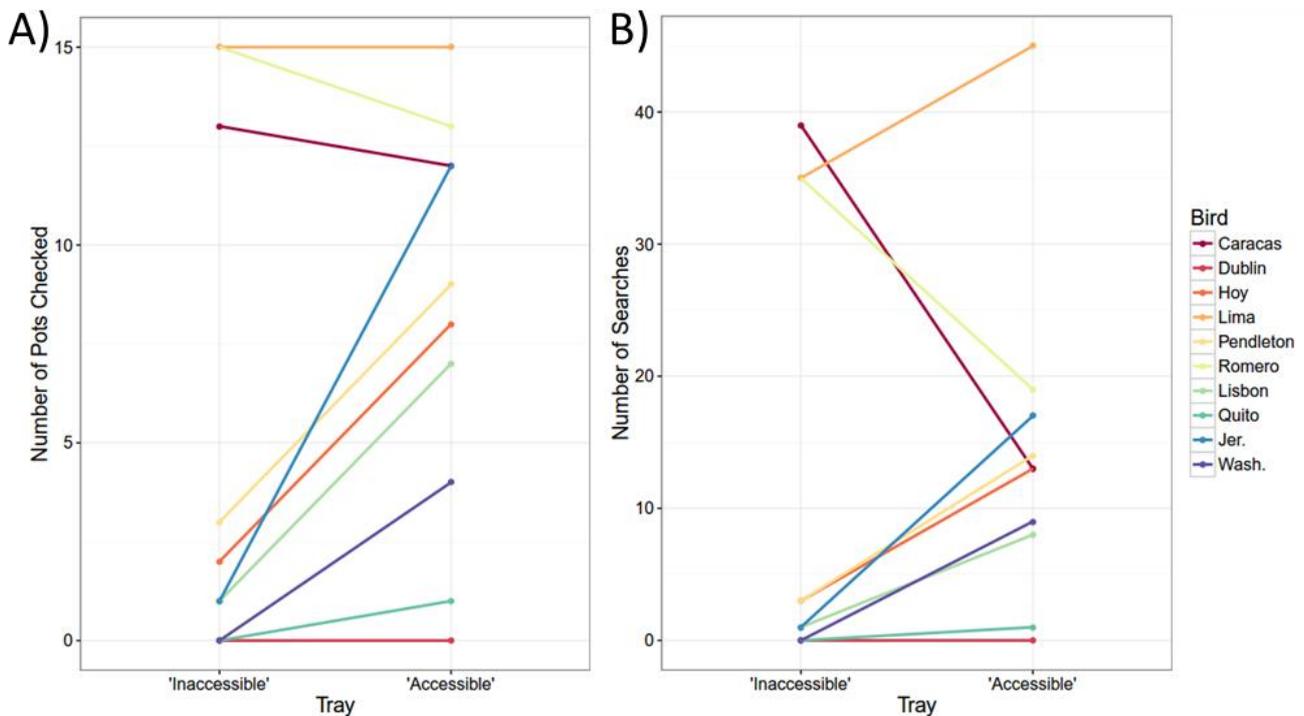


Figure 2.2. Panel A shows the number of pots checked and Panel B shows the number of searches in the ‘inaccessible’ and the ‘accessible’ tray, for each bird.

These results suggest that birds (falsely) believed the ‘accessible’ tray to be the only accessible tray because they tended to approach the ‘accessible’ tray first and they searched in more pots of the ‘accessible’ tray. However, the number of birds approaching the ‘accessible’ tray first was only significant at the trend level, which might be due to the small sample size.

While the birds from colony 1 had some experiences with lids and that they could not access objects beneath the lid (Step I), they did not have prior experience of attempting to *cache* in trays covered with a lid, and never observed other birds attempting to cache in such an ‘inaccessible’ tray. This result tentatively suggests that even without this experience, the

jays have some notion of accessibility in that they understand the fact that not being able to access a caching tray would prevent a cacher from caching in it.

Given that the jays never experienced another bird trying and failing to cache in a tray covered by a lid, birds seemed to have transferred their own experience about not being able to reach food to a novel situation, namely to what another caching bird would be experiencing. This result is consistent with previous findings suggesting that scrub-jays use their own experience to predict what others can perceive (Emery & Clayton, 2001).

Experience of the Removability of the Lid (Step III)

This training followed the observer test and was conducted 1) to ensure that they will cache in a tray that was covered by the Perspex lid after seeing that the lid had been removed, and 2) to show them that the lid will be placed back on a tray after caching. They also learned that their own caches made in a tray covered with a lid after caching would be accessible to them at a later time. Note that birds were *always* trained only after participating in Step II and without another bird present.

Method

Subjects and housing. Ten Eurasian jays (3 females) from two different colonies participated, all housed as described in the procedure of Step I and II. Birds from colony 1 were tested by me, birds from colony 2 (Romero, Hoy, and Pendleton) by Natalie Williams.

Set-up. Training was conducted in a compartment measuring 1 x 2 x 2 m with wooden platforms across the whole length of the compartment. Birds were trained in the same compartment they would later be tested in for the false (Experiment 2.1a) and the true belief task (Experiment 2.1b) Birds were monitored from a separate video room.

Procedure. Birds received two different conditions on two different days: a *tray-with-lid* condition, where a (trial-unique) caching tray was covered at the start of the session, and a *tray-without-lid* condition, where the tray was not covered at the start of the session. Each training condition lasted two days: on day 1, birds could cache, and on day 2 they were able to retrieve their caches. The order in which birds participated in the two different conditions was counterbalanced. On day 1 of the tray-with-lid condition, the lid was removed from the caching tray once the bird had settled down in the compartment. To control for the fact that the experimenter had to touch the tray to remove the lid, in the tray-without-lid condition, the caching tray was touched by the experimenter. Then, birds in both conditions were given a bowl with peanuts and left for 15 minutes. After the 15 minutes elapsed, in the tray-with-lid condition the experimenter covered the tray again with the lid and released the cacher. Caches

made in the tray were recorded. On day 2, at retrieval, the caching tray with all caches from day 1 was placed in the same position as on day 1 in both conditions. In the tray-without-lid condition, there was no lid in the compartment, while in the tray-with-lid condition the lid was positioned next to the tray. In both conditions, birds were brought into the compartment and could retrieve their caches for 10 minutes. During that time, the compartment window was open to allow access to the outside run (see Appendix A, Figure A.1) where birds could re-cache their caches for later consumption.

Both training conditions were repeated until birds cached in both trays. All but one bird that ended up caching in both conditions, did so on the first try (Quito did not cache in her first tray-without-lid training, and the training had to be repeated). Three birds (Lisbon, Jerusalem, and Dublin) did not cache in either condition even after 4 repetitions, and thus only seven birds proceeded to the false belief task. Birds cached on average median = 5 items (range: 1-26) in the tray-with-lid condition, and median = 6 items (range: 2-15) in the tray-without-lid condition.⁶

Experiment 2.1: False and True Belief Task

Birds had the possibility to cache in two different caching trays: one that was accessible all the time, and one that was only made accessible by the experimenter once a curtain restricted the observer's visual access to the compartment. Thus, according to the observer's belief, the cacher should only have access to and therefore cache in one of the two caching trays: their (false) belief was that one caching tray, the 'inaccessible' tray, could not contain any nuts. If cachers understand that the observers have a false belief about the caching trays, then they should show a higher preference, or possibly an exclusive preference, to cache in the 'inaccessible' tray because that is the tray the observer is unlikely to search in if that bird does indeed have a false belief about caching in the 'inaccessible' tray. Whether the observer had a (false) belief about the (in)accessibility of the trays had been confirmed previously in Step II.

An additional, non-social condition was conducted for two reasons. First, it ensured that any preference for the 'inaccessible' tray in the false belief condition was specific to when the birds were being observed. Second, if birds happen to prefer the 'accessible' tray in general, such a tendency could be taken into account. Due to the experimenter not having manipulated the 'accessible' tray as much as the 'inaccessible' tray it is possible that the inaccessible tray was associated with disturbance, and thus should be avoided as a location for

⁶ For raw data, see Appendix B, Table B.2.

caches. However, the ‘inaccessible’ tray could also have a higher saliency due to this manipulation. Because of this potential preference for one of the trays, in the analysis the social and the non-social condition were compared: A relative increase in the preference for the ‘inaccessible’ tray in the social compared to the non-social condition would suggest that birds protected their caches by taking into account the false belief of the observer in the adjacent compartment. The difference of number of caches made in the seemingly ‘inaccessible’ tray minus the number of caches made in the ‘accessible’ tray was calculated. This difference should be higher in the social condition than in the non-social condition.

In the true belief task, observers were able to see the removal of the Perspex lid. Only then, the curtain between compartments was closed. In this situation, the birds should not show a relative increase in preference to cache in the ‘inaccessible’ tray in the social condition compared to the non-social condition. The true belief task was carried out always after the false belief task to minimise carry-over effects after the observer finds out that the Perspex lid could be removed from the caching tray.

Importantly, and differently from previous caching studies, the birds were only in the presence of a conspecific before and after the caching period; during the caching event birds cached in private. This procedure also minimised the availability of behaviour cues of the observer during caching (see Chapter 3). The possibility that a conspecific exhibits different behavioural or appearance cues depending on her belief or knowledge has been previously brought forward to explain performance in a range of theory of mind studies investigating animals (Penn & Povinelli, 2007, 2013). According to this account, the focal animal responds to such cues and thus does not have to attribute perspective or mental states to her conspecific. In the present experiment, cachers cannot react to some form of behavioural and appearance cues by the observer at the time of caching, signalling her (false) belief.

Method

Subjects and housing. A total of seven birds were tested in the false belief and in the true belief tasks. The housing were the same as described in the procedure of the Step II. Data were collected in winter 2015/2016. Birds from colony 1 (Washington, Caracas, Lima, Quito) were tested by me, Natalie Williams tested birds from colony 2 (Romero, Hoy, Pendleton).

Procedure. The set-up was the same as described in the procedure of Step II. Birds participated in two experiments: a false belief task (Experiment 2.1a) and a true belief task (Experiment 2.1b), both either with an observer present (social condition) or no observer present (non-social condition). The order of social and non-social conditions was

counterbalanced. Birds received one trial per condition consisting of a caching phase on day 1 and a retrieval phase on day 2.

Experiment 2.1a (False Belief task). For testing, birds were brought into two separate compartments. In the *social condition*, the observer was brought in first, then the cacher (the focal bird). If birds were called in from the inside, the experimenter left the testing room for 2 minutes. This procedure was again done to keep timings constant across birds. The cacher was then given a bowl containing 50 shelled peanut halves. Then, the curtain to the observer's compartment was closed, preventing the observer's visual access to the cacher's compartment. The experimenter removed the lid from the 'inaccessible' tray and placed it between the two trays, making both of them accessible, and left the testing room for 15 minutes. Birds were monitored from an adjacent room with the CCTV system and recorded with a camcorder mounted in front of the cacher's compartment. After 15 minutes, the experimenter returned, placed the lid back on the 'inaccessible' tray that had been covered before, and opened the curtain. Then – in view of the observer – the experimenter placed an additional lid over the second tray and released first the cacher, then the observer.

The location of the 'inaccessible' tray was counterbalanced between birds, but stayed the same across all four trials. In some instances of the social condition (see Table 2.1), Step II was conducted at the same time, where it was tested whether observers had indeed formed a false belief that one of the trays was 'inaccessible'. In the *non-social condition*, the same procedure was used except that no observer was brought in.

On the next day, the caching trays with all caches intact, both covered, were placed in the cacher's compartment in the same location as during caching. The lids were removed in the cacher's presence and they had 10 minutes to retrieve any caches they made the day before. This was done to ensure they would stay motivated to cache. During this time, the compartment flap was open to allow access to the outside run. The door to the main aviary was kept closed, so that birds could re-cache their nuts without being disturbed by conspecifics.

Experiment 2.1b (True belief task). The same procedure was used as in the false belief task, with one important difference: In the *social condition*, the lid was removed from the caching tray and placed in the middle of the two trays *before* the observer's view was covered with the curtain. Note that the true belief task always followed the false belief task, and each bird had the same order of social and non-social conditions.

Analysis. Items cached in both trays were counted and recorded by the experimenter. All analyses were conducted in RStudio Version 1.0.136 (R Core Team, 2016).

Experiment 2.1a (False belief task). To assess whether birds had a preference for one of the two trays, a difference score was calculated of the mean of items cached in both trays across both social and non-social condition: $D_{\text{trays}} = \text{mean}(\text{items cached})_{\text{'inaccessible' tray}} - \text{mean}(\text{items cached})_{\text{'accessible' tray}}$. The difference score was used to obtain one independent measure for the birds' preference for caching in one of the two locations. Whether this difference was different from zero was tested with a two-tailed one-sample Wilcoxon signed rank test. A two-tailed test was used here because there was no clear prediction regarding the preference of the birds (Ruxton & Neuhäuser, 2010). Furthermore, a two-tailed permutation test was calculated with the R package coin (Hothorn, Hornik, van de Wiel, & Zeileis, 2008) to assess whether birds cached more in the social than in the non-social conditions considering both trays.

To test whether birds would take into account the observers' false belief, the difference in the number of caches made in the seemingly 'inaccessible' tray minus the number of caches made in the 'accessible' tray was compared across conditions ($D_{\text{Social/Non-Social}} = \text{items cached}_{\text{'inaccessible' tray in the social/non-social condition}} - \text{items cached}_{\text{'accessible' tray in the social/non-social condition}}$). Again, the difference score was used to obtain one independent measure for the birds' preference for caching in one of the two locations. This difference score should be larger in the social than in the non-social condition ($D_{\text{Social}} > D_{\text{Non-Social}}$). In the true belief task, however, there should be no difference between the social and the non-social condition ($D_{\text{Social}} = D_{\text{Non-Social}}$). Based on this clear prediction for the false belief task, a directional (one-tailed) permutation test was calculated with the R package coin (Hothorn et al., 2008). Alpha was set at $\alpha = .05$. P-values $< .1$ were interpreted as trends. Cohen's d s were corrected for dependence according to Morris and DeShon (2002).

Experiment 2.1b (True Belief task). For the true belief task, however, only descriptive statistics are given because four birds (Quito, Pendleton, Lima, and Hoy) stopped participating and therefore the final sample size for the true belief task was just three birds (i.e., $n = 3$).

All descriptive averages are given as median with range in brackets.

Results and Discussion

In the false belief task, irrespective of condition, birds cached a median of 3.5 (1-9.5) items in the 'accessible' and 1 (0-3.5) item in the 'inaccessible' tray. That is, considering all conditions, birds tended to cache more in the 'accessible' tray: the difference in number of items cached (median $D_{\text{trays}} = 1.5$ items, 0-8.5) was different from zero at trend level, $W = 15$, $p = .059$, Cohen's $d = 0.83$. Furthermore, in the social conditions, birds cached a median of 3

2: False Belief task in Eurasian Jays

(0-15) items in both trays. In the non-social conditions, birds cached in both trays a median of 3 (0-15) items. That is, birds did not cache more in the social condition, $Z = 0.593$, $p = .656$, Cohen's $d = 0.236$.

In the social false belief task, birds cached a median of 5 (0-15) items in the 'accessible' tray and 2 (0-4) items in the 'inaccessible' tray. In the non-social false belief task, birds cached a median of 3 (1-10) items in the 'accessible' tray and 2 (0-4) items in the 'inaccessible' tray. Figure 2.3 displays the difference in number of items cached ('inaccessible' - 'accessible'). This difference was not higher in the social condition (median $D_{\text{Social}} = -2$, range: -13-1) compared to the non-social condition (median $D_{\text{Non-social}} = -1$, range: -10-2), $Z = -0.51$, $p = .71$, Cohen's $d = -0.115$.

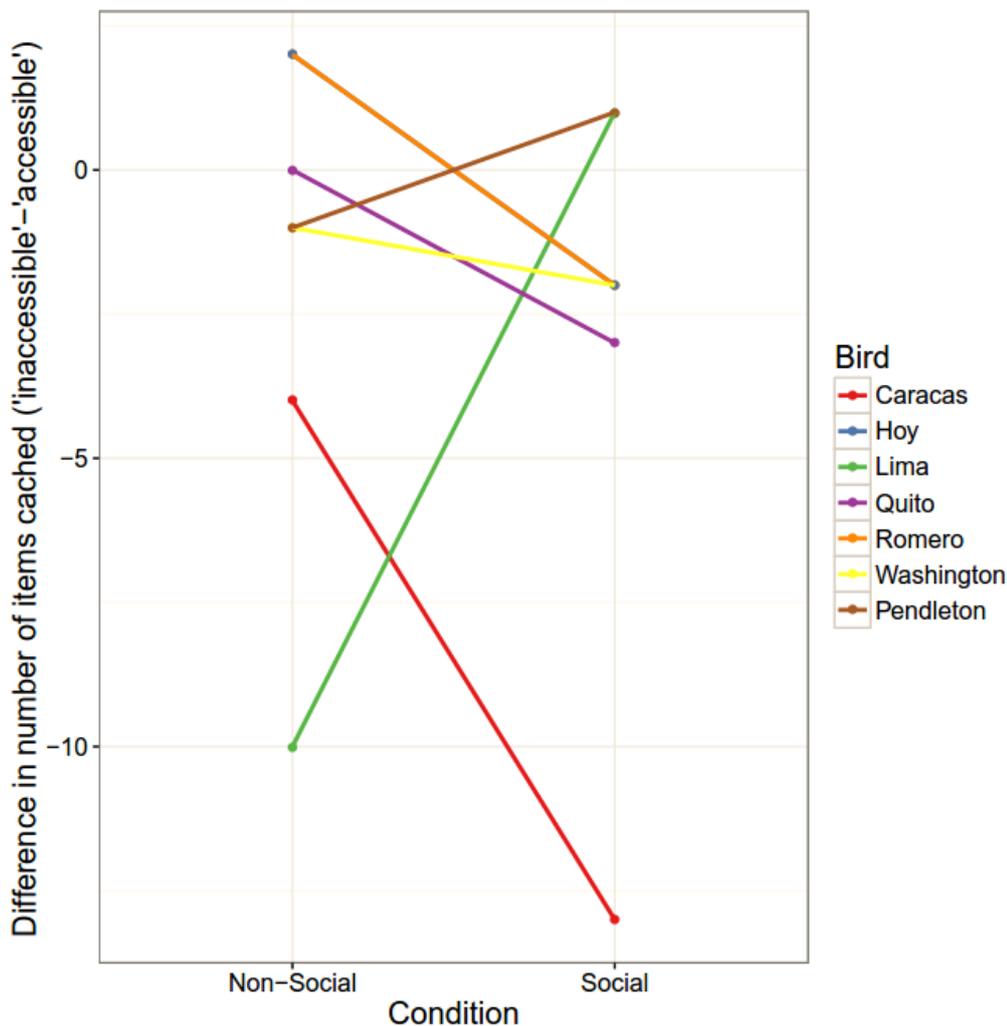


Figure 2.3. Difference in number of items cached in the 'inaccessible' tray minus the number of items cached in the 'accessible' tray in the non-social and the social condition, for each bird.

In the true belief task, irrespective of condition, birds cached a median of 4.5 (2.5-4.5) items in the 'accessible' tray and 2.5 items in the 'inaccessible' tray (median $D_{\text{trays}} = 2$ items,

2: False Belief task in Eurasian Jays

range: 0-2). In the social condition, birds cached a median of 4 (3-4) items in both trays together, and, in the non-social condition, 10 (7-10) items in both trays together.

In the social true belief task, birds cached a median of 2 (1-3) items in the ‘accessible’ tray and 2 (1-2) items in the ‘inaccessible’ tray. In the non-social true belief task, birds cached a median of 7 (3-7) items in the ‘accessible’ tray and 3 (3-4) items in the ‘inaccessible’ tray. In the true belief task, the median difference in caches made in the ‘inaccessible’ tray minus the number of caches made in the ‘accessible’ tray in social condition was $D_{\text{Social}} = 0$ (-1-0) and in the non-social condition average $D_{\text{Non-social}} = -4$ (-4-1). See Appendix B, Table B.3 for raw data.

These results suggest that birds tended to prefer caching in the ‘accessible’ tray compared to the ‘inaccessible’ tray. It is possible that birds might have perceived the ‘inaccessible’ tray as less safe for their caches because the experimenter manipulated this tray much more. Alternatively, this preference could be explained by the fact that the ‘accessible’ tray was always accessible and was accessible for longer, and thus might be perceived as a potential caching site during all times, whereas the ‘inaccessible’ caching tray was only sometimes perceived as a potential caching site.

Importantly, this preference for the ‘accessible’ tray was not reversed in the social condition of the false belief task, compared to the non-social condition. Thus, birds did not seem to have responded to the false belief of the observer. Note that there are a range of factors that could have influenced the birds’ caching behaviour. However, the pattern of results that would support the hypothesis in question was not shown.

Note that three birds ceased to cache in their first true belief trial, and one bird ceased to cache in his second trial of the true belief trial. This cessation of caching could be taken to suggest that birds understand that in the true belief condition, the observer knew about the accessibility of both trays, and might thus search both trays when given the possibility. However, it is difficult to interpret this behaviour, given that the true belief task always followed the false belief task and was conducted in early spring. Eurasian jays show marked seasonal variability in their caching behaviour, and cache food mainly in autumn (Boseema, 1979; Clayton, Mellor, & Jackson, 1996). Therefore, it is possible that the birds were simply less motivated to cache as spring approached.

General Discussion

The present study aimed to investigate false belief understanding in Eurasian jays by using the birds’ tendency to protect their caches from conspecific observers (Legg & Clayton, 2014; Shaw & Clayton, 2012, 2013, 2014). Specifically, in the false belief task the birds had the possibility to cache either in a tray that the conspecific observer believed to be accessible or in a tray the conspecific falsely believed to be inaccessible. Importantly, the cachers had access to two caching trays; one of the trays was covered at the beginning of testing. The lid covering the tray, however, was removed out of sight of the observer, and thus made accessible for the cacher. Therefore, the observer should have had a false belief about the ‘inaccessible’ caching tray. Evidence to support this claim comes from the finding that the observers did have a tendency to search preferentially in the accessible tray, suggesting that this is where they expected the cacher to have cached. If the cachers in turn understood this false belief of the observer in regard to the accessibility of one of the two caching trays, then

they should prefer to cache in the tray the observer thought to be inaccessible. However, the cachers did not show an increased preference for the ‘inaccessible’ tray in the social condition. Furthermore, birds did not cache more in the social compared to the non-social condition. This finding is similar to previous reports of with scrub-jays (e.g., Dally et al., 2004, Dally et al., 2005; Emery & Clayton, 2001) as well as Eurasian jays (Goodwin, 1956) not reducing caching in the presence of an observer.

The task presented in this experiment required several prerequisites in order to render any behaviour in the actual task meaningful. First, birds needed to be familiar with accessibility as such, i.e., they needed to experience that objects covered by a lid are not accessible. To that end, birds were presented with a bowl of worms covered with a Perspex lid (Step I). In addition, Step II provided birds with the first-hand experience 1) that observers do not know about the removal of the lid, and 2) that observers focussed their pilfering efforts on the seemingly only ‘accessible’ tray. Thus, caching in the ‘inaccessible’ tray can be considered an efficient cache-protection strategy (see also Chapter 3). In Step III, birds were made familiar with the removability of the lid. These experiences and tests prior to the false belief task mean that the lack of a difference observed in the false belief task cannot be explained by cachers not knowing what the observer (falsely) believes (Step II), or by birds being deterred from caching in the previously covered tray due to the removal of the lid (Step III).

Even though these prerequisites were given, failure to act according to predictions does not imply the lack of understanding false beliefs altogether (de Waal & Ferrari, 2010). Several other factors related to the task used here could have influenced the birds’ performance. First, it is possible that during Step II, where birds learned that one tray was not accessible to the cacher, birds also learned that pilferers, while having access to their caching trays, will not find any caches as they themselves did not find any when they were pilfering in extinction. This would imply that the birds are capable of assuming that the observer will not be able to pilfer any of their caches any more than when the cachers themselves had been observers. Given the previous findings on experience projection (Emery & Clayton, 2001) this remains a possibility and one that could be tested empirically in future studies.

Second, given that birds were not observed during the caching event as such, they might not have felt the need to protect their caches in the first place. However, previous studies suggest that *seeing* an observer during caching is not necessary to the triggering of general cache protection strategies. For example, when an observer can hear but is out of sight both scrub-jays and Eurasian jays have been reported to protect their caches by caching in a

quiet substrate like sand, as opposed to caching in a noisy substrate (Shaw & Clayton, 2013, 2014; Stulp et al., 2009). Additionally, it should be noted that the task only shows false belief *understanding* if the cacher can be assumed to have attributed the belief of a conspecific. Therefore, if the conspecific's presence, and with it, her behavioural cues, would have been necessary for the cacher then the task would not have assessed an understanding of false belief but a response to behaviour of the conspecific based on her false belief.

In human infants, it has been argued that a failure to solve false belief tasks is not necessary related to shortcomings of theory of mind but to difficulties related to the features of the task itself (Bloom & German, 2000), such as a high demand on memory capacity, and the need to inhibit one's own knowledge or to engage in counterfactual thinking (Low & Perner, 2012). For example, in order to correctly predict the behaviour of an agent with a false belief, children have to suppress their own knowledge about the state of the world (Birch & Bloom, 2004) as well as to ignore the fact that, by and large, beliefs tend to be correct (Leslie, Friedman, & German, 2004). The task presented in this study could be no different due to its reliance on a multitude of events that have to be remembered and interferences that have to be inhibited. For example, the cacher had to suppress its own 'knowledge' about the inaccessible tray being in fact accessible.

Furthermore, I have to consider the possibility that specific factors of the task presented here masked the birds' ability. Specifically, the removal of the unwieldy lid might have startled the birds. It is conceivable then that this very salient event distracted the birds from considering the observer's belief (c.f., Lurz, 2011). Similarly, these events might have led to retroactive interference that disrupted the birds' memory for the sequence of events prior to caching (Grant, 1988; Maki, Moe, & Bierley, 1977), for example that the lid was removed after the curtain was closed. In both cases, one would expect the birds to behave in the same way in the false and the true belief task. Not considering the observer's belief, regardless of its truth value, is in effect similar to relying on one's own beliefs about the world (i.e., "both trays are accessible for birds"). Similarly, if the birds' memory of the sequence of events prior to caching was impaired, and they did not remember for example that the lid was removed only *after* the curtain closed, then they would assume the observer to have the (true) belief that both trays are accessible. In both cases, that is, if cachers did not consider the false belief of the observer but their own, and if cachers did not remember when the lid was removed, their behaviour (no preference for the inaccessible tray) would be the same.

The failure to account for false belief presented here mirrors previous findings from studies with chimpanzees. In a range of different tasks, chimpanzees behave as if they do not understand that a conspecific or experimenter has a false belief (Call & Tomasello, 1999; Hare et al., 2001; Kaminski et al., 2008; Krachun et al., 2009). However, a more recent looking-time study has provided new insights (Krupenye et al., 2016). Here, chimpanzees, bonobos (*Pan paniscus*), and orang-utans (*Pongo abelii*) were presented with short videos while their gaze was tracked. In one of the videos presented, a human wearing a green shirt is attacked by someone in a gorilla suit, who then hides in one of two haystacks located left and right of the screen. In response, the human hits the haystack (X) in which the attacker is hiding with a stick. In the false belief condition, the human leaves the scene, at which point the attacker switches haystacks (unexpected transfer to Y), and then leaves the scene altogether. The human returns with the stick, and here the chimpanzees looked at the haystack (X) the human saw the attacker hide in. This looking pattern implies that they anticipated the human to act according to his false beliefs (attacker is located in X). This possible disparity between ‘explicit’ (overt behaviour) and ‘implicit’ (Low & Perner, 2012) false belief understanding in apes (Kano, Krupenye, Hirata, & Call, 2017) mirrors results from studies on infant false belief understanding (e.g., Buttelmann, Over, Carpenter, & Tomasello, 2014; Onishi & Baillargeon, 2005; Southgate, Senju, & Csibra, 2007). Before the age of four, children generally do not pass explicit false belief tasks (Wellman et al., 2001). It has been argued that their failure might be due to the fact that young children lack executive control necessary to suppress the predominant response based on their own true belief as discussed in Chapter 1. In fact, recent research proposes that children before the age of four possess at least an ‘implicit’, non-verbal understanding of false beliefs (e.g., Kovács, Téglás, & Endress, 2010; Onishi & Baillargeon, 2005; Luo, 2011) and of the fact that false beliefs have a causal relationship to behaviour (Southgate & Vernetti, 2014). However, other authors have pointed out that Krupenye et al.’s (2016) study, similar to studies in infants (Heyes, 2014; Perner & Ruffman, 2005), is missing an important non-social control (Heyes, 2017). Specifically, Heyes (2017) argues that we have to acknowledge, and empirically test, the possibility that the performance of Krupenye’s apes was due to low-level encoding, or submentalising, rather than ‘true’ mentalising (i.e., theory of mind). For example, Heyes (2017) conjectures that Krupenye’s apes could have encoded salient features of the entities involved (the green shirt moving in and out of the scene), and how they related to each other. That is, the same looking behaviour would have been found if apes were presented with a non-social control video,

where the agents from the original videos were to be replaced by inanimate objects (c.f., Heyes, 1998).

Given the limitations of the task as discussed above, it is possible that, while the birds did not perform according to false belief understanding, a different design might be able to reveal their abilities. The task presented in this study constitutes an explicit false belief task in the following sense: birds had to explicitly decide in which tray to cache more, similar to, for example, the chimpanzees in Call and Tomsello (1999) that had to choose to use the help of the knowledgeable experimenter but not the naïve experimenter. While the birds tested here did not show an ‘explicit’ understanding of false beliefs, they might do so implicitly, for example by showing ‘surprise’ if conspecifics do not act according to their false beliefs. Such an implicit understanding could be investigated further using looking time studies with the birds. Similar attempts using looking time have been reported with rhesus macaques (*Macaca mulatta*); however, there was no evidence to suggest that the macaques could represent others’ beliefs (Martin & Santos, 2014).

Conclusion

The results presented here suggest that Eurasian jays do not account for the false belief of a conspecific when protecting their caches. However, Eurasian jays have been reported to respond to the desire of their partner during courtship feeding (Ostojić et al., 2014, 2016, 2013). In relation to the present study it is important to note that such an attribution of desires has been suggested to be less demanding than attributing beliefs (Wellman & Woolley, 1990). More recent results from Ostojić and colleagues (2017) however suggest that birds might be able to respond to the desire of a conspecific by relying on behavioural and contextual cues. In Chapter 3, I explored which cues the jays could have used to do so.

Chapter 3

Changes in behaviour as a function of changes in desires

A range of studies have suggested that California scrub-jays and Eurasian jays can take into account what their conspecifics can see or hear to protect their cached food items from pilferage. More recent research shows that corvids are also able to take into account the desires of others in a caching context – that is, they take into account the changing desire of a conspecific observer. In this previous study, desire was manipulated by satiating the observers on a given food, leading to a decreased preference to eat that food. Subsequently, cachers cached more of the food the observer did not desire and thus would be less likely to pilfer. However, they also did so when they were not able to see which type of food the observer ate to satiety. Thus, cachers seem to have responded to the observer's desire state based on the observer's behaviour during the caching event. The present study built on this and investigated which cues Eurasian jays could use to do so. One possibility is that observers attend more to caching of food that they desire than to caching of food that they do not currently desire. Experiment 3.1 investigated this possibility by using peepholes to assess differences in attention towards a caching event. Specifically, it was tested whether observers' looking time at a caching event would vary as a function of their subjective desire for different foods. Here, observers looked more at a caching event involving food on which they were not sated. A second possibility is that observers might spend more time in proximity to a caching event when it involved a desired food compared to when it involved a currently undesired food. This possibility was assessed in Experiment 3.2. Here, birds could freely observe a conspecific caching in the next compartment. However, birds did not spend more time in the part of the compartment allowing visual access to the cacher's compartment when the cacher cached food the observer was not sated on. Taken together, these results suggest that, when responding to the desire of a conspecific observer in a caching context, Eurasian jays might use certain behavioural cues that correlate with this desire, such as an overt change in the observer's attention to the caching event.

Introduction

Chapter 2 explored Eurasian jays' ability to attribute false beliefs to others. The results suggested that the jays did not take into account the false belief of a conspecific observer in a caching context. However, reports of corvids' behaviours being sensitive to the perspective (reviewed in Clayton & Emery, 2007; Grodzinski & Clayton, 2010a) and desires of others (e.g., Ostojić et al., 2013, 2014, 2017) suggest that they have some elements of theory of mind-like abilities. So far, however, it is not clear what kind of cognitive mechanism underpins these achievements. Some have argued that corvids do so by *attributing* mental states to others (e.g., Dally et al., 2006; Keefner, 2016). However, others have argued that while their behaviour might appear as if they are attributing mental states, it is in fact better explained by an ability to read behavioural cues (e.g., Penn & Povinelli, 2007). In the present chapter, I explore the possibility of such alternative accounts by building on research I have participated in prior to this thesis and which investigated corvids' ability to attribute desire states in a caching context (Ostojić et al., 2017)⁷. Crucially, I extend this work by analysing the cues corvids might use to respond to the desires of a conspecific. For a better understanding of the study reported in this chapter, these previous results will also be described.

As discussed in previous chapters, corvids are well known to protect their caches from thieving conspecifics, for example by preventing a conspecific observe the caching (reviewed in Clayton et al., 2007). Their versatile cache-protection strategies seem to be enabled by their ability to take into account the perspective of a conspecific. Being able to track others' perceptual states allows an individual to make predictions about what these others might do, for example whether or not they might steal one's caches. However, perceptions and knowledge are not the only sources of action – actions also result from desires: in a caching context this means that a potential thief might or might not be *motivated* to steal one's caches (c.f., Bartsch & Wellman, 1989).

Research on human infants suggests that desire states are easier to understand than belief states: infants seem to be able to predict actions based on desires earlier (around the age of 2) than actions based on beliefs (around the age of 3; Wellman & Woolley, 1990). Given that desire reasoning pre-dates belief reasoning in infant development, it is of interest whether or not corvids, while possibly lacking a full-blown theory of mind, have the somewhat less sophisticated ability to take into account the desires of others because the ability to attribute

⁷ I tested part of the scrub-jay data presented in Ostojić et al. (2017) in 2013 during an internship as part of my degree prior to my PhD.

desires might require less cognitive sophistication (Wellman & Wooley, 1990). So far, an ability to respond to desires has been suggested in a food-sharing context: Ostojić and colleagues (2014, 2013) had previously shown that Eurasian jays respond to the desire of their partner during courtship feeding. Here, birds were shown to flexibly respond to the current desire of their mate for certain food types when sharing food with her. The question whether or not the desire of a conspecific is also relevant in a caching context was subsequently investigated by Ostojić and colleagues (2017). This study is relevant because the notion that animals are in possession of higher-order social cognition, such as mental state attribution, should ideally be supported by evidence acquired in more than one context (Heyes, 1993, Whiten, 1994). Therefore, investigating desire-state attribution in a caching context has the potential to shed light on the possible flexibility of this ability. In what follows, I shall describe the rationale and results of the experiments presented in Ostojić and colleagues (2017).

Taking Desire States into Account in a Caching Context

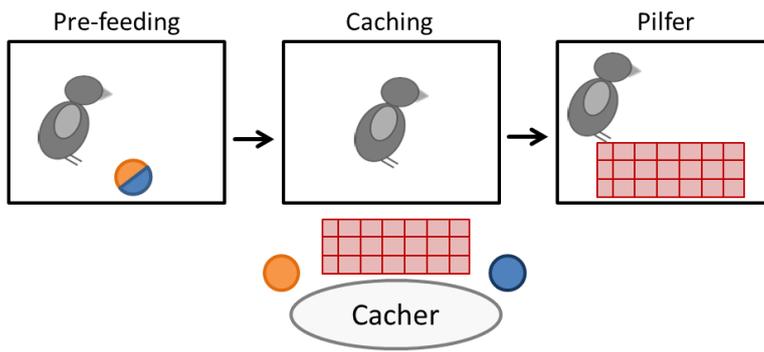
Cache-protection strategies in corvids have been mainly investigated by giving birds the opportunity to limit visual or auditory information about the location of their caches. When observed by a conspecific, scrub-jays as well as Eurasian jays will protect their caches using a number of different cache protection strategies. For example, they will hide caches behind a barrier, cache far away from conspecifics or in shaded areas (for an overview see Dally et al., 2005; Dally et al., 2010) or move previously made caches to a new location once an observer has left the scene (Dally et al., 2010; Emery & Clayton, 2001). However, it might not always be possible to fully restrict an observer's ability to know about the location of caches. In such cases, it might be beneficial for cachers to take into account the observer's desire to pilfer in order to reduce the relative risk of pilferage. More concretely, it might be beneficial to cache more of a food an observer is less likely to pilfer and eat the food they are more likely to pilfer. This potential cache-protection strategy is the focus of Ostojić and colleagues' (2017) study.

To manipulate the observer's current motivation to pilfer a certain type of food, Ostojić and colleagues (Ostojić et al., 2017) pre-fed Eurasian jays and California scrub-jays on different types of food, leading them to be satiated on that specific food. Eating one type of food to satiety decreases an animal's preference for that food for a given time, without reducing the preference for other foods (Balleine & Dickinson, 1998; Dickinson & Balleine, 1994).

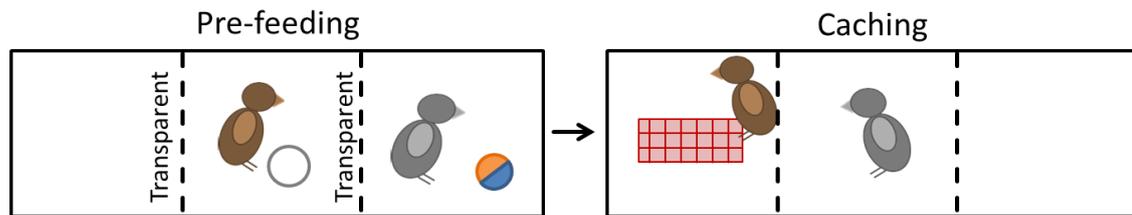
Ostojic and colleagues (2017) report two experiments. Figure 3.1 summarises the experimental procedure and set-up used in each phase of Ostojic and colleagues' (2017) experiments 1 and 2. The aim of experiment 1 was to investigate whether the jays would pilfer according to their satiety (i.e., preferentially pilfer food A after being pre-fed food B, and vice versa). This is a necessary condition for the cache-protection strategy investigated in the second experiment – taking into account an observer's current desire when caching food is only an efficient cache protection strategy if the observer would pilfer what they currently desire.

Jays were pre-fed with a particular food on different days before watching a human experimenter cache. In a subsequent pilfering phase, both Eurasian and scrub-jays pilfered according to their current motivation. Hence, it may be beneficial for cachers to cache more of a food that an observer is sated on and is thus less likely to pilfer. Additionally, this experiment 1 provided the jays with the experience that being sated on food A will reduce their desire to pilfer food A, given that experience of one's own pilfering might be crucial for the exhibition of cache protection strategies (Emery & Clayton, 2001).

A) Experiment 1



B) Experiment 2: Seen Condition



C) Experiment 2: Unseen Condition

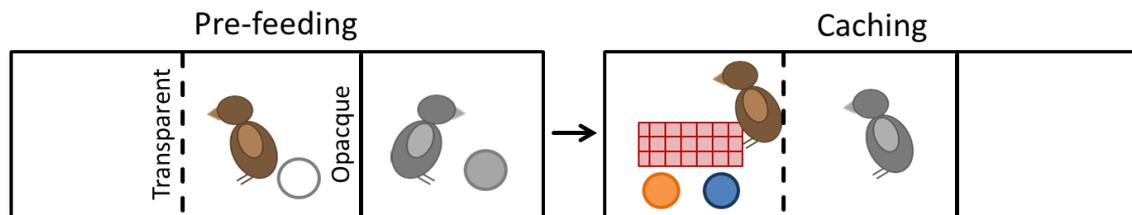


Figure 3.1. Set-up and different test phases in Ostojić et al.’s (2017) experiment 1 (Panel A) and experiment 2 (Panels B and C). During pre-feeding, observers (grey) were given different foods (food bowl depicted as two-coloured bowls). In the caching phase, an experimenter (light grey ellipse) cached two different food types in a caching tray (red) just outside the cage/compartment. In the pilfering phase, the tray was positioned in the jay’s cage/compartment. Experiment 2 consisted of two conditions. Panel B depicts the seen condition. During pre-feeding (first panel), cachers (focal bird, brown) were able to see the observers (grey) being pre-fed (two-coloured circle). During caching (second panel), cachers were given two different types of food (orange and blue circle) and a caching tray (red). The crucial difference in the Unseen condition (Panel C) was that here, during pre-feeding, the cachers could not observe the observer’s pre-feeding (grey circle).

Building on that, Ostojić and colleagues (2017) tested in experiment 2 whether cachers would adjust their caching depending on the observer’s desire. Similarly to experiment 1, an observer was first pre-fed on different food types. In a ‘seen’-condition, the cacher (the focal bird) could see this pre-feeding. Then, the cacher had access to a caching tray and two types of food, one of which the observer was pre-fed on. Here, cachers cached comparatively more of the food the observer was pre-fed on, suggesting that they adjusted their caching behaviour to the desire of the observer. Importantly, to ensure that cachers’ behaviour was due to them

attributing a desire to the observer, a further condition was included. In this ‘unseen’-condition, the cacher did not see which type of food the observer was pre-fed on. Here, cachers also cached more of the food the observer was sated on, taking into account the observer’s desire although they *could* not have attributed any desire states. Hence, they might have been responding to the cues in the observer’s behaviour.

Behaviour Reading Accounts of Theory of Mind Experiments

Some authors argue that the performance of animals in a theory of mind task are not best explained by the ability to attribute mental states, enabled by a theory of mind, but by other mechanisms that exploit behavioural and situational cues. Such approaches have been loosely summarised as ‘behaviour reading’ accounts (e.g., Heyes, 1998; Penn, Holyoak, & Povinelli, 2008; Penn & Povinelli, 2007; see also Chapter 1). This common critique suggests that the focal animal in a theory of mind task is relying on observable changes in behaviour of their conspecifics that are accompanied by changes in mental states, rather than *attributing* mental states to them (Heyes, 2014a). This relationship between observable behavioural cues and certain outcomes is learned. Recall that in Hare and colleagues’ (2001) experiment, when a dominant opponent did not observe a placement of food by an experimenter, the focal chimpanzee approached the food much faster compared to when the dominant could see where the food was being hidden. It has been argued that the dominant’s behaviour might be different depending on whether she saw the food being hidden compared to when she was ignorant (e.g., Heyes, 2014a; Lurz, 2011). For instance, when the dominant knew about the location of the food, she might have approached the food faster. The subordinate focal chimpanzee might have learned about such regularities in the behaviour of conspecifics, for example that dominant competitors generally tend to retrieve food faster when they could see the food. Similarly, in the case of desire-state attribution, the focal animal might respond to the behaviour of the opponent that changes with the opponent’s desire, without having to infer a underlying desire.

However, so far, behaviour reading accounts do not fully specify which cues are used by the behaviour-reading animal, and offer only post-hoc explanations for an animals’ performance (e.g., Call & Tomasello, 2008b; Halina, 2015; see also Chapter 1). In principle, a range of different behavioural cues could potentially tip off the focal animal. That is, there is no independent empirical research investigating which behavioural cues a conspecific could exhibit and which behaviour cues the focal bird could perceive – in the case of Hare and colleagues (2001) for example, it might be either the orientation of the conspecific’s body or the conspecific’s gaze that the subordinate responds to.

The present study set out to investigate which observable behavioural cues exhibited by a conspecific corvids could use in order to ‘read behaviour’. To that end, the caching paradigm assessing desire state attribution presented by Ostojić and colleagues (2017) was used. This study was selected because here, the condition conducted to control for behaviour-reading accounts (unseen condition) indeed suggested that the jays relied on behaviour-reading, an assumption that has so far not been directly supported in other paradigms (Halina, 2015). Recall that in Ostojić and colleagues’ (2017) experiment 2, the cacher predominantly cached food that the observer was sated on and was thus unlikely to pilfer, regardless of whether the cacher knew what food the observer was sated on. Therefore, one possible explanation for the results reported by Ostojić and colleagues (2017) is that the caching jays noticed a change in the observers’ attention towards the caching event depending on the observers’ desire. If the observers had had no interest in the cached food, they might have attended less to the caching of that food, which could have been picked up by the cacher, leading to an increased caching of food A. The aim of the present study was to directly test which overt behaviour changes as a function of an observer’s desire.

In Experiment 3.1, I used a looking time paradigm to assess changes in attention of an observer in response to a human caching currently desired and undesired food. Experiment 3.2 complemented this by observing birds in a more natural caching set-up, without peepholes and with a conspecific cacher, assessing whether observers would spend more time in close proximity to the cacher.

Experiment 3.1: Attention of Observer ⁸

Here, I tested whether or not Eurasian jays would show any overt change in attending towards the caching event depending on their specific satiety. Attending towards a desired compared to an undesired food was measured with looking times. Due to birds’ visual system, measuring looking time in birds is methodologically challenging. Most birds have two lateral eyes that allow them to monitor a large visual field (G. R. Martin, 1994), which is further aided by frequent eye, head, and body movements (Fernández-Juricic, O’Rourke, & Pitlik, 2010; Friedman, 1975). It is thus difficult to judge whether or not a bird is attending to an event at a given time. A possible solution is to measure attention by allowing animals only restricted visual access through holes in a partition (Range & Huber, 2007). This procedure also introduces a cost of attending to certain events: if the focal bird wants to observe an event, the bird cannot at the same time observe another event, and has to cease doing other

⁸ I am grateful to Michael Mendl for comments on the study design.

things, like eating (c.f., Grodzinski et al., 2012). This procedure is based on the assumption that if birds are interested in an event, they will look through the peepholes allowing access to this event (Scheid, Range, & Bugnyar, 2007).

In previous studies assessing looking time with peepholes, California scrub-jays have been reported to adjust their looking behaviour in order to gain information about the location of caches: they prefer to observe caching in an adjacent compartment compared to when only food and a tray or only a bird were presented (Grodzinski et al., 2012). They also spent more time looking through peepholes at caching events when knowledge about the caches is necessary to pilfer them later on, as opposed to when food items can be found without having to search for them (Watanabe et al., 2014).

In the present experiment, such ‘peepholes’ were thus used to assess whether and when the birds were observing caching of food (see also e.g., Bird & Emery, 2010; Grodzinski et al., 2012; Scheid et al., 2007; Watanabe et al., 2014). If the birds are motivated to pilfer food that they are not sated on, as suggested in Ostojic and colleagues’ (2017) experiment 1, and if they prefer to look at events that provide them with useful information, they should attend more to the caching of food they had not been pre-fed on (the desired food) than to the food they had been pre-fed on (the undesired food).

In the present experiment, a human was used as cacher, similar to the procedure of Ostojic and colleagues’ (2017) experiment 1. This procedure also allowed rendering caching independent of the birds’ behaviour and consistent across trials and birds. Furthermore, to avoid the experimenter’s expectation to influence her caching behaviour, the caching experimenter was blind to the testing conditions. That is, the experimenter did not know which food the bird had been pre-fed and thus which food the bird was sated on (c.f., Ostojic et al., 2016).

Method

Subjects and housing. Eleven sexually mature Eurasian jays of mixed sex were tested from November 2016 to February 2017, 9 individuals from colony 1, and 2 individuals from colony 2. All birds had previously participated in previous research (see Appendix A, Table A1) involving caching and pilfering (e.g., Legg & Clayton, 2014; Ostojic et al., 2017; Shaw & Clayton, 2013, 2014).

Note that 10 scrub-jays were part of Ostojic and colleagues’ (2017) study. However, due to the expiration of the UK Home Office project licence PPL 80/2519 in December 2016, no scrub-jays were available to be tested for this study. Birds from colony 1 were tested by

3: Changes in behaviour in Eurasian jays

Ljerka Ostojić (knowledgeable experimenter 1) and me (naïve cacher⁹; experimenter 2), birds from colony 2 were tested by me (experimenter 1) and Rachel Crosby (experimenter 2). The housing is described in Chapter 2.

Set-up. Birds were tested in three adjacent compartments as can be seen Figure 3.2, Panel A. Birds received their pre-feeding in compartment 1, and then moved to compartment 2, where a window (training step 1, see below) or a peephole (training step 2 and test, see below) allowed visual access to compartment 3, where the caching took place. The peephole had a diameter of ~2.5 cm and made it possible to assess when and where a bird was looking. A wooden perch was mounted below the peephole and at the flap leading to the run in compartment 2. All food was presented in colour unique bowls.

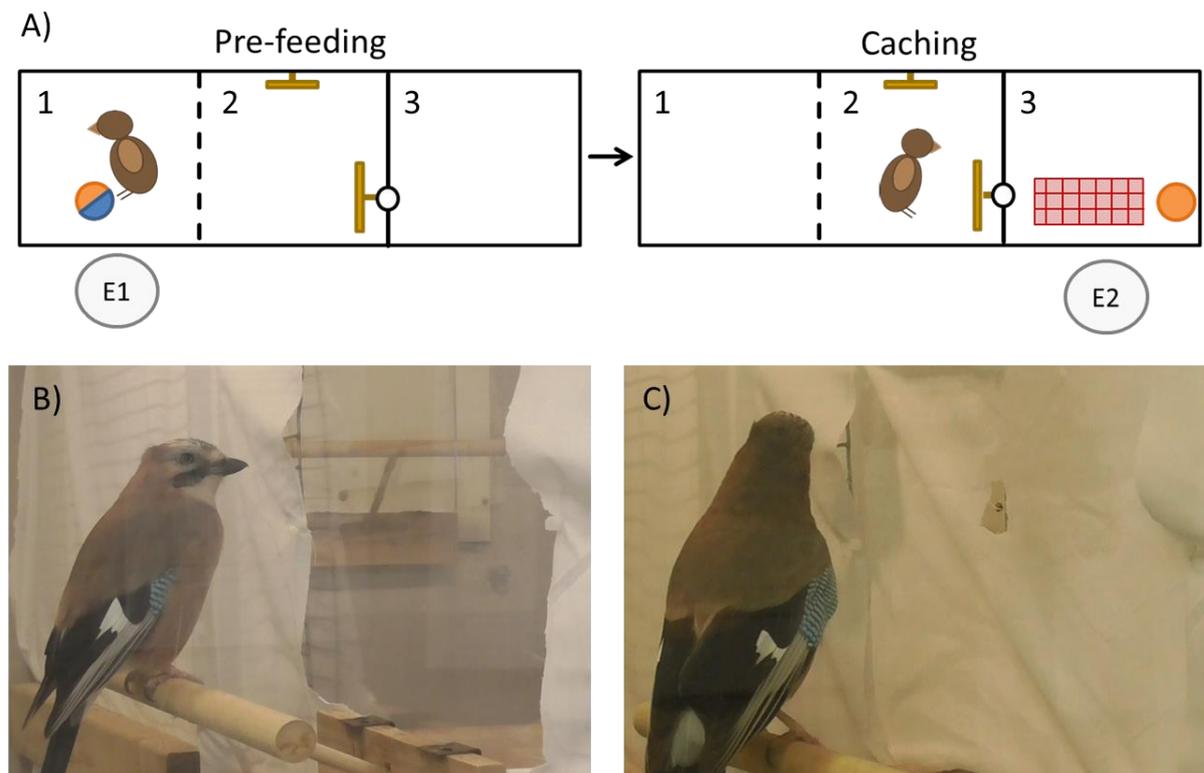


Figure 3.2. Panel A shows the set-up and procedure of the test phase of Experiment 3.3. Birds were pre-fed in compartment 1 by experimenter 1 (grey circle, E1), and then moved to compartment 2 where they were able to observe experimenter 2 (grey circle, E2) cached in compartment 3. Panel B shows a still frame of a jay during training, and Panel C of a jay looking through the peephole. Note that the sheeting with the peephole was attached to the mesh from compartment 3, and only allowed visual access to the adjacent compartment through the peephole.

Procedure. The procedure consisted of three phases. First, birds were pre-fed maintenance diet for 15 minutes in compartment 1 (*pre-feeding phase*). Then, the birds were

⁹ Note that experimenter 2 was naïve for all but one bird from colony 1, where experimenter 2 saw a bird handling the food she had been pre-fed on.

let through a window to compartment 2. This procedure ensured that, during the test, the naïve experimenter 2 would not see any pre-feeding food left in the compartment. A caching tray and a bowl with food were shown to the bird in front of compartment 2 and placed into compartment 3 by experimenter 1. The experimenter left the testing room for 2 minutes. During this time, birds could look into compartment 3 to see the caching tray and the bowl of food (*food-only phase*). This food-only-phase served to ensure that any effect found in caching was not due to increased interest in the food presented, but was instead specific to caching of that food. Then, in the *caching phase*, experimenter 2 entered the room and cached 6 (the mean number of food items cached in Ostojić et al.'s, 2017, experiment 2) larvae of the mealworm beetle¹⁰ in randomly allocated locations. Caching lasted approximately 30 seconds.

Training step 1: To familiarise birds with the procedure, birds received two training steps. In the first step, each bird received a minimum of 2 trials. The bird could observe the caching through a Perspex window shown in Figure 3.2, Panel B. Then, after caching ended, the food was taken out of the compartment, and birds were let through to compartment 3, where they were able to pilfer the larvae for approximately 2 minutes, and were released back into the main aviary. Importantly, during the caching phase birds had to sit on the perch mounted at the window to the caching compartment in order to proceed to the next step. This step was included to ensure that birds were comfortable with the presence of the experimenter 2 caching in the next compartment.

Training step 2: The procedure of the second step was the same as in the first step except that birds had to use the peephole to observe the caching, and could not pilfer after the caching phase. This second step was conducted to ensure birds would use the peephole to observe the caching. Only if the birds passed this step, that is, only if they looked through the peephole at least once during caching, birds moved on to test trials. If birds failed to look through the peephole twice in a row, they received another two trials of training step 1 before being presented with training step 2 again.

Test: The procedure of the test trials was the same as in the second training step, except that now, two types of nuts were used. Birds participated in two test trials: a *matching* and a *conflicting* condition. The type of food pre-fed to the birds was kept constant across the two conditions, but counterbalanced across birds. The caching food was then either the same (*matching* condition) or different (*conflicting* condition) to the pre-feeding food. Importantly,

¹⁰ Because Romero did not pilfer larvae of the mealworm beetle, larvae of the wax moth were used for him.

in the test trials, birds could again only use a peephole to observe the caching, as illustrated in Figure 3.2, Panel C.

Analysis. All analyses were conducted in RStudio Version 1.0.136 (R Core Team, 2016). Video recordings were coded regarding time spent looking through the peephole in the matching and in the conflicting conditions. To confirm consistency of coding, 40% randomly chosen videos were coded by a second rater (Rachel Crosby), blind to conditions and hypothesis. Inter-rater reliability is reported as an intra-class correlation coefficient (Hallgren, 2012) and was calculated with the R package irr (Gamer, Lemon, & Singh, 2012). Inter-observer reliability was high ($ICC = .97$).

The absolute time spent looking at the caching event in the conflicting condition was compared to the matching condition. If birds would attend to the caching event differently depending on their current desire, they should spend more time looking at the caching event in the conflicting condition than in the matching condition. Such a difference should be specific to the caching phase and should not be found in the food-only phase.

Due to the small sample size, data were analysed using exact permutation tests using the R package coin (Hothorn et al., 2008). Because the analysis was based on clear predictions, a directional test was used. Alpha was set at $\alpha = .05$. P-values $< .1$ were interpreted as trends. Cohen's d was corrected for dependence according to Morris and DeShon (2002). All descriptive averages are given as median with range in brackets.

Note that four birds were not included in the main analysis of the test phase because they did not look in either of the test trials (Lisbon, Jerusalem, Dublin, Hoy), resulting in a sample size of $n = 7$. One of these birds looked however in the food-only phase (Lisbon) and was thus included in the analysis of this phase.

Results

As can be seen in Figure 3.3, birds looked a median of 3.12s (0s-19.2s) in the conflicting condition and 1.92s (0s-9.84s) in the matching condition. This tendency of birds to look longer in the conflicting condition was however only at trend level, $Z = 1.528$, $p = .070$, Cohen's $d = 0.912$.

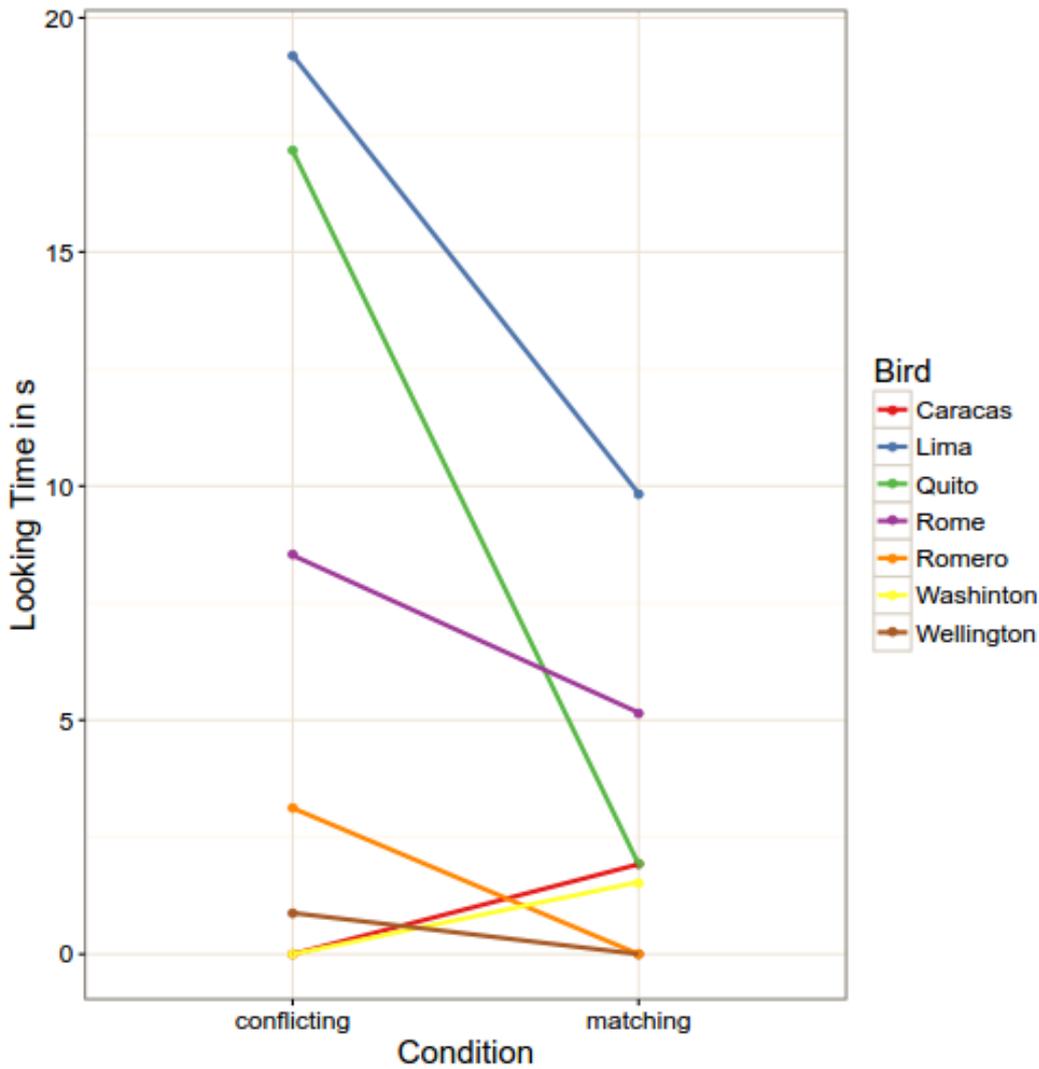


Figure 3.3. Looking time of all birds in the conflicting and the matching condition.

Additionally, to ensure that this tendency was specific to caching, the looking times during the food-only phase were analysed, where only a caching tray and the food were present. Here, birds ($n = 6$) looked a median of 5.24s (0.28s-21.42s) in the conflicting condition and 3.02s (0s-7.72s) in the matching condition. This difference in looking time was not significant, $Z = -1.158$, $p = .156$, $d = 0.552$ (see Appendix B, Table B.4 for raw data).

Thus, desire for a certain type of food seems to influence whether birds will attend to the caching of that food: birds tended to attend more to the caching when food they have not been pre-fed on was cached. This result suggests that the cachers in Ostojić and colleagues' (2017) study could have made use of a change in the observer's attentiveness.

Experiment 3.2: Behaviour of the Observer¹¹

It is possible that in Experiment 3.1 the birds had no motivation to obscure their interest in the caching as caches were made by a human experimenter. Our birds do not necessarily compete over food with humans in the same way as they compete with their conspecifics. Furthermore, the birds might have learned in the training phase that the human would not respond to their looking behaviour. In contrast, when competing with conspecifics, it is likely that the birds will react to each other's behaviours regularly. This possibility was further explored in Experiment 3.2. Here, birds were able to watch a real bird cache. This follow-up experiment thus provided an ecologically valid procedure to assess the observers' behaviour. It was assessed whether a difference in the observer's desire for certain food influences the observer's overt behaviour when observing a conspecific cache. To that end, birds were presented with a conspecific caching in the adjacent compartment. The desire of the observer was manipulated by pre-feeding different food types, and subsequently, the observer's behaviour in response to a caching conspecific was recorded. Additionally, birds had access to the cachers' tray after observing the caching. This additional step was conducted to assess whether differences in attention to a caching event would translate into differences in observational spatial memory performance given that previous research shows that corvids will attend more to caching when information about the location of caches is needed to pilfer (Watanabe et al., 2014). This pilfering phase was conducted in private and in extinction (i.e., in the absence of food, see Chapter 2).

Several variables were recorded: the proximity of the observer to the cacher in the adjacent compartment and time spent *not attending* because they were caching, eating, and flying. Importantly, it was not possible to code whether or not a bird was attending to the cacher in the adjacent cage – while it might look to a human observer as if a bird is not paying attention to a caching event, they might well be very alert. Therefore, behaviours that showed that the observer was clearly *not* attending to the cacher were coded. It was predicted that, when birds were pre-fed on a different food than the food the cacher cached, they should spend more time in close proximity to the cacher's compartment, compared to when they were pre-fed the same food.

Method

Subjects and housing. Seven sexually mature Eurasian jays of mixed sex were tested in February 2017. The housing was the same as that described in Chapter 2.

¹¹ I am grateful to Michael Mendl for comments on the study design.

Set-up. Birds were tested in two compartments as shown in Figure 3.3: the observer was in compartment 1, and the cacher in compartment 2. Cameras were positioned in front and to the left of the observer's compartment (compartment 1) as well as above the caching tray in compartment 2.

A mesh wall separated the compartment 1 and 2. This wall was additionally covered with white sheeting, leaving only a small window (20 cm x 30 cm) where birds could see each other. Here, a transparent Perspex prevented interactions between the birds.

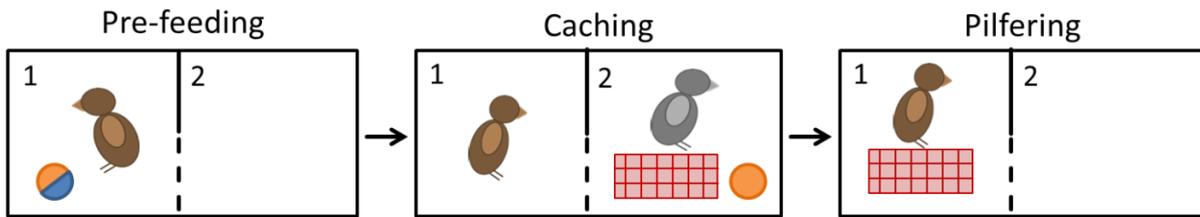


Figure 3.3. Set-up and procedure of Experiment 3.2. The focal bird (brown) received either peanuts or macadamia nuts in colour unique bowls (blue / orange circle). The brown bird denotes the observer (focal bird), and grey the cacher. The red rectangle depicts the caching tray, with the caching food next to it (orange circle).

To aid behaviour coding, the testing compartments were set up in the following way. First, only the window allowed birds to see into the compartment of the cacher. This set-up required the birds to come to the front of the compartment if they wanted to observe the cacher. Second, the floor of compartment 1 was divided into 2 sections. Section 1, the section closer to the window to the cacher's compartment, was further divided into two equally large sections with black tape stuck on the floor which was visible on camera. Lastly, during the caching phase, a bowl of maintenance diet was placed at the end of the observer's compartment. Due to the bowl's position birds could not see the caching while eating from this bowl. Figure 3.4 shows this set-up of the observer's compartment.

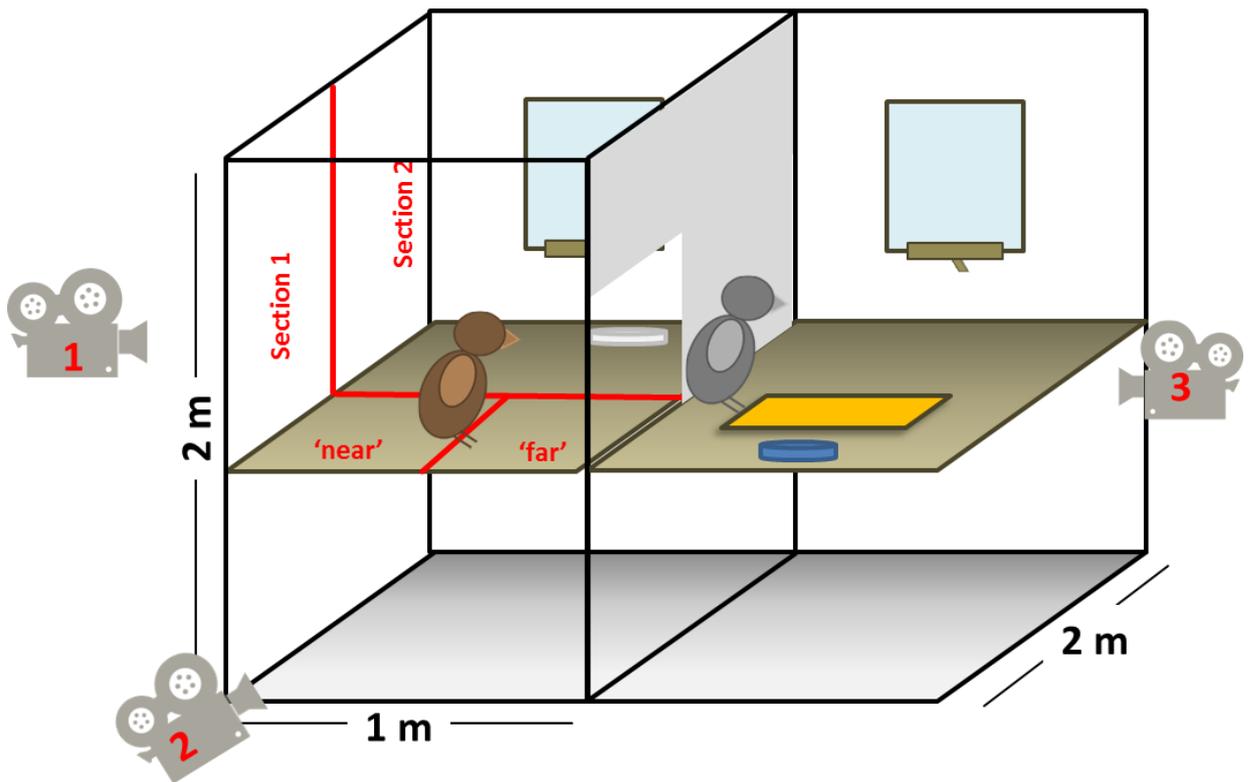


Figure 3.4. Set-up of compartment. Red lines depict the section boards, marked with black tape on the compartment floor, the brown bird depicts the observer (focal bird), and the grey bird is the cacher. The caching tray is depicted in orange and the bowl with the caching items in blue. A bowl of maintenance diet was placed in the observer's compartment, depicted in grey here. Sheeting partly obscured the observer's view to the cacher's compartment; only the caching tray and the food bowl could be seen through a window in the sheeting. Three cameras recorded the observer's behaviour.

Procedure. Similarly to Experiment 3.1, birds participated in two test trials: a *matching* and a *conflicting* condition. The food cached by the caching bird (peanuts) was kept constant across all birds. The pre-feeding food given to the observers differed between conditions such that it was either the same (*matching* condition) or different (*conflicting* condition) to the food cached in the caching event.

Focal birds were brought into compartment 1 and received a bowl of pre-feeding food (50 peanuts, or 50 pieces of macadamia nut) for 15 minutes. After the pre-feeding phase, a caching tray (a seedling tray with 5 x 3 pots, see Chapter 2) and a bowl with 100 peanuts were shown to the birds in front of their compartment, and then placed in compartment 2. The caching bird was then let into compartment 2 and the experimenter left the room. After 15 minutes, the caching tray and any leftover food were removed from compartment 2, and the cacher was released to the small outside run (see Appendix A, Figure A.1). During a 5-minute long break, the experimenter recorded the caches and their location. All caches were removed before the tray was given to the observer in order to ensure that birds rely on their memory,

rather than smell or visual cues emanating from the caches, when searching for caches (e.g., Clayton & Dickinson, 1998; see also Chapter 2). Furthermore, new sand was used to avoid the possibility of using smell to locate caches. The observer then had another 5 minutes to ‘pilfer’. As a last step, the tray was returned (the pots were replaced with the original pots, filled with caches) to the cacher for 5 minutes while the flap to his run was kept open. This procedure was used to maintain the cacher’s motivation to cache as it allowed the cacher to re-cache any caches to the outside run and consume them at a later point. Caches that were left in the tray after this period were lost to the cacher.

Birds that served as a cacher for other birds were always tested first as an observer. This procedure ensured that the experience they gained in the pilfering phase would not influence their caching behaviour. Specifically, in the pilfering phase they might learn that they, as observers, have access to the cacher’s caching tray, which could reduce their motivation to cache in the tray. Table 3.1 shows an overview of birds tested and that served as cachers.

Table 3.1. Observers and cachers tested in Experiment 3.2.

Observer (focal bird)	Cacher
Caracas	Lima*
Wellington	Lima*
Rome	Caracas
Washington	Wellington
Quito	Rome
Lisbon	Quito
Jerusalem [#]	Washington
Dublin	Wellington

Note: *Lima was not tested as an observer; he only served as a cacher. [#]Jerusalem did not participate in her second trial because she did not want to enter the testing compartment.

Behaviour coding. As mentioned above – because of the difficulties of coding birds’ looking behaviour in the absence of peepholes – the coder was agnostic with regard to whether birds were paying attention to the caching event. Only spatial proximity to the caching event was coded, a behaviour that could be measured objectively. Proximity was coded as being either in *section 1* (closer to the window into the cacher’s compartment) or *section 2* (further away from the window into the cacher’s compartment) of the compartment.

3: Changes in behaviour in Eurasian jays

Furthermore, it was coded whether birds were eating, flying, or caching – all of which would have prevented the bird from seeing the caching event.

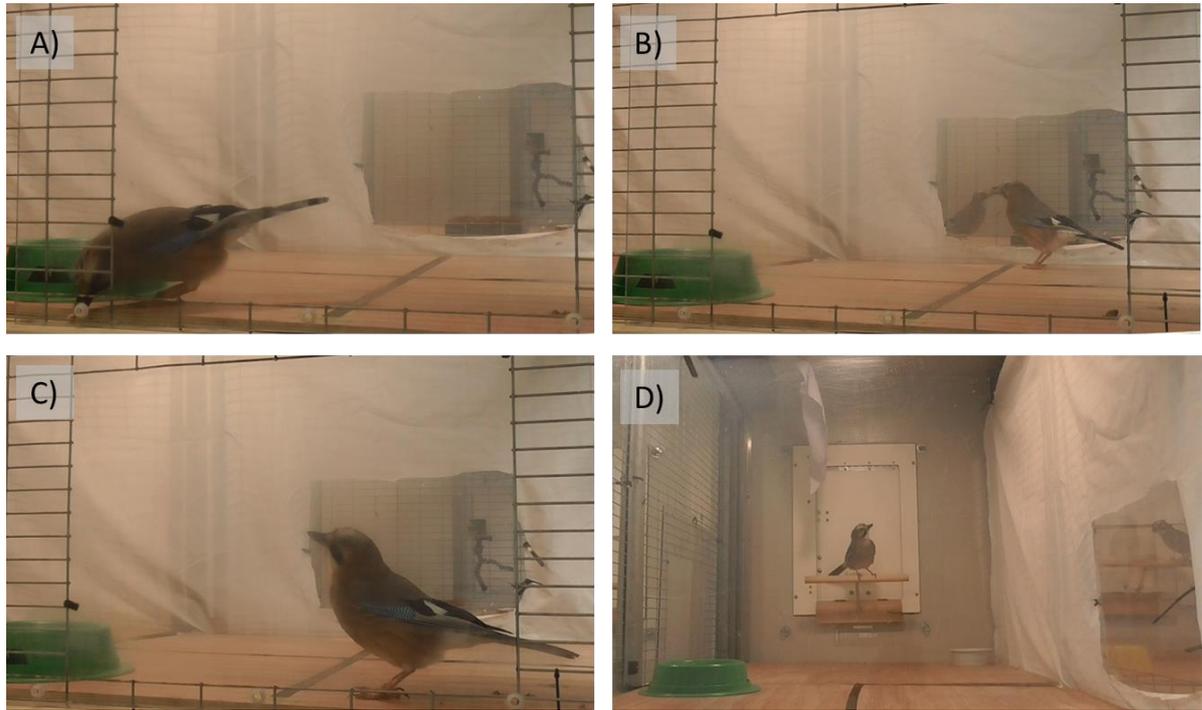


Figure 3.5. Examples of behaviours coded as seen from camera 2. In panel A) the focal bird (here: Caracas) is caching in section 1, ‘far’ from the cacher’s compartment (cacher not in view); in panel B) the focal bird is ‘near’ the cacher’s compartment (cacher in view); in panel C) the focal bird is ‘far’ from the cacher, not eating or caching; in panel D) the focal bird is in section 2 (cacher not in view).

Figure 3.5 shows four examples of behaviours coded. Being in section 1 was only coded when birds were standing on the platform, or sitting on the compartment wall. Birds often sat just beneath the ceiling in section 1, which was not coded as being in section 1 because birds could not see the cacher from there. In section 1, it was coded whether birds were *near* or *far* from the cacher’s compartment. The difference between ‘near’ and ‘far’ was marked by the black line of tape running along the middle of the platform. Time spent eating or caching was subtracted from time spent being in section 1. Additionally, I coded whether the cacher was in view of the observer (i.e., somewhere around the caching tray and the food bowl). Here, it was not assessed what the cacher was doing while being in view, as individual cachers differed in how much time they spent interacting with the tray or peeling and eating nuts.

Mainly videos taken from camera 1 were coded. Videos from camera 2 or 3 were used in case the behaviour was not seen on camera 1.

Analysis. All analyses were conducted in RStudio Version 1.0.136 (R Core Team, 2016). Videos were coded by myself using Solomon coder (Péter, 2016) to assess the proximity of the observer in relation to the cacher and the caching tray. To confirm consistency of coding, 40% randomly chosen videos were coded by a second rater (Piero Amodio), who was blind to the conditions and the hypothesis. Inter-rater reliability was calculated with the R package irr (Gamer et al., 2012) as intra-class correlation coefficient and was high ($ICC = .99$ for time spent in section 1, $ICC = .97$ for time spent ‘near’, and $ICC = .95$ for time spent ‘near’ while the cacher was in view).

Due to large individual difference in how much time was spent in one place, proportions of time spent out of total time were calculated. Three values were calculated: the proportion of time spent in section 1 (excluding time spent eating or caching) out of the total time spent not flying (henceforth called ‘total time’), the proportion of time spent near the window out of the total time, and the proportion of time spent near the window while the cacher was in view out of total time.

Due to the small sample size, data were analysed using exact permutation tests using the R package coin (Hothorn et al., 2008). Because the analysis was based on clear predictions, a directional test was used. Alpha was set at $\alpha = .05$. P-values $< .1$ were interpreted as trends. Cohen’s d was calculated correcting for dependence according to Morris and DeShon (2002). All descriptive averages are given as median with range in brackets. It was not possible to analyse observational spatial memory as too few birds ‘pilfered’ during the pilfering phase.

Results

Figure 3.6 shows the proportions of time spent in the different sections of the compartment (section 1 in general, and in the ‘near’ part of section 1) as well as the proportion of time spent in the ‘near’ part of section 1 while the cacher was in view. Additionally, the absolute time spent in section 1 for each bird is shown to illustrate the scale.

Birds spent a median of 241.4s (34.2s-561.4s) in section 1 in the conflicting condition, and a median of 76.2s (5.2s-875.2s) in the matching condition. In other words, bird spent a median of 27.6% (3.8-64%) of their time in section 1 in the conflicting condition and a median of 8.4% (0.6%-97.3%) of their time in section 1 the matching condition. This difference is not significant, $Z = 0.377$, $p = .336$, Cohen’s $d = 0.137$. They spent a median of 6.0% (0.7%-38.2%) near the window allowing visual access to the cacher’s compartment in the conflicting condition, compared to a median of 2.0% (0%-13.5%) in the matching condition. Again, this difference was not significant, $Z = 1.17$, $p = .148$, Cohen’s $d = 0.494$.

3: Changes in behaviour in Eurasian jays

When the cacher was in view, birds spent a median of 2.9% (0%-34.6%) of their time near the window in the conflicting condition compared to a median of 1.2% (0%-25.8%) in the matching condition. Again, this difference was not significant, $Z = 0.219$, $p = .438$, Cohen's $d = 0.070$.

As can be seen in Figure 3.6, panel A, this result was driven by two birds (Dublin and Wellington). Thus, 5 birds tested spent more absolute time in section 1 in the conflicting condition (median: 248.4 s, range: 34.2s-561.4 s) compared to the matching condition (median: 41.2 s, range: 5.2 s-235.8 s), $Z = 1.411$, $p < .031$, Cohen's $d = 0.78$ ($n = 5$). A similar pattern emerged for time spent near the window when the cacher was in view: 5 out of 7 birds spent a larger proportion of time there in the conflicting condition (median: 2.8%, 0%-34.6%) than in the matching condition (median: 1.2%, 0%-25.8%). This difference was however only at trend level, $Z = 1.77$, $p = .062$, Cohen's $d = 0.726$. Birds did not spend more time close to the window regardless of the cacher in the conflicting condition (median: 6.7%, 1.6%-39.9%) than in the matching condition (median: 2.25%, 0%-16.2%), $Z = 1.249$, $p = .156$, Cohen's $d = 0.072$ (see Appendix B, Table B.5 for raw data).

3: Changes in behaviour in Eurasian jays

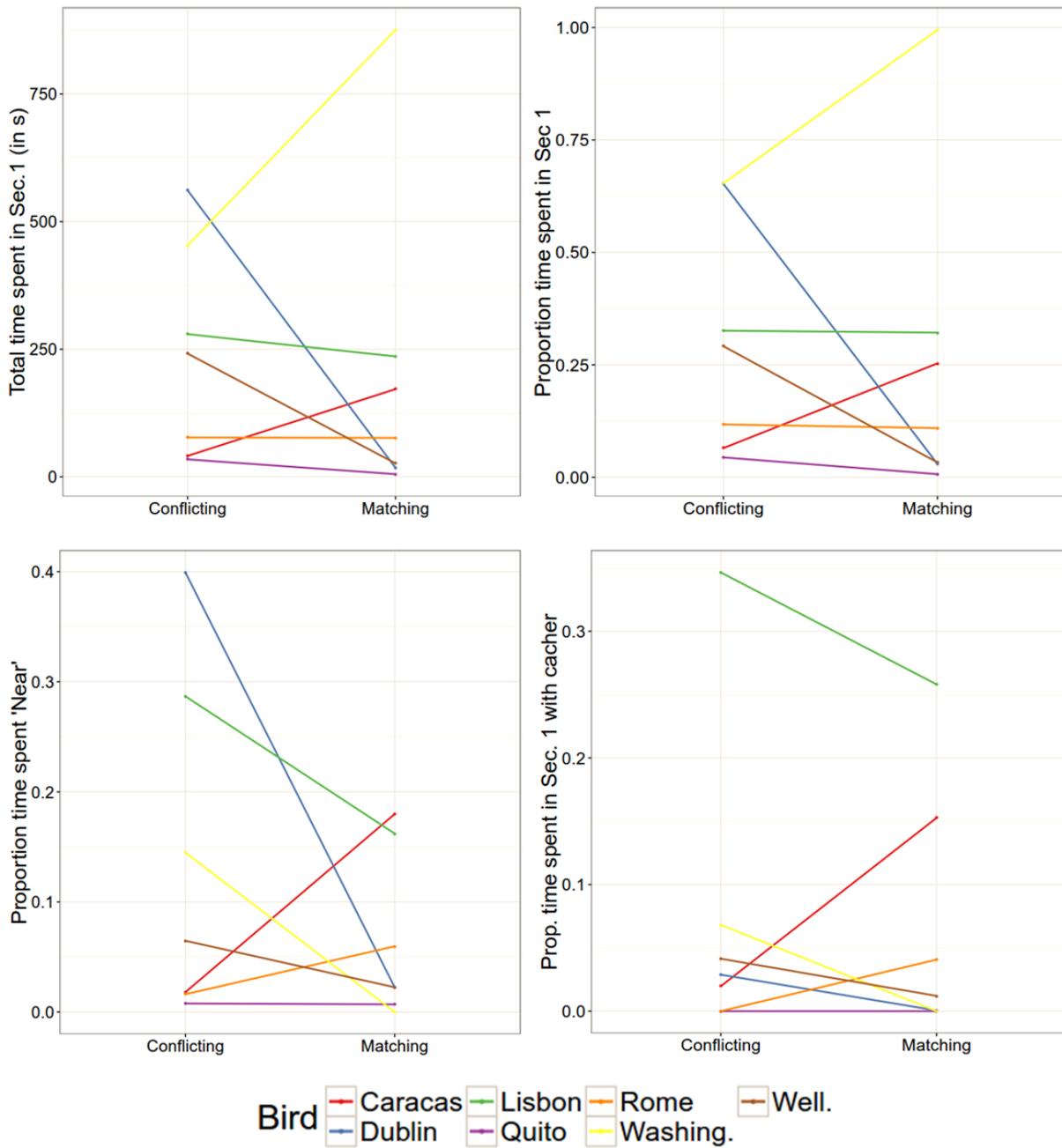


Figure 3.6. Panel A shows the total time spent in Section 1, panel B the proportion of time in spent in Section 1 out of the total time, panel C the proportion of time spent the sections nearer to the conspecifics, and panel D the proportion of time spent in section 1 while the cacher was present, for each bird in the two conditions.

General Discussion

The present chapter builds on the previously published results that show that birds take into account the desire of a conspecific during cache-protection (Ostojic et al., 2017) as well as during food-sharing (Ostojic et al., 2013; 2014; 2016). In this study, Eurasian jays and California scrub-jays had preferred to cache items not currently desired by the observers because they had been pre-fed to satiety on this type of food. Thereby, caching jays made use of the observer's reduced desire to pilfer. Importantly, however, cachers did not need to see what the observer was pre-fed on to protect their caches according to the observer's desire. Therefore, cachers might have responded to the observer's behaviour during the caching event. In the present study, it was specifically tested which cues the birds could have used to achieve this.

In Experiment 3.1, birds were first pre-fed on one type of food. Then, a human experimenter cached six items in a caching tray in the adjacent compartment, to which the birds had visual access only through a small peephole. The food cached was either the same as or different to the food the bird had just been pre-fed on (and was thus sated on). Although the difference did not reach significance, birds tended to look longer when a human experimenter was caching food that they desired compared to when they did not desire the cached food. There was no difference in looking time when only food and a caching tray were presented in the adjacent compartment. Therefore, birds' looking time behaviour changed depending on their desire in that they spent more time observing the caching of food they desired. In Experiment 3.2, birds could observe a conspecific cacher. Here, the spatial proximity of the observer in relation to the cacher and the caching tray was measured after being pre-fed the same or a different food than the food that was cached. Overall, there was no clear pattern of behaviour: some, but not all, birds spent more time in the part of the compartment allowing them visual access to the cacher and the caching tray. Similarly, some, but not all, birds tended to spend more time close to the window allowing visual access to the cacher's compartment while the cacher was present when they desired the food that was being cached. Thus, there was no clear effect of pre-feeding on the behaviours measured.

Together, these results tentatively suggest that certain behavioural cues might be influenced by the bird's current desires, while others might be less affected, or at least might not be consistently affected across different birds. For example, attending to caching might be relatively consistently increased when the observer is interested in the cached food, whereas proximity to the caching event might not always be a reliable indicator of the observer's

desire and might depend on other factors, such as dominance rank of the cacher, or boldness of the observer. Further research is needed to assess this possibility.

Ostojić and colleagues' (2017) results showed that the birds can and will use behavioural cues to protect their caches. As indicated in the present study, such a cue could be the amount of attention shown by the observer. Interestingly, this was not the case in a previous study by Ostojić and colleagues (2013) investigating desire state attribution during food sharing: here, Eurasian jays did not take into account the desire of their mated partner when they were unable to see what she had been pre-fed. This discrepancy suggests that similar behaviours (e.g., responding to the desire of a conspecific) might be based on different cognitive processes in different contexts, such as caching compared to food sharing (Ostojić et al., 2017).

The possibility that cachers responded to the pilferer's overt behaviour is at odds with the reading of previous caching experiments: so far, the cachers' tendency to limit the observer's opportunity to pilfer by caching out of sight or in difficult to see locations has been interpreted as an ability to attribute perspective and knowledge states to observers (e.g., Dally et al., 2006). Thus, Ostojić and colleagues (2017) suggests that at least certain cache-protection strategies might not necessarily rest upon a highly complex cognitive process like attributing perspective but could rely on reading behaviour. Therefore, birds' cache-protection strategies may not always and not exclusively reflect higher social-cognitive processes such as attributing mental states but could be based in part on behaviour-reading type abilities or on a combination of behaviour reading and attributing mental states (c.f., Ostojić, Legg, Mendl, & Clayton, in prep). This suggestion mirrors what has been proposed to underlie human theory of mind as well: that another's behaviour is understood and predicted using a range of different mechanisms, such as behaviour reading or the use of heuristics (c.f., Andrews, 2015; Apperly & Butterfill, 2009; Butterfill & Apperly, 2011; Carruthers, 2013; Heyes, 2014c).

One caveat of the present study is the nature of the 'cacher' used: in Experiment 3.1, the human cacher might not have been perceived as a competitor. Previous studies made use of human experimenters playing the role of a competitor (e.g., von Bayern & Emery, 2009), also in a caching context (e.g., Bugnyar & Heinrich, 2005; Bugnyar, Schwab, Schloegl, Kotrschal, & Heinrich, 2007). Here, ravens protected their caches from a competitive human but not from a passive onlooker. That is, learning that the human experimenter would steal their caches was necessary for cache-protection strategies to be elicited (Bugnyar et al., 2007). By contrast, the human cacher used in the present study was likely associated with the provision of food due to her history with the birds from previous interactions in experiments

and outside testing. It is thus possible that in Experiment 3.1 birds might not have felt the need to disguise their interest in the cached food. This in turn could explain the divergent results of Experiments 3.1 and 3.2: in Experiment 3.1 observers might have been less secretive than in Experiment 3.2 about their intentions because the human experimenter was not perceived as a competitor. Note however that in a previous study where observers had visual access to a conspecific cacher via peepholes, similar to the procedure of Experiment 3.1, the Eurasian jays did not completely hide their presence either (Shaw & Clayton, 2013). The point being made here is that they did not prefer a ‘silent’ perch from which they could look through the peephole over a noisy one. They did however vocalise less. This study thus suggests that, when being able to see conspecifics through a peephole, Eurasian jays seem to conceal some, but not all, of the cues signalling their presence.

Conclusion

In conclusion, these results suggest that Eurasian jays might be able to ‘read’ certain behavioural cues that correlate with the desire of a conspecific when protecting their caches – however, not all birds might exhibit the same behaviour. This finding highlights the notion that in order to respond to the changing mental states of a conspecific in a flexible way, animals might need to be especially tuned toward the behaviour of a conspecific, compared to other objects in the environment. Consequently, animals need to be able to differentiate between animate agents, which (re)act unpredictably and flexibly (Call, 2001), and inanimate non-agents, which can be acted on and tend to be predictable. This points to the relevance of investigating the basis of theory of mind-like abilities in animals, such as a sensitivity to the presence and behaviour of an agent, as opposed to non-agents. As stated by Andrews (2015), “seeing others as people is key” (p. 120) to successfully predict behaviour. In Chapter 4, I therefore assess the sensitivity of corvids to cues that are indicative of social agents and have been considered to be relevant for distinguishing animate from inanimate categories.

Chapter 4

Biological motion perception in California scrub-jays¹²

The concept of ‘biological motion perception’ refers to the perception of a number of individually moving stimuli as an animate living object. It has been suggested that a preference for biological motion reflects the ability to differentiate between animate and inanimate entities as one of the crucial building blocks upon which more complex social cognitive skills might rest upon. According to this ‘social cognition’-hypothesis, a preference for biological motion should be found in a variety of different non-human animal species, especially in those for which there is evidence of complex social cognition. However, previously reported biological motion preference in birds has been found specifically in precocial chicks. Therefore it has been suggested that a preference for biological motion may be functionally important in filial imprinting, where the newly hatched chick needs to follow the first moving stimulus in sight, namely the mother. According to this ‘ecology’-hypothesis, a preference for biological motion might be specific to species whose ecology requires them to identify other social agents based on their movement. To differentiate between these two hypotheses, in the present study, it was explored whether altricial California scrub-jays, a corvid species known for their highly developed social skills in the context of caching, exhibit such a preference for biological motion. First it was ascertained that the birds had a preference for observing a social agent (a conspecific) over an inanimate object that was matched for size and colour (Experiment 4.1). Subsequently, birds were allowed to observe through peepholes two different types of biological motion pattern, namely biological motion of another scrub-jay (Experiment 4.2a) and an unfamiliar biological motion pattern of a horse (Experiment 4.2b). In both experiments, birds did not prefer to observe the biological motion patterns over observing random motion patterns presented at the same time. This result supports the hypothesis that previously reported biological motion preference in animals might be linked to the ecology of certain species, in which conspecifics’ movement might be of special biological relevance such as in precocial birds or shoaling fish.

¹² The results from this chapter are being prepared for publication as Brecht, K. F., Ostojić, L., & Clayton, N. S. (in prep.). No evidence of a preference for biological motion patterns in California scrub-jays (*Aphelocoma californica*).

Introduction

In Chapter 3 I report two experiments suggesting that Eurasian jays' behaviour might change as a function of their mental states, in this case, their desire. This change could in turn be utilised by conspecifics. Therefore, in order to take into account what others want, and potentially what they know, corvids might need to be especially tuned toward the behaviour of their conspecifics. One of the most reliably found cues that tunes humans towards agents is the perception of biological motion patterns. In the present chapter, I will thus investigate this tendency in corvids.

A small number of lights attached to the body and main joints of moving human beings creates in an observer the automatic impression of a complete action, such as walking or jumping, rather than a percept of individual lights (Johansson, 1973; (Thornton, Rensink, & Shiffrar, 2002). Such dot patterns reduce movement solely to its kinematics, depriving the perceiver of any information about shape (Blake, 1993). Johansson showed that human adults are nevertheless able to recognise human activities from these dot patterns easily and rapidly (1973), and, as has been shown in later research, even when they are disguised by random dots (Cutting, Moore, & Morrison, 1988) or a scrambled masks (Bertenthal & Pinto, 1994).

Furthermore, biological motion perception has been implicated in recognising the animacy of agents (Schlottmann & Ray, 2010) and as such, it has been hypothesised to be an important pre-requisite for the development of general, flexible social cognitive abilities (Pavlova, 2012). According to this 'social cognition'-hypothesis, biological motion is a readily observable feature of animate entities that guides an individual's attention to socially relevant information (for a review see Rakison & Poulin-Dubois, 2001).

Biological motion perception can be found very early in human development (for a review see Simion, Bardi, Mascialzoni, & Regolin, 2013): looking-time studies have shown that even newborn babies that are just a few days old already show a preference for biological motion (Bidet-Ildei, Kitromilides, Orliaguet, Pavlova, & Gentaz, 2014; Simion et al., 2008). This preference extends to (some) heterospecifics, suggesting an innate preference specifically for biological motion patterns rather than a learned preference for the familiarity of human motion (Simion et al., 2008). Thus, biological motion seems to have certain characteristics that humans are sensitive to and can easily detect, independently of learning (Johnson, 2006; Simion et al., 2013), allowing us to differentiate between animate and inanimate entities (Poulin-Dubois, Crivello, & Wright, 2015; Wright, Poulin-Dubois, & Kelley, 2015).

4: Biological motion perception in California scrub-jays

The fact that biological motion preference can be found in humans only a few days old has opened up the question of whether non-human animals might be sensitive to the difference between biological and random motion, and if so which ones (e.g., Brown, Kaplan, Rogers, & Vallortigara, 2010; Troje & Westhoff, 2006). This potential sensitivity, a ‘life detector’ (Troje & Westhoff, 2006), has been proposed to be widespread among vertebrate species as a means to differentiate between animate and inanimate categories. Indeed, some non-human animals have been able to learn to differentiate between biological and random motion. For example, Blake (1993) successfully trained two cats (*Felis catus*) to differentiate biological from random dot patterns, and showed that they were able to transfer this differentiation to novel stimuli presentations. Similar results have been found with pigeons (*Columba livia*, Dittrich, Lea, Barrett, & Gurr, 1998; Troje & Aust, 2013). However, it has been suggested that while certain animals can be trained to differentiate biological from random motion, it is unclear whether they actually integrate the individual dots of a dot pattern to a coordinated percept of biological motion. For example, in more recent studies, pigeons were not able to transfer the discrimination between different type of motions learned from dot patterns to ‘full-detail’ videos of an animal performing the same movement (Qadri, Asen, & Cook, 2014; Yamamoto, Goto, & Watanabe, 2015). Consequently, the successful trainings demonstrated in previous studies need not imply that animals perceive biological motion in the same way as adult humans do.

So far, only a handful of studies on non-human animals have investigated a spontaneous preference like the one exhibited by humans. For example, Vallortigara, Regolin, and Marconato (2005) found that visually inexperienced chicks (*Gallus gallus domesticus*) preferred to approach a biological motion pattern when it was presented alongside a rigid motion or a random motion sequence. This preference was shown for both a walking hen stimulus and a walking cat stimulus, suggesting a general preference for biological motion. Furthermore, medaka fish (*Oryzias latipes*) spontaneously respond to biological motion displays with increased shoaling behaviour (Nakayasu & Watanabe, 2014), and female common marmosets (*Callithrix jacchus*; Brown, Kaplan, Rogers, & Vallortigara, 2010) will spend more time inspecting videos showing biological motion patterns. The studies on fish and chicks suggest an ‘ecology’-hypothesis of biological motion preference, wherein biological motion preference is closely linked to the species’ ecology and the need to identify agents based on their movement, for example the need of precocial birds to imprint on their mothers (Miura & Matsushima, 2016).

4: Biological motion perception in California scrub-jays

In summary, two alternative hypotheses regarding the evolution of biological motion preference have been proposed. The ‘social cognition’-hypothesis proposes that the perception of biological motion is associated with the development of flexible social cognitive abilities because it allows distinguishing animate from inanimate categories (e.g., Poulin-Dubois et al., 2015). Following this idea, if biological motion is relevant for detecting social agents, animals that have sophisticated social cognition should be attuned to biological motion, comparable to what has been reported in humans, and should prefer biological motion over random motion. The alternative, ‘ecology’-hypothesis states that biological motion preference in animals might be closely linked to specific innate behaviours, such as filial imprinting or shoaling, and might not necessarily relate to flexible social cognitive abilities. In this case, biological motion perception is expected to be confined to animals that rely on their conspecifics’ movement for survival.

To differentiate between these two hypotheses, in the present study, biological motion perception in California scrub-jays was investigated. Scrub-jays are an altricial species of bird known for their social cognitive abilities such as their ability to take into account what others can see or hear when protecting their food from pilferage (Grodzinski & Clayton, 2010a, 2010b). Evidence for preference for biological motion over random motion patterns in scrub-jays would support the notion that biological motion perception in animals is related to detecting and attending to social agents, an ability relevant for animals equipped with sophisticated social cognition.

To explore whether or not scrub-jays were attuned to biological motion, a looking time paradigm was employed in which the birds could look through peepholes, using a procedure similar to what has been used in Chapter 3 and in previous studies on this species (Grodzinski et al., 2012; Watanabe et al., 2014). The use of peepholes made it possible to measure their preference for biological compared to random motion patterns.

In Experiment 4.1, it was first assessed whether or not California scrub-jays preferred to attend to a full-display animate conspecific over attending to an inanimate object. This was done both ‘live’ and as video playback. In corvids, video playback had previously been used with rooks (*Corvus frugilegus*, Bird & Emery, 2008). However, using video playback in birds has to be validated due to the potential issues associated with the presentation of videos on monitors designed for the human eye (D’Eath, 1998; Lea & Dittrich, 2000); hence, in Experiment 4.1, I concurrently validated the use of video playback in scrub jays. Then, their preference to look at a biological motion pattern depicting a scrub-jay (Experiment 4.2a) was measured by allowing them to choose between looking at a biological motion pattern and a

4: Biological motion perception in California scrub-jays

random motion pattern, both presented on a video screen. To eliminate the possibility that a preference for biological motion depicting a conspecific is only due to greater familiarity with the stimulus than with the random motion pattern, I subsequently contrasted random motion with an unfamiliar stimulus by presenting the birds with the biological motion pattern of a walking horse (Experiment 2b). If scrub-jays are sensitive to biological motion, birds should allocate more time to looking at the biological motion than at random motion, regardless of whether the stimulus presented is a conspecific or a heterospecific (Simion et al., 2008).

Experiment 4.1

Previous studies measuring how much time is allocated to looking at each of two simultaneously presented events have revealed that the birds prefer to look at social than non-social events or stimuli. For example, scrub-jays preferred to look at another bird caching over looking at a caching tray (Grodzinski et al., 2012), and rooks preferred to look at a novel conspecific over an empty compartment, both live and when presented as video playback (Bird & Emery, 2008). I used a similar paradigm to validate the use of video playback with scrub-jays. Using both a live and a video presentation method, scrub-jays were presented with a social stimulus, a familiar conspecific, and a non-social stimulus, an inanimate object. If scrub-jays – like other corvids – prefer to look at a social stimulus, they should prefer to look at the conspecific than at the object with the live presentation method. If the birds could also discriminate these different stimuli presented on a video screen, they were expected to show the same preference with the video presentation method.

Methods

Subjects. Five female and three male adult California scrub-jays participated and were housed at the Sub-department of Animal Behaviour at the University of Cambridge. All of the birds were originally collected in 2007 as wild nestlings from California, USA. During the experimental period, subjects were housed in pairs in three to four joined cages (each measuring 1 x 1 x 1m). When resting, birds were kept together with one to 3 individuals in larger outdoor aviaries (measuring 2 x 6 x 3m) constructed of wood and mesh with gravel floors. Birds had also access to inside compartments (3 x 9 x 2m). Outside of testing, birds were fed a maintenance diet consisting of bread, seeds, eggs, cheese, vegetables, fruit and dog kibble. During all times, birds had ad libitum access to water and various forms of enrichment. The work was conducted under the UK Home Office project licence PPL 80/2519.

4: Biological motion perception in California scrub-jays

Birds were tested between May and August 2015. Two birds (one male, one female) died while resting between trials and thus their data were excluded, resulting in a sample of $n = 6$ scrub-jays.

Set-up. The birds were tested in the middle of three cages (each measuring 1 x 1 x 1 m), separated from each other by opaque dividers as depicted in Figure 4.1, Panel A. The birds had visual access into the adjacent cages (cages 1 and 3) through peepholes in the opaque dividers (3cm diameter, 55 cm off the cage floor) (Grodzinski et al., 2012; Watanabe et al., 2014).

4: Biological motion perception in California scrub-jays

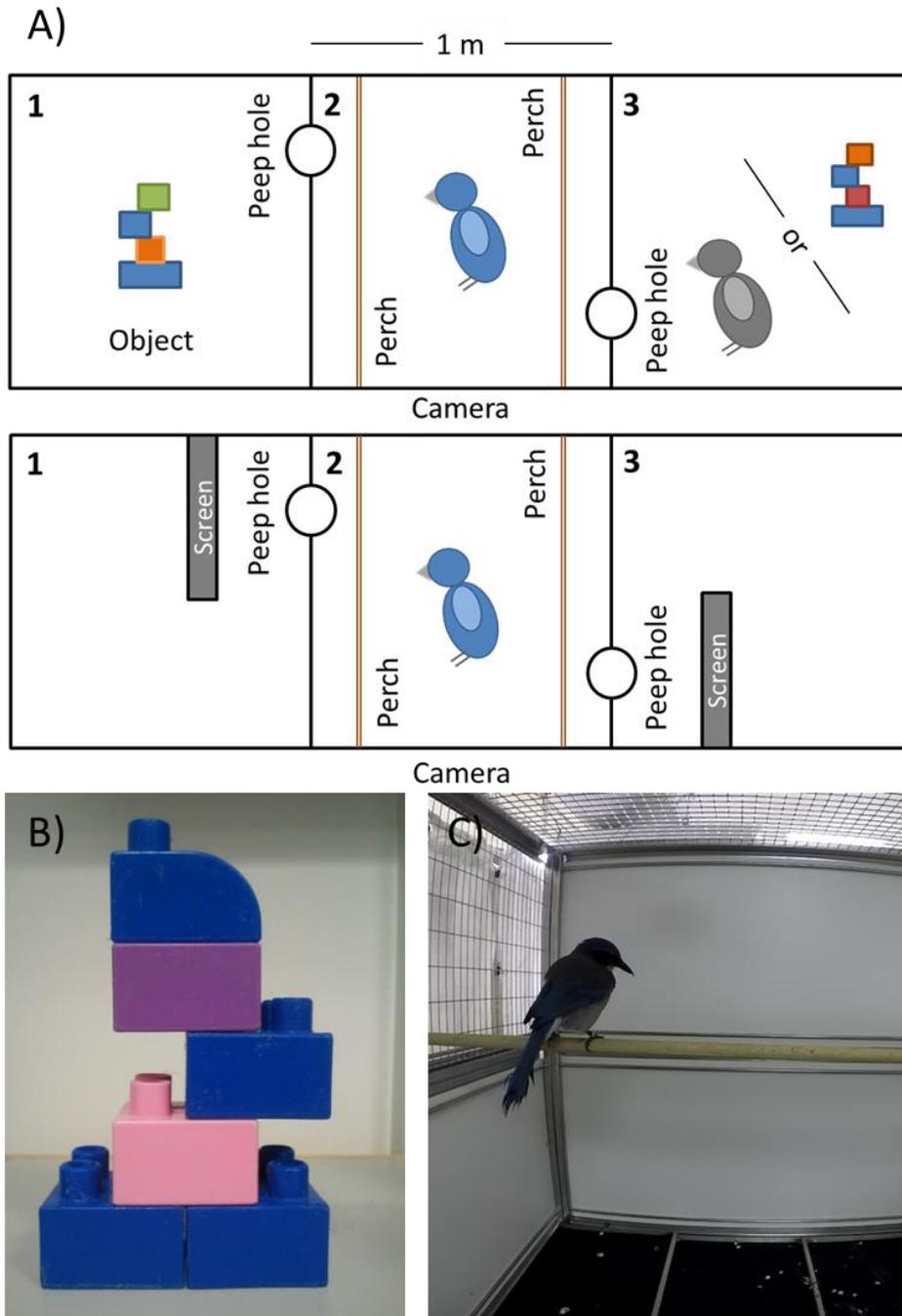


Figure 4.1. Panel A shows an aerial view of the experimental set-up, with the focal subject in cage 2, and the object and or the partner in the adjacent cages in the live condition. In the video condition, the screens depicted the partner and the objects respectively. Peepholes were positioned at the near and far end of the cage, respectively. Perches were mounted on both sides of the cage. Panel B shows one of the objects (left) and the partner (right) as a still frame of one of the videos used.

Perches were mounted running parallel to the dividers and 52 cm off the cage floor such that the birds had to slightly hunch down in order to see through the peepholes, making it easier to determine when a bird was looking. Figure 4.2 shows an example of a bird looking through a peephole. Additionally, a third perch was mounted in the middle of the cage. From

4: Biological motion perception in California scrub-jays

this middle perch, birds had the opportunity to explore the room, and to explore the peepholes. However, note that ‘looking’ was only counted when birds approached one of the two peepholes and looked down to see through them.



Figure 4.2. Example of bird looking through one of the peepholes.

Both with the live and the video presentation methods, the birds could see either a conspecific agent in one and a scrub-jay sized inanimate object made out of Lego Duplo® bricks in the other cage (Agent-Object condition; see Figure 4.1, panel B) or an object in both cages (Object-Object condition). The Object-Object-condition was introduced to account for the housing situation of the birds. Birds were always housed in pairs in four cages, of which three were used for testing. In the video presentation method, the conspecific partner would always be adjacent to one of the cages where the video screen was mounted (i.e., on the left of cage 1 or on the right of cage 3). To avoid a side bias, induced by the scrub-jays’ interest in conspecifics (e.g., Grodzinski et al., 2012), that could have interfered with a preference for one of the two videos the Object-Object condition was introduced. This condition allowed comparing the time birds choose to look at an object, for example on the left, over another object on the right (Object-Object condition) in one trial to the time they choose to look at the agent on the left over an object on the right (Agent-Object condition) in the other trial. Hence, in this setup, it was possible to compare looking times into the same peephole. If birds show an interest in an agent presented as video playback, they should spend more time looking through the peephole showing the agent on day 1 (or day 2) compared to the time they spent looking through the same peephole showing an object on day 2 (or day 1).

Sides and trial order was counterbalanced across birds. For all birds except one (Nr. 215) the conspecific in the Agent-Object condition was their cage partner, i.e. the bird they

4: Biological motion perception in California scrub-jays

were housed with. For Nr. 215, the conspecific agent was Nr. 223 (male) who lived in the adjacent cage. Each bird was tested with the same conspecific agent with the live and the video presentation methods.

Material. For the video presentation method, a 10-minute long video playback of both Agent and Object respectively were shown on a computer screen with a size of up to 5 cm, which corresponds to a visual angle of maximum 12.4° (variability due to moving agent). For the Agent-Object trials, videos of the conspecific were filmed such that the bird was moving as little as possible (see supplementary material for videos of the Agent-Object condition). To account for the high flicker rates perceived by birds (D'Eath, 1998; Ware, Saunders, & Troje, 2015), videos were filmed using a GoPro® Hero 4 Black with 60 frames per second and a resolution of 930p and presented with a Lenovo® Thinkpad Edge E330 (50 to 60 Hz refresh rate, graphic card Intel HD graphics 4000) on a 17" portable Lenovo® LCD monitor (60 Hz refresh rate), on which pixels did not go black between frame changes.

Procedure. Firstly, it was established that the birds had a preference to look at their partner. Thus, all birds were tested with the live presentation method first. The order in which the birds experienced the Agent-Object and the Object-Object conditions was counterbalanced across birds but remained the same for both presentation methods for each bird. Birds thus received four trials in total, one trial per day. A trial was repeated if a bird did not look through either of the peepholes— this happened once, namely for Nr. 202 for the Object-Object with the video presentation method such that this trial was repeated. Approximately one and a half to two hours prior to testing, scrub-jays were visually isolated from their partner. For the duration of testing, all food was removed from the cages.

After positioning all stimuli in the adjacent cages (objects and agents or video screens respectively), the experimenter opened the peepholes and left the test room for the duration of the experiment (10 minutes). The birds' behaviour was recorded with a Multicam Surveillance Camera System and a GoPro, mounted to the cage mesh (GeoVision GV-900, London, UK).

Analysis. All analyses were conducted in RStudio Version 1.0.136 (R Core Team, 2016). Video recordings were coded regarding time spent looking through each peephole. To confirm consistency of coding, 15% of all videos were coded by a second rater (Rachel Crosby), blind to conditions and hypothesis. Inter-rater reliability is reported as an intraclass correlation coefficient (Hallgren, 2012) and was calculated with the R package irr (Gamer et al., 2012). Inter-observer reliability was high ($ICC = .80$).

4: Biological motion perception in California scrub-jays

To obtain an independent measure of preference while taking into account that birds differed in the time spent looking through the peepholes overall, the following percentage scores were calculated. For the Agent-Object condition, the duration of looking at the agent was divided by the duration of looking through the two peepholes together, $LT_{\text{Agent}} / LT_{\text{Object}+LT_{\text{Agent}}}$. For the Object-Object condition, the duration of looking at the object presented on the same side as the agent in the Agent-Object condition was divided by the duration of looking through both peepholes together, $LT_{\text{Object}} / LT_{\text{Object}+LT_{\text{Object}}}$. Thus, the percentage of looking through the target peephole can be interpreted as the birds' relative preference of looking at that particular stimulus. If scrub-jays, like other corvids, prefer to look at social agents rather than at inanimate objects, then this proportion should be higher in the Agent-Object than in the Object-Object condition. In addition, if scrub-jays recognise these different types of stimuli on a computer screen, this effect should not only be shown using the live but also using the video presentation method.

Due to non-normality, data underwent aligned rank transformation with the R package ARTools (Kay & Wobbrock, 2016; Wobbrock, Findlater, Gergle, & Higgins, 2011). The transformed data were analysed using a repeated measures ANOVA with the factors *Condition* (Agent vs. Object) and *Presentation method* (Live vs. Video playback). Alpha was set at $\alpha = .05$. P-values $< .1$ were interpreted as trends. Cohen's *ds* were corrected for dependence according to Morris and DeShon (2002).

To ascertain that the same preference was exhibited in both presentation methods, a repeated measure ANOVA was run with condition as a within-subject factor separately for each presentation methods as planned contrasts. All descriptive averages are given as median with range in brackets.

Results and Discussion

When presented with a live agent and a 'live' object, birds spent a median of 67.0% (57.5%-98.9%) of their time looking through the target peephole in the agent-object condition, and 37.0% (0%-45.0%) of their time looking through the target peephole in the object-object condition. When presented with video playback of the agent and the object, birds spent a median of 82.4% (61.4%-100%) of their time looking through the target peephole in the agent-object condition, and 19.2% (0%-75.7%) of their time looking through the target peephole in the object-object condition.

As can be seen in Figure 4.3, regardless of presentation method, birds looked more through the target peephole in the Agent-Object (median = 79.1%, range: 67.2%-99.5%) than in the Object-Object (median = 29.9%, range: 0%-49.3%) condition (main effect of condition:

4: Biological motion perception in California scrub-jays

$F(1,20) = 9.10, p = .007$, Cohen's $d = 1.53$). In addition, this effect did not differ between the live and the video presentation methods (no interaction condition \times presentation method: $F(1,20) = 0.005, p = .982$).

The planned contrasts further confirmed that with each presentation method, the birds looked longer through the target peephole in the Agent-Object than in the Object-Object condition (main effect of condition in the live presentation method, $F(1,5) = 10.44, p = .023$, Cohen's $d = 2.74$; video presentation method, $F(1,5) = 12.1, p = .018$, Cohen's $d = 1.35$; see Appendix B, Table B.6 for raw data).

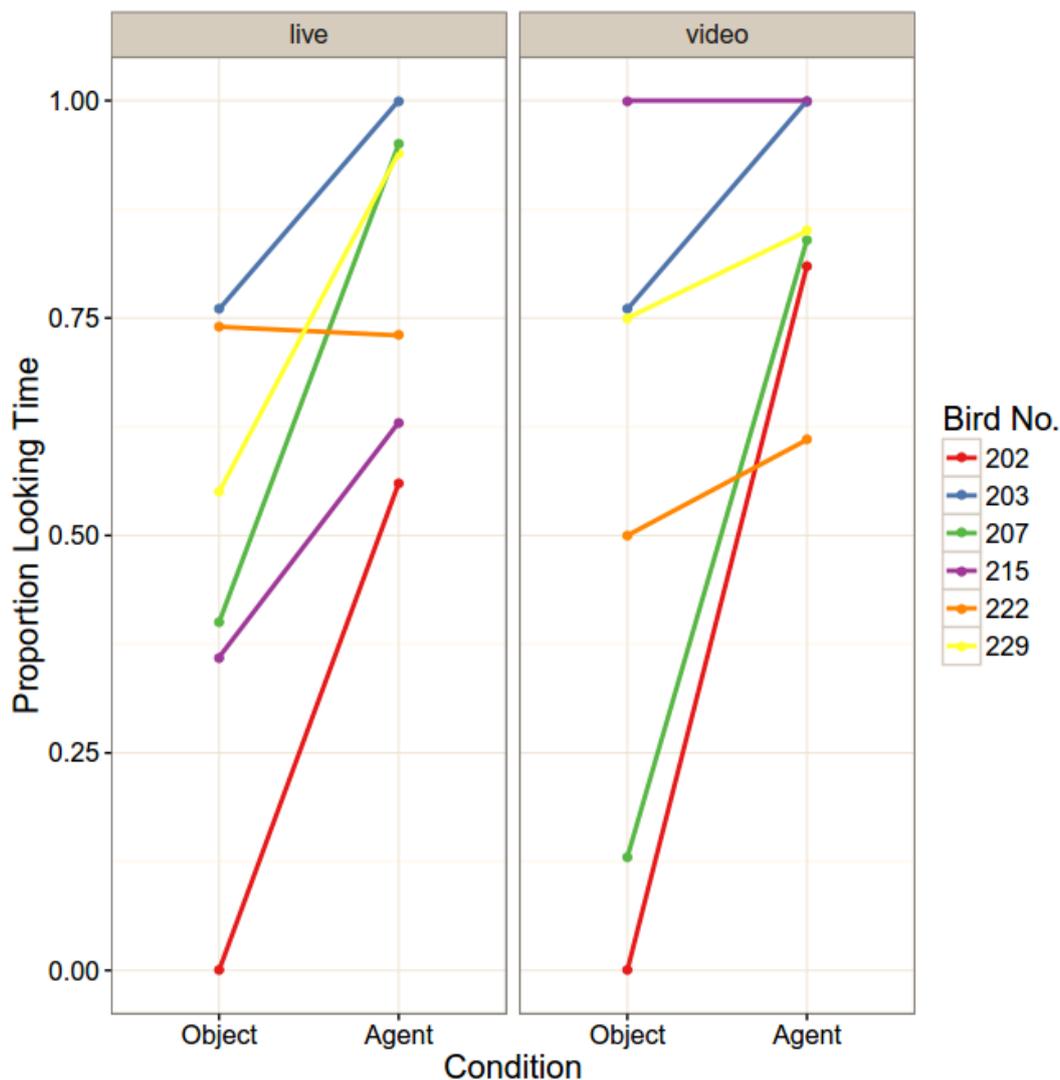


Figure 4.3. Proportion looking time for each condition for each bird separately.

These results show that firstly, the scrub-jays preferred observing an animate agent over observing an inanimate object, and secondly, that the birds reacted to the stimuli presented on the video screen similarly to the live stimuli. Thus – in agreement with what has been found previously in rooks (Bird & Emery, 2008), Eurasian jays (Davidson, Miller,

4: Biological motion perception in California scrub-jays

Loissel, Cheke, & Clayton, 2017), and other birds (Galoch & Bischof, 2007; Rieucan & Giraldeau, 2009) – video playback can be used as a means with which to present stimuli to scrub-jays in the subsequent experiments.

Experiment 4.2

As in Experiment 4.1, the time birds spent looking at the biological motion pattern depicting a conspecific (Experiment 4.2a) or a horse (Experiment 4.2b) was compared to random motion. Specifically, the percentage of time that the birds looked at the biological motion patterns (conspecific/heterospecific) out of the total time they looked at either the biological motion or the random motion pattern was calculated. To avoid side-bias, two trials were conducted and on each trial, the biological and random motion patterns were shown on different sides. Thus, the proportion of looking time at the biological motion was averaged across trials. If birds had a preference for biological over random motion patterns, they should spend more time looking at the biological motion more often than expected by chance (> 50% of the time).

Method

Subjects. Three female and two male adult California scrub-jays that all had previously participated in Experiment 4.1 were tested under the same housing conditions.

Set-up. The set-up was the same as in Experiment 4.1. The biological motion videos were presented with video screen mounted to the peepholes.

Material. Birds were presented with the biological motion pattern and random motion. To avoid any bias, the number, brightness and size of dots as well as the video frame rates were identical for both the biological and the random pattern.

For Experiment 4.2a, the biological motion clip was created by filming a scrub-jay (No. 223; male) hopping along a straight line. The stimuli creation is depicted in Figure 4.4. For each frame, the dots were positioned on predetermined points of the scrub-jay's body. Thirty-eight frames were created. For the final clip, the frames of the original video were replaced by a white background. The dot-frames were combined into a clip using Windows Movie Maker. For the random motion patterns, 13 dots were randomly scattered throughout the frame. Dots were moved by a set amount of pixel in each frame and in such a way that they returned to where they were at the beginning of the sequence of frames. Both the biological and random motion pattern clips consisted of 38 frames that were presented in a loop (30 frames per second). For both random motion and biological motion, 13 black dots on white background were presented.

4: Biological motion perception in California scrub-jays

For Experiment 4.2b, the biological motion pattern depicted a walking horse. Stimuli were produced frame-by-frame from a video retrieved online of a horse walking in profile. Nineteen dots were ‘attached’, and frame-by-frame re-adjusted according to the horse’s movement. Similarly to Experiment 4.1, the random motion pattern was matched to the biological motion in that the same number of dots and the same amount of frames was used for both clips (25 frames per second). Both the clips of the conspecific and the horse elicited the impression of a biological motion pattern in a human viewer (the experimenter).

Procedure. All birds participated in two trials each, both in Experiment 4.2a and 4.2b. In both trials, the biological motion and the random motion pattern were presented. To avoid side-bias, the different videos were shown on two different sides in the two trials. As in Experiment 4.1, birds were isolated from their partner 20 to 30 minutes prior to testing, and only shortly before testing, they were deprived of their maintenance diet and all food was removed from the testing cage.

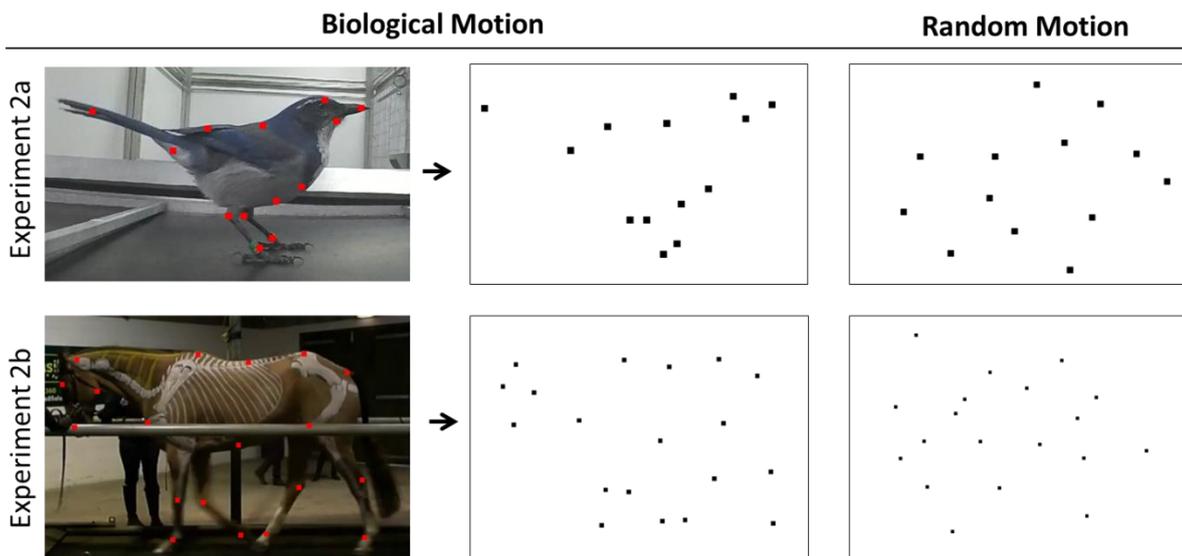


Figure 4.4. Stimulus creation (Experiment 4.2a and 4.2b). To create a biological motion pattern of a scrub-jay, dots were ‘attached’ frame-by-frame to predetermined points of the video playback of a hopping scrub-jays body and walking horse, respectively.

Analysis. To confirm consistency of coding, 6 out of 40 videos (15%) were coded by a second rater blind to conditions and hypothesis (Corina Logan). Interrater reliability was measured as intra-class correlation coefficient (Hallgren, 2012) and showed a strong agreement between raters ($ICC = .78$). The mean percentage of time looked at the biological motion out of the time looked at the two videos in total, was analysed using RStudio, Version 1.0.136 (R Core Team, 2016). If birds have a preference for biological over random motion, they should spend more time looking at the biological motion more frequently than expected by chance (50% of the time). A one-sample one-tailed Wilcoxon signed-rank test was

4: Biological motion perception in California scrub-jays

calculated, with a test-value of 50%, reflecting the prediction that the average proportion of looking time should be higher than 50%. Because the analysis was based on clear predictions, a directional test was used. Alpha was set at $\alpha = .05$. P-values $p < .1$ were interpreted as trends. Cohen's d s were corrected for dependence according to Morris and DeShon (2002). All descriptive averages are given as median with range in brackets.

Additionally, I calculated a Bayes Factor (BF) with a Bayesian one sample t -test (test value $> .5$) (see Appendix C) for both Experiments 4.2a and 4.2b.

Results and Discussion

In Experiment 4.2a, birds looked a median of 11.05 s (4.45s-90.26) at one of the two displays across both trials. Birds spent a median of 50% (27.0%-64.9%) of the time looking at the biological motion pattern. Thus, as can be seen in Figure 4.5, the amount of looking time towards the biological motion as a proportion of the total time looking at both the conspecific and random motion did not significantly differ from chance, $W = 5.00$ $p = .781$, Cohen's $d = -0.171$).

4: Biological motion perception in California scrub-jays

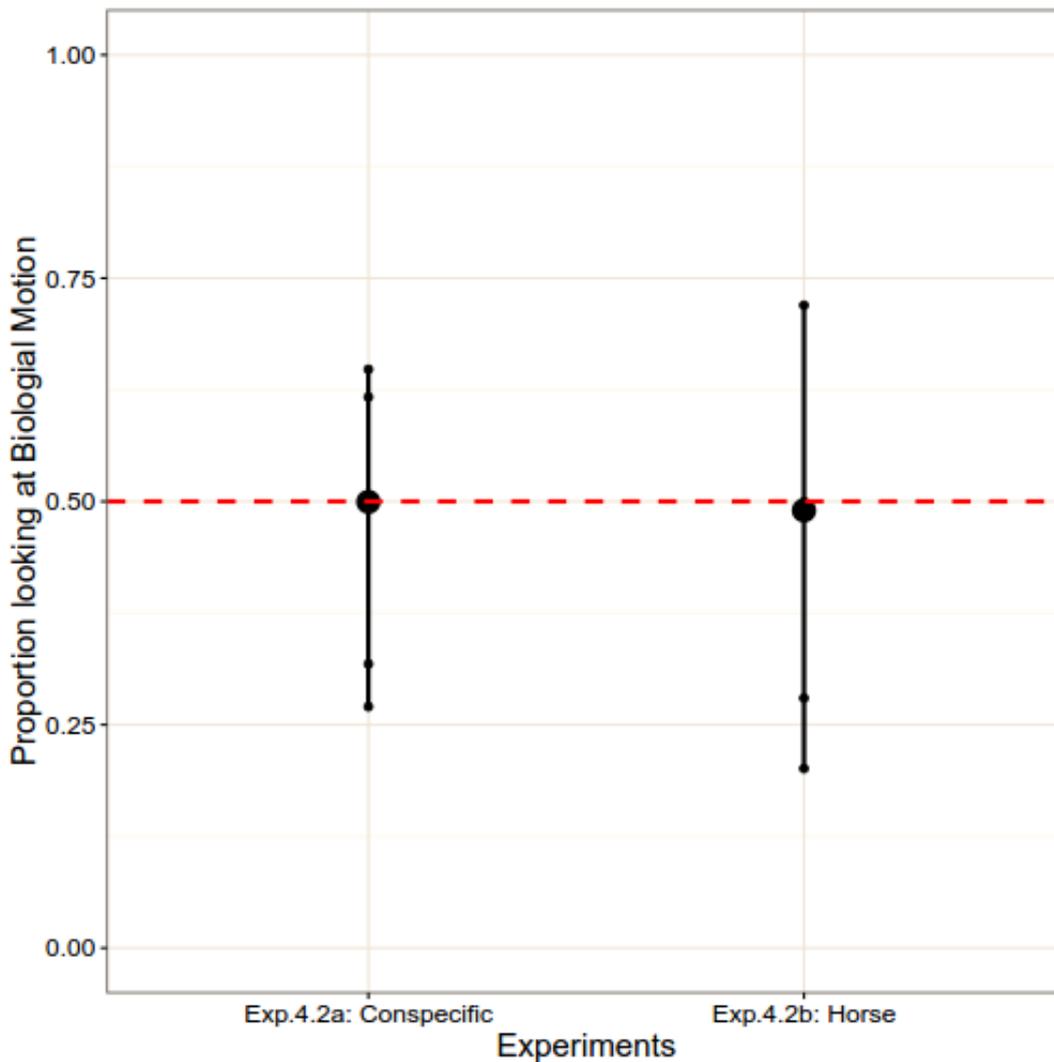


Figure 4.5. Proportion of time looked at biological motion for Experiments 4.2a and 4.2b. Black dots show the mean proportion of time looked towards the biological motion, with smaller black dots donating the individual values. Red dotted line denotes chance.

In Experiment 2b, birds looked with a median of 3.37s (0.73s-13.99s) at one of the two displays across both trials. Birds spent a median of 49.9% (20.0%-72.0%) of the time looking at the biological motion pattern depicting a horse. As can be seen in Figure 4.5, this percentage was not significantly different from chance, $W = 3.50$, $p = .769$, Cohen's $d = -0.291$ (see Appendix B, Table B.7 for raw data).

General Discussion

The results from Experiment 4.1 suggest that, in principle, video playback can be used to mirror real-life situations when testing California scrub-jays, a conclusion that is supported by previous research with other species of birds in general and corvids in particular (Bird & Emery, 2008; Davidson et al., 2017; Rieucan & Giraldeau, 2009; Ware et al., 2015). In Experiment 4.2a and 4.2b, the preference of California scrub-jays to attend to biological

4: *Biological motion perception in California scrub-jays*

motion patterns over random motion patterns was investigated, presenting birds with different biological motion stimuli. Regardless of the type of biological motion (a conspecific in Experiment 4.2a or unfamiliar heterospecific in Experiment 4.2b), it was found that the scrub-jays did not show a preference for looking at biological motion patterns. This result is at odds with the ‘social cognition’ hypothesis, namely the notion that biological motion perception is related to flexible social cognition in animals.

The lack of a preference for biological motion in scrub-jays, in the context of Vallortigara and colleagues’ (2005) positive results with chicks, is in line with the suggestion that the preference for biological motion patterns in birds is related to filial imprinting rather than social cognitive abilities (‘ecology’ hypothesis; see also Miura & Matsushima, 2016; Regolin, Tommasi, & Vallortigara, 2000). Thus, a preference for biological motion over random motion patterns might exist in species for whose survival it is necessary to identify conspecifics based on their movements (see also the induction of shoaling behaviour in medaka fish, Nakayasu & Watanabe, 2014). It is also possible that a preference for biological motion is a tendency that only young birds show – that is, it would be of interest whether young corvids have such a preference. To my knowledge, there is no research on whether the initial preference for biological motion patterns in chicks is preserved into adulthood.

It is important to note that in Experiment 4.1, scrub-jays showed a preference to look at a live conspecific as well as at video playback of a conspecific over an inanimate object. Thus, it is unlikely that the indifference of the birds regarding motion patterns in Experiments 4.2a and 4.2b could be explained by the procedure used: scrub-jays will choose between looking at one of two stimuli, and will allocate comparatively more time to look at an agent, a biologically and socially relevant stimulus, than at a novel but inanimate object, even when presented by video playback. Their indifference towards biological motion pattern shown in Experiments 4.2a and 4.2b suggests that for scrub-jays biological motion patterns alone do not constitute socially relevant cues, that is, in the absence of other cues about the animate stimulus.

It is possible that a different experimental approach could uncover an ability to *distinguish* biological from random motion at least when trained, for example by using operant conditioning techniques that have been used with cats (Blake, 1993), pigeons (Dittrich et al., 1998; Troje & Aust, 2013), and chicks (Ryan, Lea, Alkind, & Dittrich, 2001). However, the fact that scrub-jays did not show a spontaneous *preference* for biological motion patterns suggests that they do not readily perceive a dot pattern as a biological agent

4: Biological motion perception in California scrub-jays

That is, the scrub-jays might literally fail to ‘connect the dots’, as has been suggested to be the case with pigeons (Qadri et al, 2014; Yamamoto et al, 2015).

In summary, the results of this study suggest that scrub-jays might not use biological motion as a cue to differentiate between animate and inanimate objects. Thus, together with results from recent studies on pigeons (Qadri et al., 2014; Yamamoto et al., 2015), the findings challenge the notion that a ‘life detector’ based on a preference for biological motion cues is present in birds. Instead, the preference for biological motion previously found in chickens might be confined to precocial birds, which rely on imprinting and thus might have a higher need to identify social agents based on their movement. Further research is needed to illuminate the possibility that biological motion preference is limited to animal species that heavily rely on the movements of their conspecifics, such as precocial birds or shoaling fish.

This also opens the question which other ‘social’ cues that have previously been implicated in the development of social cognitive abilities in humans, might be relevant for scrub-jays. Given that scrub-jays do not appear to be particularly interested in biological motion patterns, less impoverished stimuli might be of importance. In humans, a highly relevant precursory ability for social cognition seems to be the sensitivity to the direction of gaze. Responding to gaze has been linked to theory of mind abilities in humans (Baron-Cohen & Cross, 1992; Leekam, Baron-Cohen, Perrett, Milders, & Brown, 1997) and has been shown in other corvid species (von Bayern & Emery, 2009). The question whether scrub-jays display a similar sensitivity to the direction of gaze is investigated in Chapter 5.

Chapter 5

Assessing the sensitivity to direction of gaze in California scrub-jays¹³

Summary

When observed by a conspecific, food-caching California scrub-jays employ a number of different strategies to protect their caches from potential theft. For example, they cache in visually inaccessible locations or re-cache items that the observer previously saw them cache. This has been interpreted as an ability to take into account the perspective of others. Such an understanding of visual perspective would assume that the birds also take into account the direction of gaze. The aim of this study was to determine whether or not scrub-jays are sensitive to 1) the direction of gaze of a human experimenter and 2) the direction of gaze of a conspecific observer in a caching context. In Experiment 5.1, birds could retrieve food whilst being presented with a human experimenter looking either towards or away from them. Birds took longer to approach the food reward when the experimenter was looking at them compared to when she was looking away from them. In Experiments 5.2 and 5.3, video playback was used to manipulate the gaze of an observer during a caching event: scrub-jays were presented with videos of a conspecific either facing towards or facing away from them whilst being allowed to cache either out-of-view or in-view of the observer bird. The stimuli presented on the video screen did not influence their caching and re-caching behaviour: the birds did not protect their caches from a forward facing observer by caching preferentially in the out-of-sight location and did not re-cache caches that the observer had had visual access to. Together, these results suggest that while scrub-jays appear to be sensitive to the direction of gaze of a live human experimenter, video playback of a conspecific might not be a sufficiently salient cue to elicit the jays' cache protection strategies.

¹³ The results of this chapter are being prepared for publication as Brecht, K. F., Ostojić, L., Legg, E. W., & Clayton, N. S. (in prep). Sensitivity to direction of gaze in different context in California scrub-jays (*Aphelocoma californica*).

Introduction

Chapter 4 showed that while scrub-jays have a preference to observe a conspecific over an object, they did not prefer to look at biological motion patterns. A preference for biological motion found in humans has been suggested to reflect the fact that biological motion cues provide an important basis to distinguish between inanimate and animate objects, and as such, constitute important social cues that are associated with the development social cognitive abilities. The present chapter investigates another potential precursor of theory of mind in corvids: the sensitivity to the direction of gaze. Being sensitive to gaze is related to understanding what others (can) see and therefore know (Povinelli et al., 2000). Specifically, this chapter assesses how scrub-jays respond to gaze of humans and conspecifics. In doing so, this work extends previous research into cache-protection strategies in scrub-jays (reviewed in Clayton et al., 2007).

California scrub-jays cache excess food for later consumption (Vander Wall, 1990), and they can flexibly adjust their caching strategies based on what they expect will happen at the time of recovery (Clayton, Dally, Gilbert & Dickinson, 2005). Caching also has its risks, however, as up to 30% of caches can be lost to pilferage (Vander Wall & Jenkins, 2003). Observational spatial memory allows these birds to efficiently pilfer caches they have seen other conspecifics make (Watanabe & Clayton, 2007). To protect their caches from being pilfered in the future, scrub-jays have been found to employ a suite of different strategies (Dally, Clayton, & Emery, 2006). These either take place at the time of caching or at a later time, namely after the observer has left the scene. Specifically, when observed by a conspecific, scrub-jays preferentially cache in locations that limit the observer's visual access to the cache site, such as in the shade, behind a barrier, or far away from the observer (Dally et al., 2005). Alternatively, if a conspecific has auditory but no visual access, jays preferentially cache in a quiet substrate (Stulp et al., 2009). Finally, if scrub-jays cannot obscure the location of their caches from the observer at the time of caching (Dally et al., 2005), scrub-jays move previously made caches to different, novel locations (re-caching) once the potential threat is no longer present (Dally, Emery, et al., 2006; Emery & Clayton, 2001).

Three important controls suggest that these cache protection strategies are specific to the situation in which the caching event is observed by a conspecific competitor: the same caching behaviours do not occur when the birds are caching without a conspecific present ('in private'; Dally et al., 2005), when they are caching in front of their mate with whom they share their caches (Dally, Emery, et al., 2006), or in front of their own mirror image (Dally et al., 2010). This specificity of the reported cache protection strategies has been interpreted as

indicative of scrub-jays responding to what observers can and cannot see (Clayton et al., 2007; Dally et al., 2005; Dally, Emery, et al., 2006; Emery & Clayton, 2004a).

Important support for the hypothesis that scrub-jays understand others' perspectives as well as knowledge states would be provided by evidence that the birds exhibit a prerequisite of these abilities, namely a sensitivity to where a conspecific is looking at and thus whether or not the conspecific is attending to the cacher and the cacher's actions during the caching event. Such a sensitivity to where others are looking presents an important prerequisite for the ability to understand others' visual perspective: an individual can only see things that are in her line-of-sight (for a similar argument in primate theory of mind research see Povinelli, Bering, & Giambrone, 2000). In the context of caching, therefore, caches only need to be protected when conspecific observers are actually watching the caching process. Outside of a caching context, there is some evidence that corvids are sensitive to gaze cues and might understand that individuals facing them are attending to them. In a cooperative context, rooks and jackdaws have been found to successfully use human gaze to locate food (Schmidt, Scheid, Kotrschal, Bugnyar, & Schloegl, 2011; von Bayern & Emery, 2009). In a different context, human gaze has been shown to be aversive to corvids: jackdaws took longer to approach food when an unfamiliar human was facing in their direction compared to when the human was facing away (von Bayern & Emery, 2009), and American crows escaped faster from humans approaching them with direct gaze compared to humans approaching them whilst looking away (Clucas, Marzluff, Mackovjak, & Palmquist, 2013).

The aim of the current study was to determine whether or not the direction of gaze of another social agent affects scrub-jays' behaviour in two different contexts: when competing with a human, and when being observed by a conspecific during caching. In three experiments, I therefore tested whether a) scrub-jays responded to a human's direction of gaze in a food competition context, and whether b) scrub-jays exhibited different caching behaviours depending on the direction of an observer's gaze. In Experiment 5.1, birds were presented with a human experimenter either looking at them, or looking away from them. If, like other corvids (von Bayern & Emery, 2009) scrub-jays were averse to human gaze, then they would be expected to approach food more slowly when the experimenter was looking towards them than when she were looking away. In Experiments 5.2 and 5.3, caching birds were presented with video playback of conspecific observers with differing gaze directions. Scrub-jays have a blind area at the back of their head ranging from 25° to 46°, depending on the position of their eyes (Fernández-Juricic et al., 2010). Using video playback allowed manipulating of the conspecific's gaze direction (see Chapter 4 for the validation of the use of

video playback in scrub-jays). Two different cache-protection strategies were assessed: caching out of the observer's view (Experiment 5.2) and re-caching once the observer had left (Experiment 5.3). If scrub-jays understood the importance of the observer attending to their caching, they should selectively protect their caches when confronted with a conspecific directing its gaze towards them but not when confronted with a conspecific not looking their way.

Experiment 5.1

Experiment 5.1 tested whether or not California scrub-jays are sensitive to the direction of gaze of a human experimenter. To this end, the latency to approach food when a human experimenter was looking in the bird's direction was compared with the latency when a human experimenter was looking away.

Method

Subjects and housing. Housing of the California scrub-jays was the same as described in Chapter 4. Three female and two male sexually mature scrub-jays served as subjects and were tested between January and February 2016. All birds had previous experience with caching and pilfering, both in experiments (e.g., Thom & Clayton, 2013) and during resting periods, in which they were routinely given caching trays as enrichment. Birds were deprived of their maintenance diet to ensure they were motivated to approach the food used in the experiment.

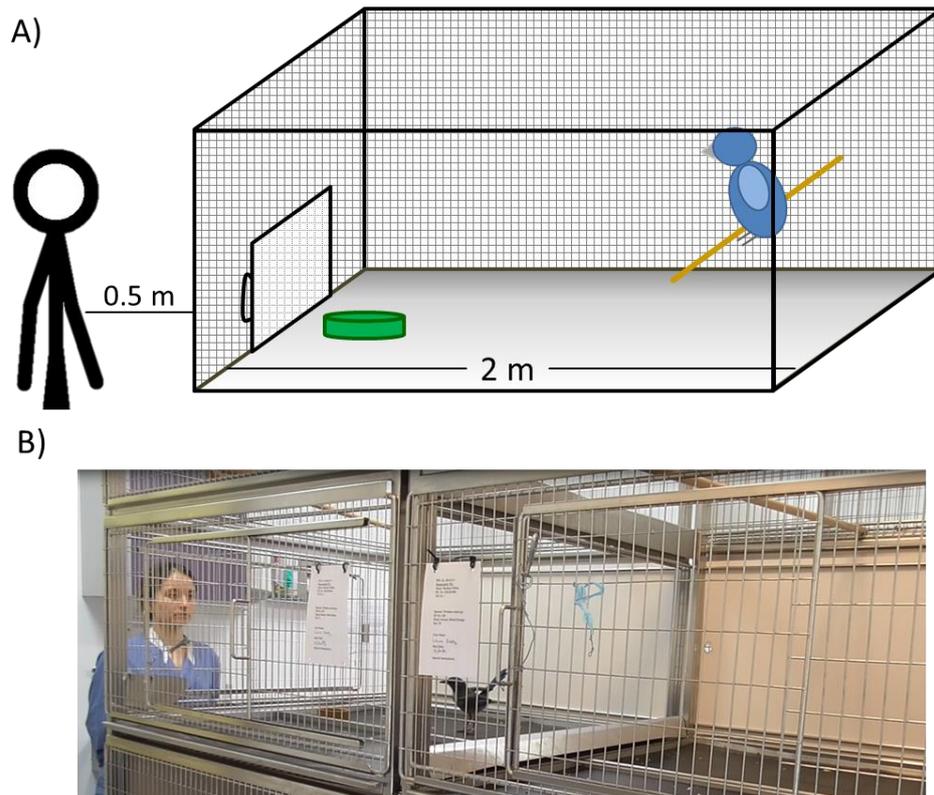


Figure 5.1. Experimental Set-up. Panel A shows a schematic view of the testing area. Panel B shows an example trial (Bird No. 207, Condition: Facing Forward).

Set-up. Testing took place in a testing area over two cages (2 x 1 x 1 m). Cages were empty except for a perch at the far end of the experimental area, a water bowl, and a porcelain food bowl at the near end of the cage as depicted in Figure 5.1. The near end of the cage also had a small door, allowing the experimenter access to the bowl. During testing, birds were isolated from their partner (in those cases in which birds were housed with their partner). A camera was positioned at the back of the room.

Procedure. Before starting testing, birds were given a wax moth larva in the bowl, in order to check whether they were willing to come down to feed at all in this set-up on the testing day. Birds had 10 minutes to approach and take the food. Birds that did not approach within this time were assigned 10 minutes.

At the beginning of each test trial, subjects were usually sitting on the perch. The experimenter was positioned one arm's length (~ 50 cm) away from the cage and placed one wax moth larva in the bowl by using the little door in the cage wall. Birds were given 10 minutes to approach and take the food. The birds' latency to take the food was determined from the moment the experimenter was in position and said "Start". Trials were also video recorded. The order of the Facing Forward and the Facing Away conditions was

counterbalanced across birds. Birds received one trial per condition and experienced the two conditions on separate days.

Analysis. Latencies were timed live by the experimenter with a stop watch. Timing started once the experimenter was in position, and ended once the bird took the worm. In the facing away conditions, the sound of the birds taking the worm from the porcelain bowl signalled the end of the trial. When uncertain to the exact end time, which happened once, videos were used to time the latency, from the ‘start’ signal from the experimenter to the moment the bird took the food from the bowl. All analyses were conducted in RStudio Version 1.0.136 (R Core Team, 2016). Due to the small sample size, permutation tests were calculated with the R package coin (Hothorn et al., 2008), comparing latency to approach in seconds for the Facing Forward compared to the Facing Away condition. Because the analysis was based on clear predictions, directional tests were used. Alpha was set at $\alpha = .05$. P-values $p < .1$ were interpreted as trends.

Results and Discussion

Birds took a median of 52.92s (3.92s-600s) to approach the food. When the experimenter was facing forward birds took a median of 426.8s (17.52s-600s) to approach, when the experimenter was looking away a median of 17.18s (3.92s-102.08s). Thus, as can be seen in Figure 5.2 the direction of the experimenter’s gaze affected the birds’ latency to approach and take the food, $Z = 1.789$, $p = .031$, $d = 1.899$ (see Appendix B, Table B.8 for raw data).

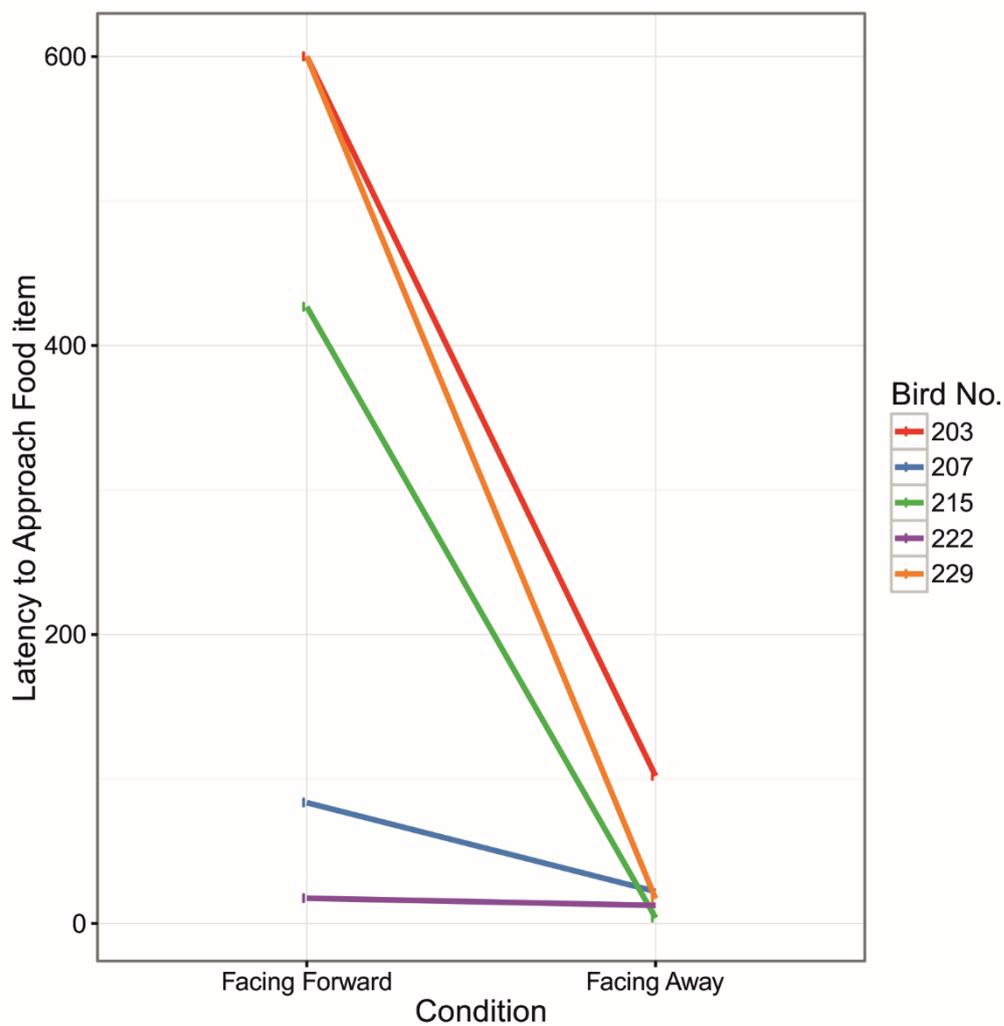


Figure 5.2. Latency to approach the food (in seconds) for each bird in the Facing Forward and the Facing Away conditions.

Similar to other corvids (e.g., Davidson, Clayton, & Thornton, 2015; von Bayern & Emery, 2009), scrub-jays showed an increased latency to approach food when faced with an experimenter looking forwards, compared to when the experimenter was looking away. Thus, scrub-jays seem to be sensitive to the direction of gaze of a human heterospecific.

Experiment 5.2

In Experiments 5.2 and 5.3, it was investigated whether or not the scrub-jays were also sensitive to the direction of gaze of a conspecific when given the experience of watching a video playback of the conspecific's gaze. To this end, a conspecific's gaze direction was manipulated within a caching context. The set-up was similar to methods previously used to assess cache-protection strategies in scrub-jays, in that scrub-jays were able to choose between a caching site in-view and a caching site out-of-view of the observer (e.g., Dally et al., 2010).

In Experiment 5.2 it was tested whether scrub-jays preferentially cached in locations out of the observer's view when an observer faced towards them. To that end, in Experiment 5.2a, scrub-jays were presented with videos of an observer facing either towards or away from them. Scrub-jays could cache food in two different locations – one 'in-view' of the video screen and one 'out-of-view', behind an opaque barrier. Previous studies suggest that scrub-jays understand that only caches an observer could see being made are in danger (reviewed in Clayton et al., 2007; Grodzinski & Clayton, 2010a). Therefore, if birds are responding to video playback of birds similarly to how they would to live birds, they should cache more in the 'out-of-view' than in the 'in-view' location when presented with the video of the conspecific observer facing towards them than when presented with the observer facing away.

In addition, a non-social control condition was included, in which the birds were presented with a video of an empty cage¹⁴. In the case that the birds did not show any differences in their behaviours between the two experimental conditions, this non-social control condition could assess whether the birds treated the observer in the video in the same way as they would treat a 'live' observer. Previous studies found that jays protected their caches specifically when they were presented with an observer but not in a non-social condition (Dally et al., 2005, 2010). Regardless of the results regarding the two experimental conditions – if the birds treated the observer in the video in the same way as a 'live' observer, they would be expected to cache more in the 'out-of-view' than in the 'in-view' location when presented with a video of a conspecific irrespective of its direction of gaze (social conditions: average between the Facing Forward and the Facing Away conditions) but not when they were presented with the video of the empty compartment. Alternatively, if the birds showed no difference in their caching behaviour between the social and the non-social conditions, this would suggest that they did not perceive the conspecific in the video as a threat to their caches, and thus that the video and live conditions trigger different behavioural responses.

A control experiment (Experiment 5.2b) was conducted to ensure that any effects found in the Experiment 5.2a were specific to caching behaviour and not due to a general preference for one of the locations. Here, subjects were presented with the same videos but this time they had access to powdered food only, which they could not cache, in both the 'out-of-view' and in the 'in-view' locations.

¹⁴ As an additional non-social control, I ran a trial in which birds were presented with a video of a rope hanging from the cage ceiling. This condition was run to ascertain that a difference between the social conditions (Facing Forward and Facing Away) and the empty compartment would not be due to movement on the screen. As there was no significant difference between the conditions Empty Compartment and Rope (one-tailed permutation test, $Z = 0.56, p = .31$), this condition is not included in this report.

Method

Subjects and housing. Five female and five male sexually mature scrub-jays were tested between December 2014 and February 2015. Housing conditions were the same as in Experiment 5.1.

Material. In both Experiments 5.2a and 5.2b, birds were presented with a 15-minute long video that consisted of a looped sequence of 4 to 5-second long recordings. The screen with the video was mounted to the wall of cage 2, see Figure 5.3. The videos displayed either an empty cage (Empty Cage condition), a conspecific facing the focal animal (Facing Forward condition), or a conspecific facing away from the focal animal (Facing Away condition; see Figure 5.4). On screen, conspecifics were between 6.4 cm to 8 cm in height, corresponding to a visual angle of 3.3° to 4.2° (assuming the cacher stands on the caching tray).

Birds serving as actors were kept mildly hungry by removing all food from their cage 30 minutes prior to filming. For filming the Facing Forward condition, actor birds were presented with food behind the camera to ensure that they attended to the direction of the camera and thus would appear to be attending to the cacher during the test trials. For filming the Facing Away condition, the experimenter left the room for 30 minutes to allow the birds to settle down and eventually turn away from the camera. Three sets of videos were shot with three different birds to prevent pseudo-replication.

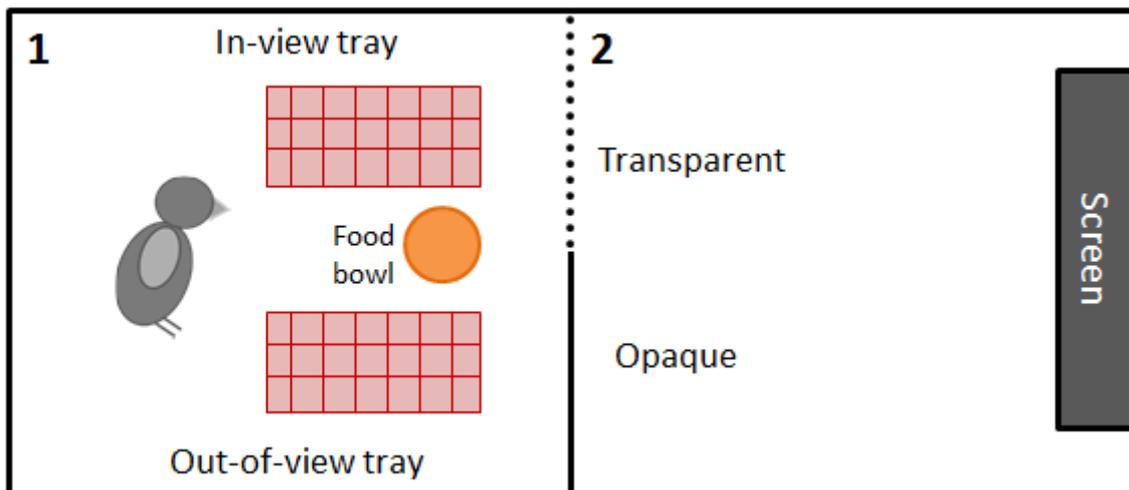


Figure 5.3. Aerial view of the testing set-up for Experiment 5.2a. The cacher (bird in grey) had access to two caching trays (red rectangle) and a bowl of food (orange circle). One tray was ‘out-of-view’ behind the opaque barrier (thick grey line) and the other one was ‘in view’ behind a transparent barrier (dotted grey line). The screen was mounted to the far wall of cage 2. The set-up for Experiment 5.2b was the same except that the caching trays were replaced by two food bowls, and the food in the bowls was powdered.

In Experiment 5.2a, birds were given the opportunity to cache food in two plastic ice-cube trays (each 2x7 of 2.5 cm cube moulds filled with corn kibble). These caching trays were made visually trial-distinctive with Lego Duplo® blocks attached to one long side of the tray. A bowl containing 50 food items (type of food depended on the cacher's known food preference) was placed equidistantly to both trays. In Experiment 5.2b, birds received two bowls, each containing approximately 200 g of ground peanuts that they could eat but not cache.

Procedure. Individuals could either cache (Experiment 5.2a) or eat (Experiment 5.2b) in a location hidden behind the opaque side of a Perspex barrier ('out-of-view' location) or behind a transparent side of a Perspex barrier ('in-view' location). Which side of the barrier was opaque was counterbalanced across subjects but held constant across conditions and experiments.

In a pre-test, two trials were conducted to ensure that birds were comfortable with caching in the experimental set-up, particularly in the presence of the computer screen. In these pre-test trials, birds were given access to a bowl containing food items and a single caching tray, which was placed either behind the opaque or behind the transparent side of the Perspex barrier. Birds were allowed to cache for 15 minutes whilst the video on the computer screen showed an empty cage. The order in which the birds experienced the caching tray being behind the opaque or the transparent sides of the barrier was counterbalanced across birds. Trials were repeated until each bird cached in both trays with a maximum of two trials per side.

In Experiments 5.2a and 5.2b, each bird completed three trials. Trial order was pseudo-randomised across birds but kept the same across Experiments 5.2a and 5.2b. Two hours prior to testing, individuals were separated from their cage partner, and maintenance diet was removed to ensure that birds were mildly hungry and thus motivated to cache or eat at the time of testing. Birds were tested in cage 1. At the start of a trial, dividers to cage 2 were removed and the screen, mounted onto the back wall, was showing one of the three videos. Birds were given a 15-minute long test phase during which they could cache (Experiment 5.2a) or eat the provided food (Experiment 5.2b). In Experiment 5.2a, birds were then released into their home cage and caching trays were removed for a 15-minute long break. During this break, caches were counted and placed back in the tray. Any caches made outside the tray were removed. Birds were again allowed into cage 1 and allowed to retrieve any caches made previously, a procedure that has been successfully used to prevent extinction of caching in previous caching studies (reviewed in Clayton et al., 2007). During this 15-

minute long retrieval phase, the screen was covered. Subsequently, the caching trays were removed, and birds were released into their home cage and maintenance diet was returned. Experiment 5.2b ended after the 15-minute long test phase in which the birds could eat the powdered food.



Figure 5.4. Still frames of the video clips, from left: a conspecific facing towards the subject, a conspecific facing away from the subject, or an empty compartment control (non-social control).

Analysis. For Experiment 5.2a, items cached in the trays during the caching period were counted and recorded by the experimenter, as well as the number of items left in the bowl, cached elsewhere in the cage or left on the cage floor. In Experiment 5.2b the amount of ground peanuts eaten was recorded. To obtain one independent measure for the birds' preference for caching in one of the two locations ('in view' versus 'out-of-view') in Experiment 5.2a, the difference of the number of caches made in the 'out-of-view' tray minus the number of caches made in the 'in-view tray' was compared across conditions. If scrub-jays were sensitive to the conspecific's direction of gaze, this difference should be larger in the Facing Forward condition than in the Facing Away condition.

Similarly, to obtain one independent measure for the birds' preference for eating in one of the two locations in Experiment 5.2b, I compared the difference between the amount of powdered peanuts eaten from the bowl 'out-of-view' minus the amount from the bowl 'in-view' across the different conditions. If a preference for the 'out-of-view' location in Experiment 5.2a represents a cache protection strategy, then it should be specific to the

caching situation and thus no such preference should be shown in the eating situation in Experiment 5.2b.

All analyses were conducted in RStudio Version 1.0.136 (R Core Team, 2016). Aligned rank transformed data (Wobbrock et al., 2011) were submitted to a repeated measures ANOVA with the within-subject factor Condition (Empty Cage vs. Facing Forward vs. Facing Away) with the R package ARTool (Kay & Wobbrock, 2016). Permutation tests were calculated with the R package coin (Hothorn et al., 2008) as a planned contrast between the Facing Forward and Facing Away conditions, and between the social conditions (average from the Facing Forward and Facing Away conditions) and the empty cage condition. Because the analysis was based on clear predictions, directional tests were used. Alpha was set at $\alpha = .05$. P-values $p < .1$ were interpreted as trends. All descriptive averages are given as median with range in brackets.

Results and Discussion

One male subject (bird no. 210) was excluded from the analysis because he failed to cache for the duration of all test trials. Birds cached in the in-view tray a median of 8 (0-22.5) items in the Empty Cage condition, 2.5 (0-22) items in the Facing Forward condition, 6 (0-19) items in the Facing Away condition. In the out-of-view tray, birds cached a median of 5 (0-17) items in the Empty Cage condition, 4 (0-8) items in the Facing Forward condition, and 4 (0.5-11) items in the Facing Away condition.

The average difference of caches made in the ‘out-of-view’ minus caches made in the ‘in-view’ tray was -3 ($-5.5-3.5$) in the Empty Cage condition, -1 ($-14-7$) in the Facing Forward condition, and -2 ($-15-2$) items in the Facing Away condition. As can be seen Figure 5.5, the different videos presented on the computer screen did not influence the difference of caches made in the ‘out-of-view’ minus caches made in the ‘in-view’ tray (no main effect of Condition: $F(2,16) = 0.117$, $p = .892$, Cohen’s $d = 0.231$). Planned contrasts showed that this difference was not higher in the Facing Forward (Median = -1 , range: $-14-7$) than the difference in the Facing Away condition (Median = -2 , range: $-15-3.5$; $n = 9$; $Z = 0.71$, $p = .258$, Cohen’s $d = 0.205$). Further, the difference of caches made was not higher in the social conditions (average of Facing Forward and Facing Away, median = 0 , range: $-12.25-1$) than the difference in the Empty Cage condition (Median = -3 , range: $-5.5-3.5$; $n = 9$, $Z = -0.232$, $p = .586$, $d = 0.316$, Cohen’s $d = 0.075$; see Appendix B, Table B.9, for raw data).

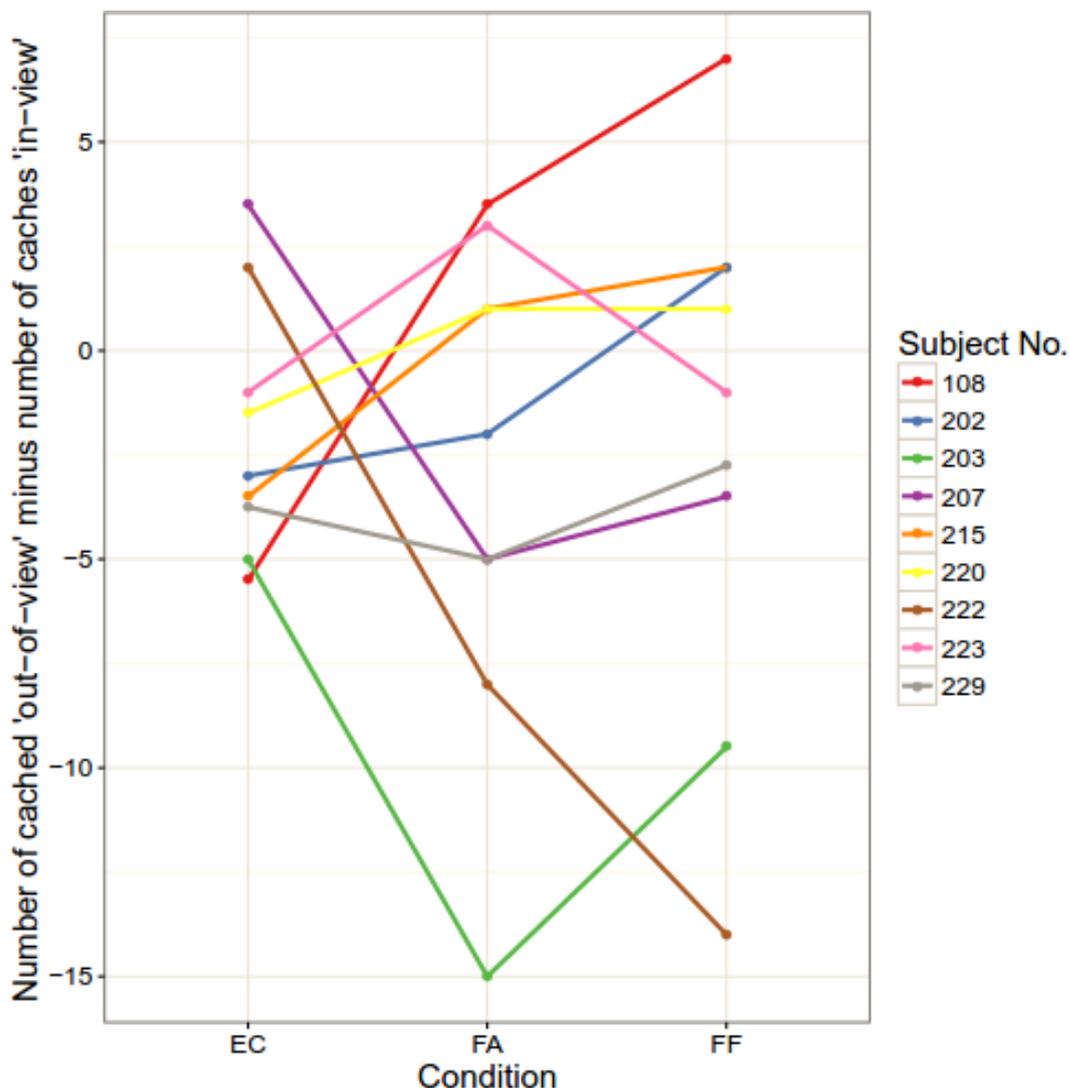


Figure 5.5. Number of caches cached in the ‘out-of-view’ tray minus the number of caches cached in the ‘in-view’ tray in all three conditions, for each bird.

Eight birds were tested in Experiment 5.2b because one bird fell sick (not related to the study) after Experiment 5.2a. One bird (No. 207) was later excluded from the analysis because 7.75g of food were missing from the ‘in-view’ bowl in the Facing Forward condition (average amount eaten was 0.40g) due to the bird having tossed food out of the bowl.

The amount of powdered peanut eaten from the ‘in-view’ and the ‘out-of-view’ bowl is given in Table 5.1. The different videos presented on the screen did not influence the difference of food eaten in the ‘out-of-view’ location minus the food eaten in the ‘in-view’ location (no main effect of Condition: $F(2,14) = 0.033, p = .967$). Planned contrasts showed that the difference of food eaten in the ‘out-of-view’ bowl minus food eaten in the ‘in-view’ bowl in the Facing Forward condition (Median = $-0.19g$, range: $-0.41g-0.02g$) was not higher than the difference in the Facing Away condition (Median = $-0.25g$, range: $-0.7g-0.26g$; $Z = 0.184, p = .430$, Cohen’s $d = 0.105$). Further, the difference in the social conditions (average

of Facing Forward and Facing Away, median difference = -0.22g , range: -0.56g - 0.14g) was not higher than the difference in the Empty Cage condition (median difference = -0.13g , range: -0.6g - 0.04g , $Z = -0.210$, $p = .547$, Cohen's $d = 0.072$).

Table 5.1. Amount of powdered peanut eaten in g in the 'in-view' and the 'out-of-view' tray.

	Amount of powdered peanut eaten in g	
	'In-view'	'Out-of-view'
	Median (Range)	Median (Range)
Facing Forward	0.43g (0g-7.75g)	0.08g (0g-0.3g)
Facing Away	0.3g (0.03g-0.8g)	0.1g (0.02g-0.55g)
Empty Compartment	0.25g (0 g-0.87g)	0.08g (0g-0.44g)

These results suggest that the scrub-jays' caching and eating behaviours were not affected by the observer's direction of gaze or the general presence of the conspecific as displayed on the video screen. Additionally, the scrub-jays' caching behaviour did not differ between when a conspecific was present (social situation) or absent (non-social situation): The birds did not employ more cache protection strategies when presented with a video of a conspecific (irrespective of whether the conspecific was looking at them or away from them) compared to the non-social control in which they were presented with a video of an empty cage alone.

Experiment 5.3

In addition to employing cache-protection strategies while caching, scrub-jays also re-cache items into novel locations once the observer has left the scene (Emery & Clayton, 2001). Experiment 5.3 addressed the question of whether the jays' re-caching behaviour was influenced by the observer's direction of gaze. Cachers had access to two caching trays, both 'in-view', and, after a break of 15 minutes, they had the opportunity to re-cache any caches made in the initial caching period. As in Experiment 5.2, birds were presented with different videos during the caching period: a video of an observer facing towards or away from them, or a video of an empty cage. Similarly to Experiment 5.2, the video of the empty compartment was used to assess whether the birds treated the observer in the video in the same way as they would treat a 'live' observer. The proportion of re-caches (number of re-caches divided by the total number of caches) made was investigated. If the scrub-jays were sensitive to the observer's direction of gaze, they were expected to re-cache a larger proportion of initially

made caches after having had cached in front of a video showing the observer facing towards them than after having had cached in front of a video showing the observer facing away.

Method

Subjects. Four female and four male sexually mature scrub-jays were housed and tested under the same conditions as laid out in Experiment 5.2 between February and June 2015. All scrub-jays had previously participated in Experiment 5.2. The overall setup was the same as in Experiment 5.2, except that a fully transparent divider was placed between cage 1 and 2 such that there was no difference in the visual accessibility of the two caching locations.

Procedure. Each bird completed three trials. Trial order was pseudo-randomised across scrub-jays. Two hours prior to testing, individuals were separated from their cage partner, and maintenance diet was removed to ensure that scrub-jays were mildly hungry and thus motivated to cache or eat at the time of testing. As in Experiments 5.2a and 5.2b, scrub-jays were tested in cage 1 (see Figure 5.3). At the start of a trial, dividers to cage 2 were removed and the screen, mounted onto the back wall, was showing one of the three videos¹⁵. Note that new videos were made to avoid habituation.

Testing was separated into 3 phases. First, the scrub-jays had a 15-minute long caching phase during which they could cache the provided food. Similarly to Experiment 2a, during a 15-minute long break in the home-cage, caches were counted and placed back in the tray. Any caches made outside the tray were removed. The scrub-jays were again allowed into cage 1 to retrieve or re-cache any previously made caches. During this 15-minute long re-caching phase, the screen was covered, thus re-caching took place in ‘private’. Then the caching trays were removed, the birds were released into their home cage and maintenance diet was returned.

Analysis. To ensure that birds could re-cache items, birds had to initially have cached at least one food item in each condition. The number of items that changed location was counted, either by being taken out of the tray to eat or hide elsewhere in the cage, or by being cached somewhere else in one of the trays (henceforth called re-cached) during the re-caching period in private. As the number of items that can be re-cached depends on the number of items cached, I analysed the proportion of re-cached items (number of re-cached items divided by total number of items cached) in the same manner as in Experiment 5.2 with a repeated measures ANOVA (factor *Condition*) and one-tailed permutation tests as planned

¹⁵ Note that here again, we presented birds with a non-social Rope condition. There was again no significant difference between the Rope and Empty Compartment condition (one-tailed permutation test, $Z = -0.14$, $p = .55$) and thus the description of the Rope condition is not included in this manuscript.

contrasts. Alpha was set at $\alpha = .05$. P-values $p < .1$ were interpreted as trends. All descriptive averages are given as median with range in brackets.

Results and Discussion

Bird No. 215 was excluded from the analysis because she failed to cache across all test trials ($n = 8$). Birds cached a median of 9.75 (1.5-23) items in the empty cage condition, 7.5 (3-24) items in the facing forward condition, 6.5 (1-27) items in the facing away condition. Birds re-cached a median of 3 (1-22.5) items (or 40%, range: .24-1) in the empty cage condition, 6.25 (1-10) items (or 44%, range: 30%-62%) in the facing forward condition, and 3 (0-11) items (or 38%, range: 15%-81%) in the facing away condition.

As can be seen in Figure 5.6, a median of, birds did not adjust the proportion of re-cached items depending on condition, $F(2,14) = 0.529$, $p = .600$. Birds did not re-cache a larger proportion of caches in the Facing Forward (Median = 44%, 31%-62%) than in the Facing Away condition (Median = 38%, 0%-100%), $Z = 0.355$, $p = .359$, Cohen's $d = 0.210$. Moreover, birds did not re-cache a larger proportion of caches in the social conditions (average of Facing Forward and Facing Away; Median = 38%, 15%-81%) than in the Empty Cage condition (Median = 40%, range: 24%-100%), $Z = -0.88$, $p = .816$, Cohen's $d = 0.315$ (see Appendix B, Table B.10, for raw data).

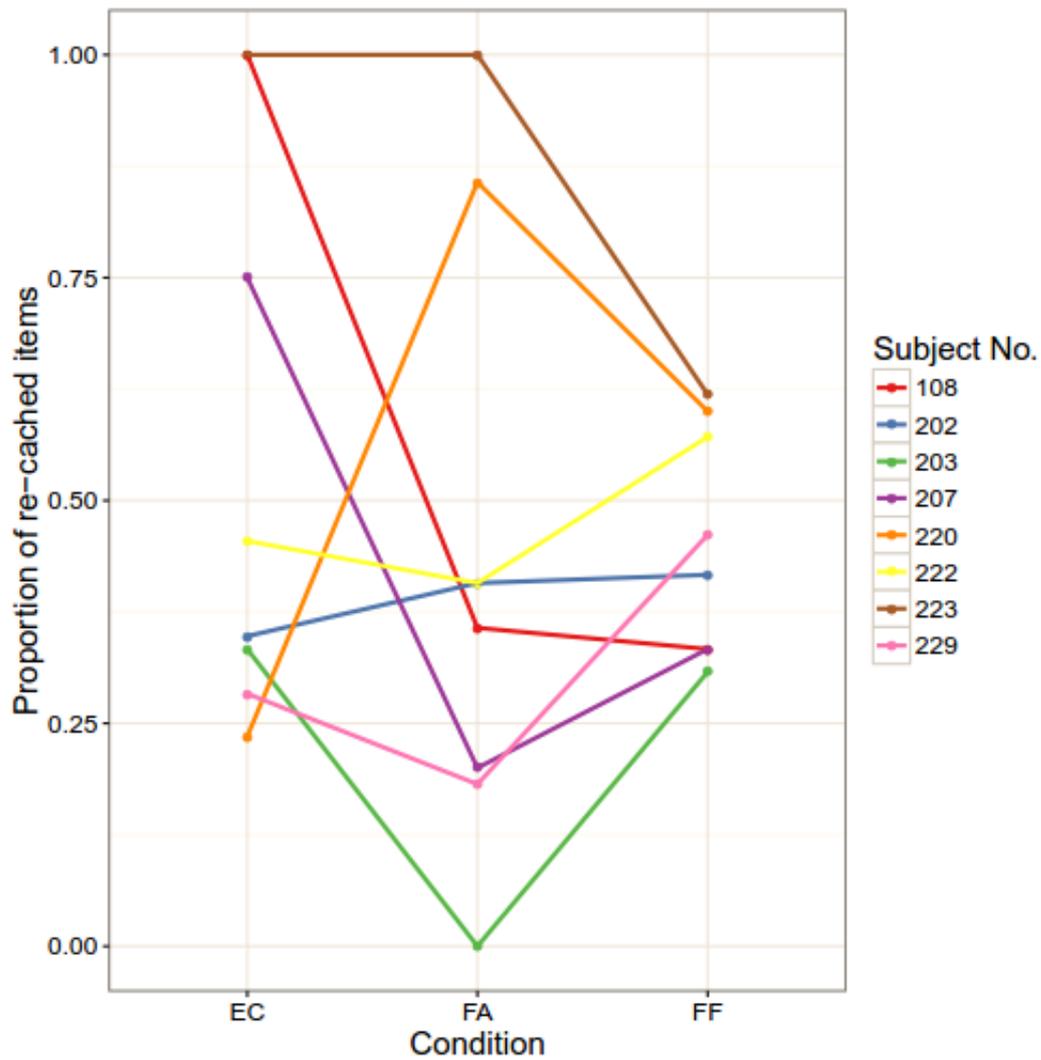


Figure 5.6. Proportion of re-cached items in all three conditions, for each bird.

Thus, the scrub-jays' re-caching behaviour was not affected by the observer's direction of gaze or the general presence of the observing conspecific.

General Discussion

In Experiment 5.1, California scrub-jays showed a longer latency to approach food when presented with a human experimenter facing towards than facing away from them, which suggests that they were sensitive to the gaze of the human experimenter. Experiments 5.2 and 5.3 aimed to extend these findings and investigated the birds' sensitivity to a conspecific's gaze in a caching context. Specifically, in Experiments 5.2 and 5.3 video playback was used to assess whether or not the birds' cache protection strategies were sensitive to direction of gaze of a conspecific observer as shown by video playback. However, in this context, scrub-jays did not adjust their behaviour to where the conspecific was looking

nor to the presence of the conspecific in general, suggesting that they do not respond to a video playback in the same way as they respond to a live conspecific observer.

The results obtained in Experiment 5.1 are in line with work indicating that head and gaze orientation serve as relevant cues for birds in different contexts (Davidson et al., 2014). Other corvids, namely jackdaws, have been found to respond to direction of gaze of a human experimenter in a competitive context, both live and as photographs (von Bayern & Emery, 2009). However, sensitivity to eye gaze as such need not be related to higher social cognition (see also Davidson et al., 2015). Many animals are fearful of eyes (reviewed in Davidson et al., 2014), however, this fear does not necessarily indicate an understanding of what the presence of eyes *means*. Furthermore, it is possible that the birds took longer to approach the food in the Facing Forward condition because they have learned that humans act more towards food or objects when their gaze is directed at them (see also von Bayern & Emery, 2009).

In Experiments 5.2 and 5.3, it was investigated whether or not birds were sensitive to the direction of gaze of a conspecific observer in a caching context and thus possibly acknowledge the relevance of the observer's direction of gaze for their knowledge of cache locations in the context of video playback. In both experiments, scrub-jays did not adjust their cache-protection strategies as a function of different gaze directions of an observing conspecific presented using video playback. In Experiment 5.2, scrub-jays did not prefer to cache in an 'out-of-view' tray over an 'in-view' tray when presented with a conspecific facing their way compared to one looking the other way. Similarly, in Experiment 5.3, the birds did not re-cache more when they were presented with a video of a conspecific during caching, irrespectively of direction of gaze, compared to the non-social control. Moreover, their cache-protection strategy did not differ between when a conspecific was present (social situation) or absent (non-social situation).

Importantly, both cache-protection behaviours investigated did not differ between when a conspecific was present, irrespectively of whether the conspecific was looking at them or away from them (social situations) or absent (non-social situation). This finding is at odds with results from previous studies using live observers, which suggests that the birds do not respond to video playback conditions in the same way as to a live conspecific. In previous experiments, scrub-jays preferentially cached in the 'out-of view' location or re-cached previously made caches when presented with a real conspecific observer during caching but not when they were caching in private (Dally et al., 2004, 2005; Emery & Clayton, 2001). Thus, the failure to find an effect of the observer's direction of gaze on the scrub-jays' cache-

protection behaviour might have been related to the certain characteristics of the medium of presentation, namely that the conspecific observer was presented using video playback as opposed to a real life scenario.

Video playback has been successfully used to display test stimuli to birds in previous studies. For example, Bird and Emery (2008) showed that rooks are able to differentiate between individual conspecifics presented on a video screen. Further, video playback of a group of conspecifics produced similar effects on foraging in nutmeg mannikins (*Lonchura punctulata*) compared to when real conspecifics were present (Rieucan & Giraldeau, 2009). Furthermore, in Chapter 4, scrub-jays preferred to look at their conspecific partner compared to an object, a pattern that was also observed when both stimuli were presented as video playback. It is thus unlikely that the lack of cache-protection strategies in Experiment 5.2 and 5.3 can be fully explained by a failure of the birds to attend to video playback per se. That said it is clear that real-life situations are quite different from video playback, particularly in tracking real time responses to the other individual's behaviour, and perhaps this is why the scrub-jays failed to differentiate social context in the video playback conditions in Experiments 5.2 and 5.3. There are a number of reasons why this might be so. One possibility is that, while stimuli shown on video screens can in principle elicit similar behaviour to live stimuli, scrub-jays might not perceive the conspecific presented on the screen as a threat to their caches. This could be due to several factors related to how the stimuli were depicted: the lack of depth cues or the smaller size of the conspecific. Further, the lack of auditory cues elicited by the birds displayed on the screen could pose a problem (Evans & Marler, 1991), although auditory cues made by conspecifics living in the same room were available. Further, it has been argued that, in pigeons, an important factor facilitating the recognition of a video image of another pigeon as a conspecific is the dynamic motion of the video image (Shimizu, 1998). In Experiments 2 and 3, looped material was used because scrub-jays seldom sat still and looked in one direction for more than a few seconds, which might have created an unusual deficiency of motion. Finally, videos of conspecifics might not have been sufficient to elicit cache-protection strategies due to what they depicted. In reality, it might be rare that a conspecific is only facing away or only facing forward for a prolonged amount of time and does not interact with the cacher. The mere image of a moving conspecific that does not react to the focal birds' behaviour might not be perceived as a threat. This proposal is supported by the lack of cache-protection strategies shown by jays when they are presented with their own mirror image (Dally et al., 2010). Thus, the observer's behaviour may play an important role in eliciting cache-protection strategies (see also Chapter 3 and Ostojic et al., 2017).

In summary, while scrub-jays were sensitive to a human's direction of gaze, they did not show sensitivity to a potential pilferer's gaze of direction in a caching context when the pilferer was presented as video playback. Therefore, the current study adds to the data showing that corvids find eye stimuli aversive in a competitive context (Davidson & Clayton, 2015; Davidson et al., 2015; von Bayern & Emery, 2009). However, overcoming the limitations of video playback in the context of caching found in the present study will be necessary before it can be assessed whether or not scrub-jays also use the direction of gaze to determine which caches might be at risk of being pilfered and therefore need protection.

As mentioned above, the perception of direction of gaze is generally thought to be crucial in learning about others' intentions and beliefs (Farroni et al., 2002; Langten et al., 2000). The results presented here suggest that scrub-jays are sensitive to the eye gaze; however, it is not clear whether that means that eye and gaze are also accounted for in social-cognitive contexts. In the last chapter, I present a study on whether or not the face of a conspecific in corvids has any special relevance. Human infants are very interested in human faces from a young age (Sherrod, 1979) and neurological and cognitive research suggests that human faces are processed differently than other cues. The possibility that corvids also process faces differently than other objects is addressed in Chapter 6.

Chapter 6

Face Inversion Effect in Carrion Crows

For humans, faces pose an important social cue. It has been argued that the special relevance of faces is reflected by the effect orientation of a presented picture has on the recognition of faces, namely that an inverted presentation of the picture of a face will lead to an impaired recognition of this face. Importantly, this impairment is much less pronounced when recognising objects other than faces. This so-called face inversion effect is a robust phenomenon in human perception, and has also – albeit less reliably – been found in other non-human species, most notably in primates. Consequently, it is of interest whether or not other animal species that have similar socio-cognitive abilities to humans and non-human primates, such as the ability to attribute mental states, also show a face inversion effect, which would indicate a special relevance of faces, compared to non-social stimuli. In the present chapter, I investigated the face inversion effect in corvids. More specifically, I used a delayed matching-to-sample task¹⁶ to investigate the face inversion effect in two carrion crows (Experiment 6.1). In the task, crows had to recognise the profile of crow faces as well as matched controls. Additionally, the crows were presented with upright and inverted pictures of human faces, given that previous research suggest that crows base their discrimination of human on their faces. Both crows tested did not show a face inversion effect. Interestingly, they showed an overall better performance with crow faces compared to human faces, and some impairment when responding to inverted pictures compared to upright pictures. To ensure that the stimuli and procedure used could in principle elicit a face inversion effect, human adults were tested on the same delayed matching-to-sample task used with crows (Experiment 6.2). Here, a clear face inversion effect emerged: the human adults' recognition was impaired when responding to inverted human faces compared to upright faces. This impairment was more pronounced for human faces than for control stimuli. The current study tentatively suggests that crows – unlike humans – do not seem to process faces in a different way to stimuli of other categories.

¹⁶ Crows used in the chapter had previously been trained on delayed matching-to-sample tasks and have shown good performance in such tasks (e.g., Veit & Nieder, 2013).

Introduction

Chapters 4 and 5 investigated two different social stimuli in corvids that are of relevance in the development of human social cognitive abilities: biological motion perception and sensitivity to eye gaze. Another disposition that has been implicated in social cognitive skills in humans is a special interest in faces. Faces carry a range of information, most notably about identity of individuals. Due to their high relevance, it has been suggested that faces are processed differently than other visual stimuli (Kanwisher & Yovel, 2006; Yovel & Kanwisher, 2004). Therefore, it would be of interest whether faces constitute a special stimulus for corvids, too, given their sophisticated socio-cognitive abilities. The relevance of faces is thought to be reflected in the face-inversion effect, a pronounced impairment of the recognition of inverted pictures of faces, compared to inverted pictures of other stimuli. Thus, in the present chapter, I explored the face inversion effect in carrion crows.

Compared to stimuli of other categories, recognition and memory of faces is disproportionately impaired when faces are presented upside down although both upright and inverted stimuli carry the same physical information (Rhodes, Brake, & Atkinson, 1993; Rossion, 2009; Yin, 1969). This inversion effect is an impairment that is especially pronounced when recognising faces – here inversion reduces accuracy by about 25%. With other non-face stimuli, inversion reduces performance by only 10% (Carey & Diamond, 1977; Diamond & Carey, 1986).

Inversion of a stimulus impedes the configural processing of this stimulus (Towler & Eimer, 2016). The term ‘configural’ processing refers to the encoding of spatial relations between features, such as the distance between two features. Human face recognition seems to be based largely on such configural (or holistic) processing (e.g., Bartlett & Searcy, 1993; Rhodes et al., 1993) and seems to be the reason for our overall good performance in recognising faces (reviewed in Maurer, Grand, & Mondloch, 2002). Typically, humans do not attend to the local features of a face (Collishaw & Hole, 2000) and have trouble recognising such features in isolation (Tanaka & Farah, 1993). Some researchers argue that this configural processing is innate and domain-specific for faces. Therefore, the face-inversion effect has been argued to reflect the fact that the processing of faces is based on different mechanisms than the perception of most other stimuli (Farah, Tanaka, & Drain, 1995).

However, other authors argue that the inversion effect can be explained by our frequent exposure to faces that allows us to gain expertise when recognising faces (e.g., Diamond & Carey, 1986). This expertise is achieved by exploiting, if possible, a configural

assembly of an object's features, and can thus be achieved with any type of stimulus where individual stimuli share a lot of similar features (Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998). Diamond and Carey (1986) for example show that 'dog experts' demonstrate an inversion effect for dog pictures. Furthermore, certain non-face stimuli are also sensitive to inversion, for example words or body postures (Reed, Stone, Bozova, & Tanaka, 2003). Thus, the face inversion effect is not necessarily confined to conspecifics' faces and need not reflect a domain-specific process of face perception.

Whatever stance is taken concerning the developmental origin of the face inversion effect, the face inversion effect can be interpreted as an indicator for specialised or proficient processing of faces compared to other stimuli (Liu & Chaudhuri, 2003). Whether this specialised processing stems from an innate 'face-exclusive' mechanism or a domain-general mechanism that is shaped by repeated exposure to faces is however beyond the scope of this chapter.

Arguably, humans process faces in a specialised manner because faces represent highly relevant cues offering a range of information about for example identity, age, sex, or emotional states of social partners (reviewed in Todorov, Said, Engell, & Oosterhof, 2008). But humans are not the only animals that need to differentiate between individuals. Thus, the existence of a face inversion effect as an indicator for specialised face processing has also been investigated in non-human animals. This previous research has mainly focused on primates, with mixed results (Parr, 2011a). Chimpanzees seem to exhibit a face-inversion effect (Dahl, Rasch, Tomonaga, & Adachi, 2013a; Parr, Dove, & Hopkins, 1998) whereas rhesus monkeys do not (Parr, 2011b). However, there seems to be some inconsistency in regard as to which primates show a face inversion effect. This has been attributed to the use of unsuitable methods. For example, Dahl and colleagues (2013) argue that task-irrelevant features of stimuli used in previous studies have often not been controlled appropriately, with pictures showing background or external facial cues (e.g., the head shape or hairline).

Aside from primates, so far only a handful of other non-human species have been investigated. Pigeons, for example, did not show a face inversion effect (Phelps & Roberts, 1994). In the present study, the face inversion effect was investigated in corvids. Corvids, similarly to humans and great apes, show a range of socio-cognitive abilities that require them to differentiate between individuals. For example, they might need to differentiate between different observers when protecting their caches from them – indeed, scrub-jays and ravens have been found to keep track of which individuals do and do not know about their caches and thus do or do not pose a threat to their caches (Bugnyar, 2011; Dally, Emery, et al., 2006).

Furthermore, ravens are known to be aware of relationships between members of their social group (Massen, Pašukonis, Schmidt, & Bugnyar, 2014) and adjust their willingness to cooperate with a partner based on her identity (Massen, Ritter, & Bugnyar, 2015). Thus, corvids seem to attend to the identity of their social partners both in cooperative and in competitive situations.

Moreover, there is research suggesting that several bird species are able to differentiate conspecifics from pictures (Brown & Dooling, 1992; D'Eath & Stone, 1999; Ryan & Lea, 1994; Trillmich, 1976). Corvids are no different: they are able to recognise conspecifics using visual cues alone. Rooks can differentiate between their partner and other conspecifics shown on videos as well as in still pictures (Bird & Emery, 2008), and carrion crows can be trained to differentiate between full-body pictures of conspecifics (Braun, 2013).

Taken together, the ability to recognise conspecifics and the relevance of the identity of different conspecifics suggests that for corvids, conspecifics represent a relevant stimulus. The first aim of the present study was therefore to investigate the face inversion effect in carrion crows as an indicator of this potential special relevance. Note though that it is unclear whether they can also differentiate between conspecifics based on *facial* cues alone. To date, there is research on budgerigars (*Melopsittacus undulates*, Brown & Dooling, 1992) and pigeons (Nakamura, Croft, & Westbrook, 2003), showing that both species can differentiate between individuals based on pictures of conspecifics' head. Specifically, Brown and Dooling (1992) used the 'profile' of the budgerigars' head. In line with this research, in the present study profiles of carrion crows' head were used rather than their faces. Furthermore, there is some indication that for jungle crows (*Corvus macrorhynchos*) the shape of the beak might be used to discriminate between individuals (Bogale, Aoyama, & Sugita, 2011). Consequently, due to the loss of information about beak size and shape when viewed frontally, the profile might be relevant when recognising conspecifics. Lastly, using the profile was also a practical decision: it was not feasible to acquire a range of portraits of crows facing straight forward. One reason for this might be that carrion crows exhibit a lot of head movements to scan their environment (Fernández-Juricic et al., 2010) and thus rarely look straight into a camera.

The second aim was to investigate whether another stimulus of everyday relevance for captured crows could elicit a face inversion effect: the human face. Given the repeated exposure of captive crows to human faces, crows might have developed an expertise for human faces, similarly to the case where a particular group of humans develops an expertise for dogs (Carey & Diamond, 1986). Previous research supports this prediction because both hand-raised (von Bayern & Emery, 2009) and wild corvids (Clucas et al., 2013; Marzluff et

al., 2010) have been found to attend to human faces. Furthermore, American crows (*Corvus brachyrhynchos*) recognize humans based on their face more than two years after the initial presentation (Marzluff et al., 2010) and can differentiate between male and female human faces from coloured pictures (Bogale et al., 2011). Thus, it is likely that crows can use facial cues to differentiate between humans.

To test the hypothesis that birds of the crow family show performance disruption when recognising inverted compared to upright faces, I administered a delayed matching-to-sample task to Carrion crows. If faces are ‘special’ for crows, they should have an impaired performance for inverted images compared to upright images. This impaired performance should further be *more pronounced* when responding to faces compared to when responding to non-face objects. Specifically, I compared performance when birds had to differentiate 1) between a crow face and a non-face control stimulus (side view of a fish), both inverted and upright and 2) between a human face and a non-face control stimulus (interior of a room). Non-face controls were chosen based on their similarity to the human / crow face stimuli.

Experiment 6.1

Method

Subjects and housing. Two male carrion crows, aged 3 years (Walt) and 2 years (Hugo), participated in the experiment. The birds were housed in large indoor aviaries (360 x 240 cm x 300 cm) side by side in groups of four at the University of Tübingen, Germany. The birds had been taken from the institute’s breeding stock (Animal Physiology, University of Tübingen).

The birds were kept on a controlled feeding protocol (at a minimum of 80% of their free-feeding body weight) for the duration of the experiment and earned food during and, if necessary, after the daily test and training sessions. Body weight was measured daily. Outside of testing, the birds’ diet consisted of chick meat and mashed birdseeds. Water was provided ad libitum in the aviary and during testing. Care and procedures were approved by the local ethical committee and authorised by the national authorities (Regierungspräsidium Tübingen). Training and data collection lasted from July to October 2016.

General Procedure. The birds were trained and tested on the matching-to-sample task in a darkened operant conditioning chamber. The CORTEX program (National Institute of Mental Health, MD, USA) was used for stimulus presentation and measuring the birds’ performance as error rates. Visual stimuli were displayed on a touch screen monitor (3 M Microtouch, 15”, 60-Hz refresh rate), allowing the birds to respond by pecking at stimuli

shown on the screen. Leather jesses secured birds loosely to their perch. Figure 6.1 shows the conditioning chamber.

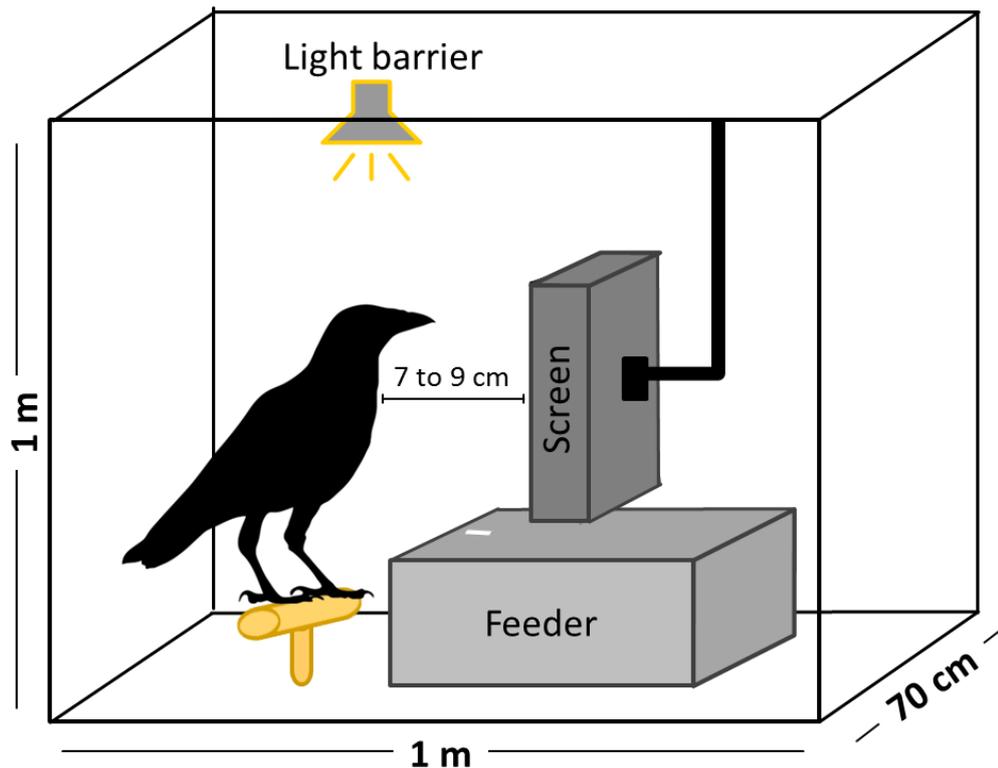


Figure 6.1. Set-up for Experiment 6.1. Birds sat in an operant conditioning chamber measuring 100 x 76 x 100 cm. During testing, the doors of the box were kept closed to minimise disruption and to avoid reflections on the screen.

Rewards (Beo Special pearls or larva of the mealworm beetle) for around 75% of correct trials were delivered with an automated feeder below the screen. Additionally, birds received auditory feedback with specific tones for correct and incorrect trials. Birds could initiate a trial by placing their head in an infra-red light barrier: in combination with a reflector foil attached to the birds' head¹⁷ the light barrier was activated when the bird was positioned in front of the screen and facing it. Trials were aborted and not counted when birds left the light barrier during sample presentation. A Go-stimulus (a small white square) was presented on the screen to indicate a new trial. A short click indicated activation of the light barrier and the Go-stimulus disappeared (pre-sample phase). Next, the birds saw a sample stimulus (i.e., one of the images described below). After a short delay, two test stimuli, the match and the non-match stimuli, were shown left and right of the centre. The birds had to respond within 3000 ms by pecking one of the stimuli. During training, delay between sample

¹⁷ The retainer of the reflector of the light barrier was implanted under anaesthesia onto the birds' skull for experiments conducted prior to the present study. For a description of surgical procedures, see e.g. Wagener & Nieder, 2016.

and test stimuli as well as time-out after incorrect responses were adjusted depending on performance. For example, time out was increased to punish incorrect choices if birds seemed to not pay attention. If birds were frustrated (often indicated by increased flapping of wings or increased delay between trials), time-out was decreased. Inter-trial interval was set at 500 ms. Figure 6.2 summarises the task procedure and the durations of each step.

In case of an incorrect response, the particular trial was presented again after all stimuli combinations were shown once. However, occasionally during training the retry took place immediately after an incorrect trial. This was done when birds started to develop a side bias or when performance dropped to chance level once a new stimulus type was introduced.

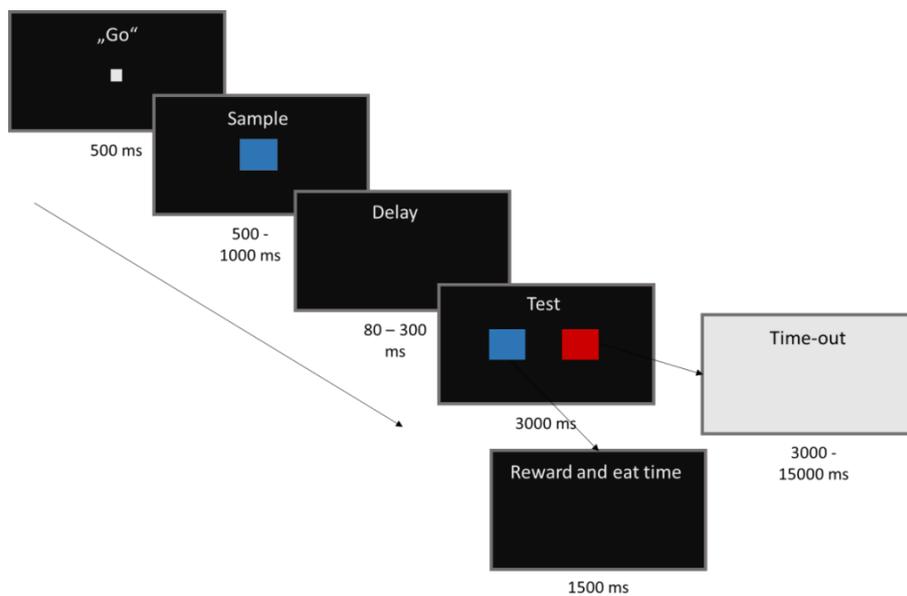


Figure 6.2. Delayed identity matching-to-sample task used in Experiment 6.1 and 6.2. Presentation times varied depending on training progress.

Birds received between 300 and 480 trials a day during training. When birds increasingly delayed entering the light barrier, stopped responding, or when more than 2 hours elapsed, birds were brought back to their aviaries.

Material. The pictures used were downloaded from google images and flickr.com. Pictures of human faces were selected with permission from the face database provided by the Max Planck Institute of Biological Cybernetics in Tübingen, Germany (Troje & Bühlhoff, 1996). Pictures of all stimuli were achromatic and brightness was equalised. Pictures were between 45x43 and 77x47 pixels in size.

For data collection, four different categories of stimuli were used: crow profiles (see above), human faces, interiors, and fish. Examples of all stimuli used are shown in Figure 6.3 (see Appendix A, Figure A.2 for an overview of all crow and human face stimuli and controls used). Pictures of fish served as controls for the crow profiles (type ‘crow’) and pictures of

interiors of houses as controls for the human faces (type ‘human’). All pictures were presented both upright and inverted.

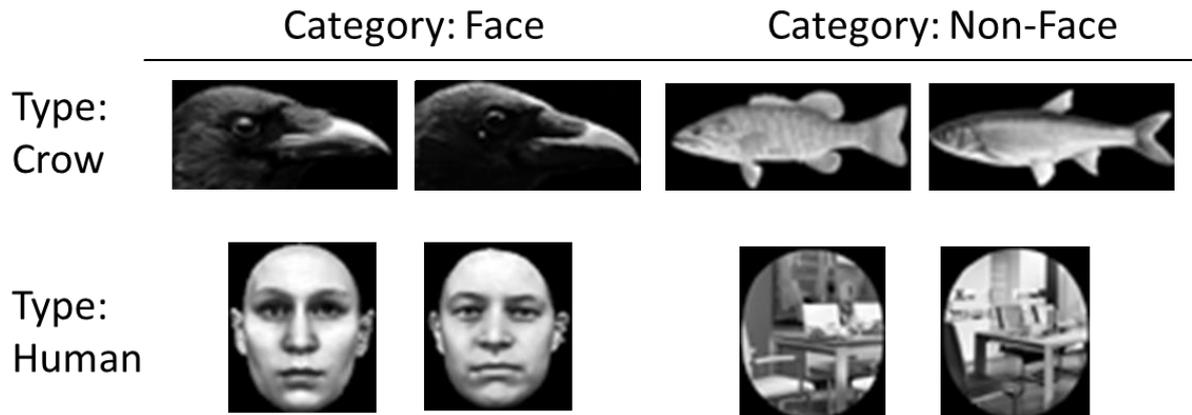


Figure 6.3. Example stimuli used for testing. Birds were tested on four classes of stimuli: crow profiles and corresponding controls (i.e., fish; type = ‘crow’), and human faces and corresponding controls (i.e., house interior; type = ‘human’).

When performing the tasks, the distance between the birds’ eyes and the screen was around 7 cm (Walt) and 9 cm (Hugo), creating an angular diameter of 17.1 and 16.3 respectively.

Behavioural protocol. Both crows had previously participated in other experiments using the same set-up and were thus habituated to the set-up and general procedure.

Matching-to-sample task. An overview of example stimuli used during training can be seen in Figure 6.4. Birds had to first match colours (blue and red) and chromatic ‘abstract’ pictures taken from Veit and Nieder (2013) until they reached criterion (defined as percentage of correct responses > 70%, Step 1). In Step 2, birds had to match achromatic abstract patterns. In Step 3, birds had to match achromatic pictures of the same category (e.g., footballs). In Step 4, birds had to recognize two pictures of four different categories (mugs, tires, flowers, and keys).

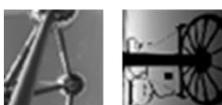
A) Training step 1



C) Training step 3



B) Training step 2



D) Training step 4



Figure 6.4. Example stimuli used for training on the matching-to-sample task.

Data Collection. During data collection, six pairs of stimuli per class were used. Each correct test stimulus appeared once at the right and once at the left side of the screen, and each stimulus was twice the match and twice the non-match. Trial order was blocked, such that pictures of one category were blocked together. Order of blocks and trials within each block was randomised.

The birds were presented with a minimum of 192 correct trials during a session (4 different pairings per stimuli x 6 stimuli pairs x 2 orientations x 4 stimuli classes). Therefore, birds saw each picture at least 4 times during one session. During data collection, birds received between 384 and 576 trials each day (2 to 4 sessions).

Analysis. Data were extracted from CORTEX (National Institute of Mental Health) using MATLAB R2016a. The face-inversion hypothesis would predict 1) a lower performance for inverted than for upright stimuli (effect of *Orientation*), and 2) a larger effect of *Orientation* for face than for non-face stimuli (interaction of factors *Face* and *Orientation*). Performance was calculated as percentage of correct responses per stimulus class and separately for upright and inverted trials. That is, the proportion of correct responses to all pictures of one category (i.e., for all 4 pairings of one stimuli) was calculated as one performance score for each category during each session (e.g., 70% correct responses to upright fish stimuli in session 1). This was done for both upright and inverted stimuli separately.

Due to the small sample size ($n = 2$), mainly descriptive statistics are presented here. Whether overall performance differed from chance was analysed using binomial tests in RStudio Version 1.0.136 (R Core Team, 2016) and for Hugo and Walt separately. For readability, performance presented in Figure 6.6 refers to the difference of percentage of correct responses on upright trials minus the percentage of correct responses on inverted trials. This difference should be higher for the face than for the non-face stimuli.

Results

Figure 6.5 shows that – for both birds – the performance on matching-to-sample for the test stimuli became increasingly stable over time. It can also be seen that performance on human faces was comparatively low for the whole duration of data collection. Furthermore, performance for upright stimuli appears to be slightly better than for inverted ones.

6: Face inversion effect in the carrion crow

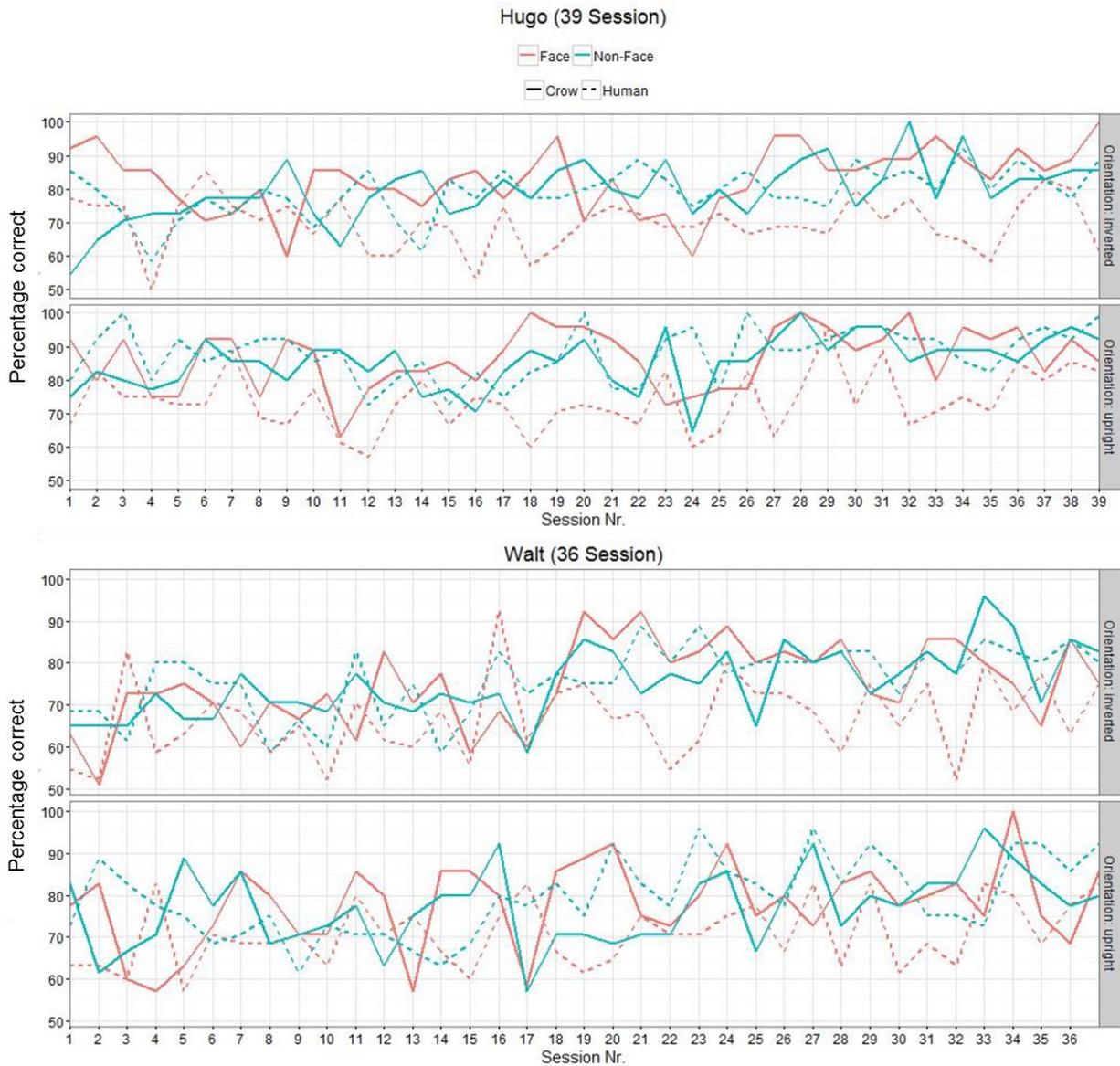


Figure 6.5. Percentage correct over all testing sessions for both crows. Red lines show percentage of correct responses on faces, and blue lines on non-face controls. The solid lines represent percentage of correct trials with stimuli of type ‘crow’, the dashed lines for the stimuli of type ‘human’.

The following results are mainly based on the descriptive statistics given in Table 6.1. Both crows performed the task better than chance (50%) for all stimulus categories (Binomial tests, all p 's < .001). Overall, Hugo performed better than Walt. Both crows performed better when crow profiles were presented compared to when human faces were presented. Similarly, Hugo was better at differentiating the crow profiles than the fish. Walt's performance with the crow profiles was similar to his performance with the fish. Furthermore, both crows generally performed better when responding to upright than to inverted stimuli, regardless of category.

Table 6.1. Overview of performance for all stimulus categories for both birds (for raw data, see Appendix B, Table B.11), averaged across all sessions given as mean.

	Mean (<i>SD</i>) performance in %	
	Hugo	Walt
Fish	82.6 (6.9)	76.1 (7.40)
Interior	83.7 (8.6)	77.7 (8.85)
Crow profile	85.0 (7.3)	76.4 (7.64)
Human face	71.9 (6.2)	68.9 (6.94)
Upright	83.6 (9.7)	76.3 (9.6)
Fish	85.7 (7.7)	77.0 (9.0)
House interior	88.0 (7.8)	79.4 (9.3)
Crow profile	86.9 (9.0)	77.9 (10.0)
Human face	73.8 (8.9)	70.8 (7.8)
Inverted	78.0(10.1)	73.3 (9.6)
Fish	79.5 (8.8)	75.2 (8.1)
House interior	79.3 (7.2)	76.1 (8.2)
Crow profile	83.2 (9.5)	75.0 (10.0)
Human face	69.9 (7.9)	67.0 (9.5)
Overall	80.8 (10.2)	74.8 (9.7)

As can be seen in Figure 6.5, for both birds the difference between performance on inverted and upright was similar for the face and the non-face control stimuli. This was the case for stimuli of both crows and humans. Thus, crows do not seem to show a face inversion effect in their error rates; inversion of a stimulus, while impairing performance, does not seem to be more pronounced for face than for non-face stimuli.

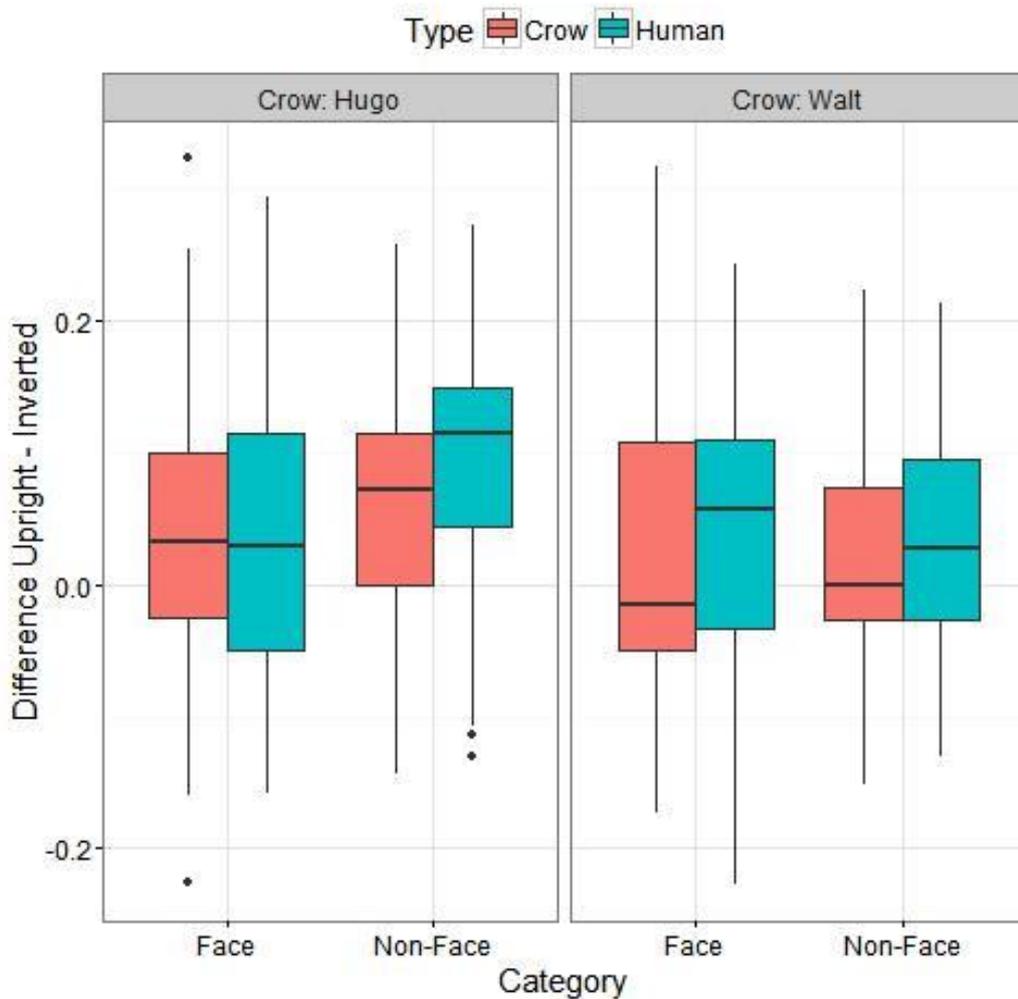


Figure 6.6. Box-and-whiskers plot showing the difference in percentage of correct responses for trials with upright stimuli minus trials with inverted stimuli for the two crows separately (red = stimulus type 'crow', blue = stimulus type 'human'). The boxes signify the upper and lower quartiles; the median is represented by the thick black horizontal lines. The whiskers extend from the box to values no further than $\pm 1.5 * \text{IQR}$ from the box. Black dots signify outliers.

These results indicate that the crows tested were not sensitive to inversion of faces, regardless of whether the face was of a conspecific or a human: both crows did not show a more pronounced decrease in their performance when presented with inverted crow profiles or human faces compared to inverted control stimuli. However, birds performed slightly better with upright than inverted stimuli in general, and their accuracy for inverted stimuli never reached the accuracy shown for upright stimuli. These results suggest that crows' accuracy is susceptible to inversion, similarly to humans. Furthermore, while not being the main focus of this study, it should be noted that birds were better at recognizing profile pictures of crows compared to recognizing human faces. Interestingly, Hugo was also better at

recognizing crow profiles, compared to a control stimulus that shared superficial features with the crow profile.

Experiment 6.2

One possible explanation for the lack of a face inversion effect in carrion crows reported above is that the stimuli and set-up used are not suitable to produce an inversion effect in general (c.f., Dahl et al., 2013a). Thus, in Experiment 6.2, the above described paradigm and the stimuli were validated using human participants.

Method

Participants. Twenty participants were recruited and tested by Lysann Wagener at the Institute of Biology at the University of Tübingen, Germany, aged 21 to 35 ($M = 26.7$), of which 13 were female.

Set-up and Material. The same test stimuli as in Experiment 6.1 were used. The set-up was the same as in Experiment 6.1 except that the touch screen was moved to face the participants sitting in front of the box. The room was darkened. Piloting the original task on myself and Lysann Wagener showed that humans were likely to perform at ceiling if the same timings as in the crow task were used. Thus, the presentation time of the sample was reduced to 500 ms and the delay between sample and test stimuli was increased to 500 ms. Furthermore, the time until a trial was aborted was reduced to 710 ms.

Procedure. Participants were instructed verbally. They were asked to complete 192 correct trials each. Similarly to the birds, humans received a retry for incorrect trials. The experiment took 20 minutes in total.

Analysis. Data were extracted from CORTEX (National Institute of Mental Health) using MATLAB R2016a and were analysed in RStudio Version 1.0.136 (R Core Team, 2016). For data analyses, a difference index was calculated for percentage of correct responses in upright minus inverted trials ($DI = \text{Upright} - \text{Inverted}$). Due to non-normality, data underwent aligned rank transformation (Wobbrock et al., 2011) with the R package ARTool (Kay & Wobbrock, 2016). The transformed data were submitted to a 2 (Factor *Type*: Crow vs Human) x 2 (Factor *Face*: Face vs Non-Face) ANOVA. One-tailed permutation tests were calculated using the R package coin (Hothorn et al., 2008) as planned comparisons between face and non-face stimuli for stimulus type ‘crow’ and stimulus type ‘human’. Because the analysis was based on clear predictions, directional tests were used. Cohen’s *ds* were corrected for dependence according to Morris and DeShon (2002).

If humans showed a face-inversion effect, the DI should be larger for faces than for non-face stimuli of the type ‘human’. However, there should be no such difference for stimuli of the type ‘crow’.

Results

Percentage correct when responding to upright pictures was $M = 94.27\%$ ($SD = 8.68\%$) for human faces, $M = 96.56\%$ ($SD = 6.99\%$) for house interiors, $M = 96.46\%$ ($SD = 5.93\%$) for fish, and $M = 88.75\%$ ($SD = 14.77\%$) for crow profiles. Percentage correct when responding to inverted pictures was $M = 87.40\%$ ($SD = 17.87\%$) for human faces, $M = 96.56\%$ ($SD = 6.99\%$) for house interiors, $M = 94.69\%$ ($SD = 8.12\%$) for fish, and $M = 85.10\%$ ($SD = 20.52\%$) for crow profiles.

As can be seen in Figure 6.6, the difference in percentage correct on inverted minus accuracy on upright trials was influenced by the different stimuli presented. The ANOVA confirmed a significant main effect of the factor Face, $F(1,76) = 6.26$, $p = .015$. There was no significant main effect of the factor Type, $F(1,76) = 0.317$, $p = 0.58$. For stimuli of type ‘human’, the difference in responding to upright and inverted stimuli was larger for face (human face: $M_{DI} = 13.8\%$, $SD_{DI} = 15.2\%$) than for non-face stimuli (interior: $M_{DI} = 0.8\%$, $SD_{DI} = 8.5\%$), which was confirmed by a planned comparison, $Z = -2.97$, $p < .001$, Cohen’s $d = 0.953$. For stimuli of type ‘crow’, there was no such difference, in that performance between upright and inverted stimuli was similar for face (crow profile: $M_{DI} = 7.3\%$, $SD_{DI} = 21.6\%$) and non-face stimuli (fish: $M_{DI} = 3.5\%$, $SD_{DI} = 10.8\%$), $Z = -0.691$, $p < .253$, Cohen’s $d = 0.162$ (raw data see Appendix B, Table B.12).

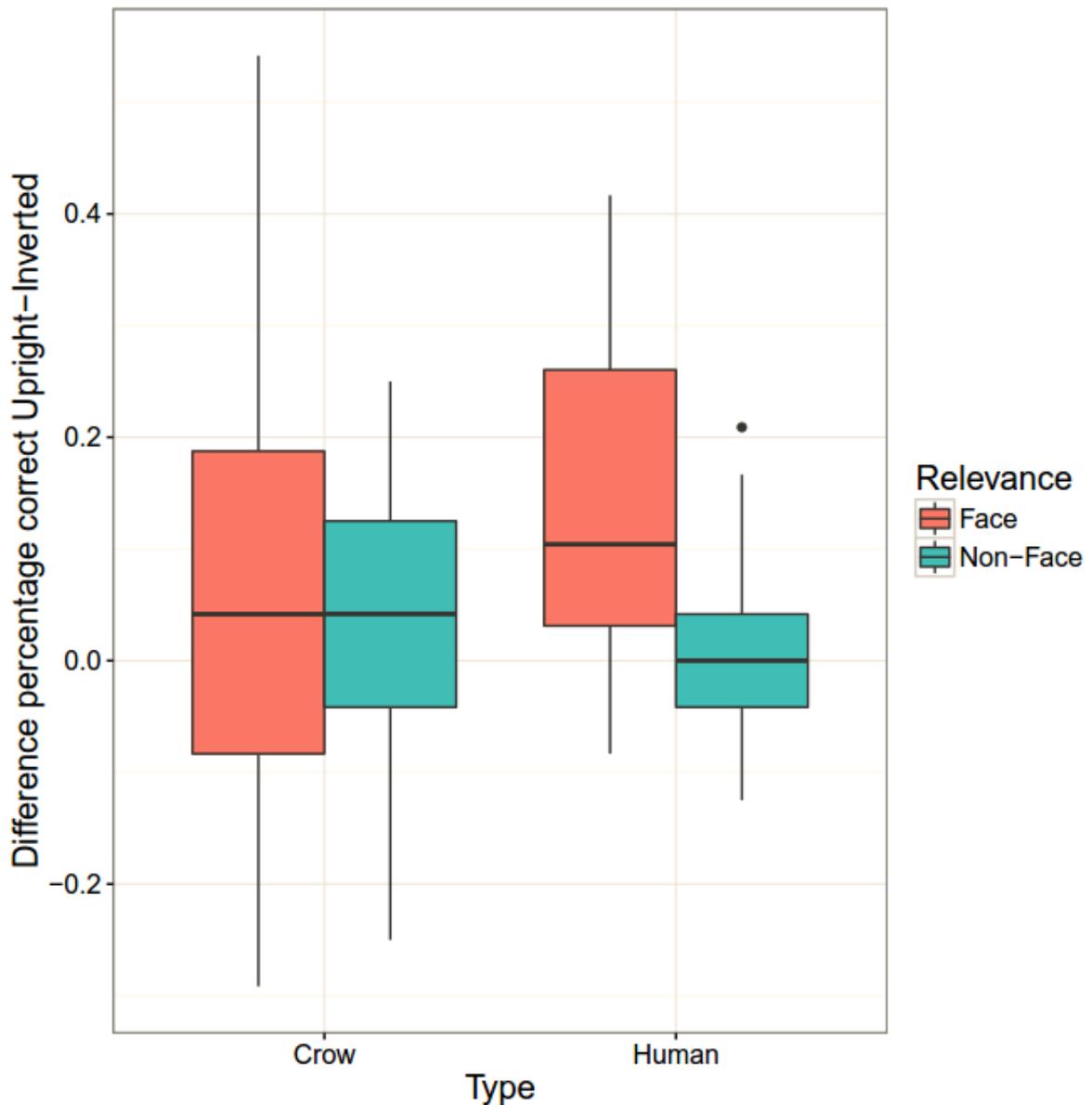


Figure 6.7. Box-and-whiskers plot showing the difference in the percentage of correct trials with inverted stimuli minus trials with upright stimuli (red = face stimuli, blue = non-face stimuli) of the participants tested in Experiment 6.2. Data are shown for stimuli of type 'crow' and 'human' respectively. The boxes signify the upper and lower quartiles; the median is represented by the thick black horizontal lines. The whiskers extend from the box to values no further than $\pm 1.5 * IQR$ from the box. Black dots signify outliers.

General Discussion

The face inversion effect refers to a pronounced impairment in the ability to recognize and remember faces compared to other stimuli once the pictures are turned upside-down (Diamond & Carey, 1986; Yin, 1969). As such, the face inversion effect has been suggested to reflect a special processing of faces. The aim of Experiment 6.1 was to investigate whether or not carrion crows also show the face inversion effect, both with crow faces and with human

faces. In experiment 6.1 using a matching-to-sample task, the two crows tested did not show such a face inversion effect. Although the birds performed slightly worse when stimuli were inverted, regardless of type of stimulus, there was no pronounced impairment of performance specifically when faces were inverted compared to controls for either the human faces or the crow faces. This lack of a face inversion effect in crows might appear puzzling given that 1) corvids can identify specific individuals (e.g., Bird & Emery, 2008; Bugnyar, 2011; Dally, Emery, et al., 2006; Massen et al., 2015) and can also do so from static pictures (e.g., Bird & Emery, 2008; Braun, 2013), 2) that corvids can also recognise specific human faces (Clucas et al., 2013; Marzluff et al., 2010) and 3) that corvids can learn to discriminate pictures in general (Veit & Nieder, 2013), and pictures of conspecifics specifically, as shown in Experiment 6.1. In what follows, two possible issues with the present study will be discussed, firstly the stimuli used in this study and secondly, the cues crows (might) use to differentiate individuals.

In principle, it is possible that the stimuli used here simply do not elicit inversion effects. It has been argued that the dissent found in the primate literature with regard to whether or not primates show a face inversion effect is due to differences in methods and stimuli used (Dahl et al., 2013a). For example, some studies used natural pictures of full primate heads, sometimes with some scenery in the background (e.g., Parr, Winslow, & Hopkins, 1999; Phelps & Roberts, 1994; Wright & Roberts, 1996), while newer studies have used very controlled pictures only showing a face without any surrounding that might allow viewers to determine head shape (Dahl et al., 2013a). Similarly, controls used differ between studies. For example, some studies used cars (Parr et al., 1999) or outdoor scenes (Phelps & Roberts, 1994) as non-face controls.

In order to directly test whether the stimuli used were responsible for the lack of a face inversion effect in carrion crows, Experiment 6.2 aimed to validate the procedure and stimuli used in Experiment 6.1 by testing humans in the same set-up and with the same stimuli as the crows. As expected, humans showed a strong face inversion effect: their performance in recognising faces was impaired to a greater extent when pictures of human faces were inverted compared to pictures of non-face controls. This result suggests that, in principle, the stimuli used should induce a face inversion effect, and indeed they do in human participants. This in turn suggests that the null result found in Experiment 6.1 likely reflects a lack of face inversion effect in carrion crows and is not purely a methodological problem.

However, Experiment 6.2 cannot rule out the possibility that the short delay used in Experiment 6.1 was responsible. In Experiment 6.2, the delay had to be increased to 500ms,

in order to avoid ceiling effects in the humans' performance. Dahl and colleagues (2013) argue when the match-distractor-pair is presented directly below the sample and temporal separation is missing completely, viewers might use picture-based matching rather than processing the pictures in a potentially configural manner. Such a procedure could therefore obscure a possible inversion effect. Thus, it is possible that in Experiment 6.1 with a delay of 0s birds could also have used picture-based matching.

Another important issue to consider when interpreting the current results is that it is not yet known whether crows use facial cues to identify conspecifics. There are reports of certain bird species using facial cues to discriminate between conspecifics (e.g., Brown & Dooling, 1992; Nakamura et al., 2003; Trillmich, 1976), for example the diverse plumage of the face (Leopold & Rhodes, 2010). Especially, budgerigars have previously been reported to use configural cues when recognising conspecifics (Brown & Dooling, 1992). Such data are lacking for corvids.

One possibility is that crows in the wild use the whole body as a cue, rather than the face alone. Notably, research on conspecific discrimination in crows has so far mainly used whole bodies. Thus, it would be of interest to see whether crows have a 'body-inversion' effect. Reed et al. (2003) found that humans display a body inversion effect in that their performance in recognising human bodies is impaired by inversion whereas recognition of houses is not. Another cue that corvids might use for identity discrimination is ultraviolet differences in plumage. Ultraviolet light perception has been reported to be relevant for mate choice in a range of bird species (for a review see Rajchard, 2009, but for opposing views see Stevens & Cuthill, 2007). For example, Steller's jays' plumage UV reflection signals mate quality. Note however that extra-pair copulations play a relatively big role for Steller's jays, compared to other corvid species (Overeem, Gabriel, Zirpoli, & Black, 2014). It is thus unclear whether the importance of UV perception in Steller's jays' sexual behaviour is indicative of visual features that might be relevant for monogamous and largely unassisted breeding carrion crows. Still, it is worth noting that the failure to find a face inversion effect might be due to the lack of UV light of in the crow profile stimuli used in the current study.

Previous research suggests that crows can use facial cues to differentiate human individuals (Bogale et al., 2011; Marzluff et al., 2010) and can be trained to discriminate between male and female faces based on pictures (Bogale et al., 2011). However, this alone does not imply that human faces constitute a 'special' cue for crows. This notion is tentatively supported by the results presented here, because the birds did not show an inversion effect when presented with human faces. Therefore, it is possible that crows used local features to

differentiate them. Such feature recognition would not be impaired by inversion. There are of course a range of different features they could have used, such as for example the shape or size of the eyes. Future research is therefore need to assess whether they indeed used local features to solve the matching-to-sample task, and if so, which ones.

In summary, the results presented here suggest that crows can learn to discriminate between human as well as crow faces, with fewer errors when responding to crow faces. However, the crows tested did not show a face inversion effect. Based on the rationale from human and other primate studies, this result would suggest that crows are no ‘experts’ for faces such that they might process faces in a different way to other stimuli. Given the limitations discussed above, however, future research is needed to determine how crows differentiate between conspecifics, and whether they can differentiate between individuals exclusively based on visual cues of a still picture of a face.

Chapter 7

Discussion and Conclusion

The aim of this thesis was to investigate theory of mind-like abilities and its basis in corvids, specifically Eurasian jays, California scrub-jays, and carrion crows. In Chapter 1, I introduced ‘theory of mind’ as the ability to attribute mental states, such as perception, desires, and beliefs, to others. The field of theory of mind has generated a large body of research, mostly revolving around the abilities of infants and non-human animals (e.g., Lurz, 2011). So far, there is no consensus whether animals are able to attribute mental states to others, or whether they mainly rely on behavioural cues when they respond to their conspecifics. Therefore, I have referred to animals’ abilities as ‘theory of mind-like’ abilities.

In corvids, most research has focused on an ability to attribute perceptual and desire states to others (reviewed for example in Clayton et al., 2007); however, it is not clear whether corvids also respond to the beliefs of a conspecific. Furthermore, while a range of studies have focused on theory of mind-like abilities in corvids, relatively little is known about the basis of such sophisticated abilities. Human theory of mind seems to rest on the ability to differentiate between animate agents and inanimate objects, and a sensitivity towards animate agents and their behaviour. Yet, the basis which corvid theory of mind-like abilities could build upon has not been uncovered. Therefore, and as discussed in Chapter 1, there are still several unanswered questions in regard to animals’ theory of mind-like abilities. My thesis was thus guided by two main questions:

- i) What are the limits of theory of mind-like abilities in corvids?
- ii) What mechanisms could be at the basis of corvids’ abilities?

In what follows, I will first summarise the main results of the experiments reported in this thesis. Subsequently, I will address the implications of these results for the questions asked in the introduction. Finally, I will relate my results back to the broader debate about animal theory of mind in general.

The ability to understand false beliefs is considered to be a litmus test of a ‘full-blown’ theory of mind. In **Chapter 2**, I report what, to the best of my knowledge, is the first paradigm designed to test such a false-belief understanding in corvids. Initially, an observer watched a cacher have access to only one of two caching trays because the other tray was

covered with a transparent Perspex lid. Then, an opaque curtain was drawn between the compartments of the two birds. Unbeknown to the observer, the lid was now removed by the experimenter, making both trays equally accessible. Consequently, the observer should have formed a false belief about the cacher's ability to cache in the previously inaccessible tray. If the cacher had understood that the observer has such a false belief, then that bird should have cached more in what the observer thought to be the inaccessible tray than in what the observer thought to be the accessible tray. I report two key findings. The first is that the observers tended to search more in the 'accessible' tray than in the 'inaccessible' one, suggesting that the belief induction worked. The second finding, however, was that the cachers did not show a pattern of caching that would be indicative of an understanding of the observer's false belief. They did not increase caching in the 'inaccessible' tray when an observer was present, compared to when no observer was present. This result suggests that the birds did not take into account the observer's mental state, which should discourage the observer to search in what they falsely believed to be the 'inaccessible' tray.

A range of previous studies suggest that Eurasian jays take into account the visual and auditory perspective of a conspecific observer (reviewed in Clayton et al., 2007; Grodzinski and Clayton, 2010a) and respond to their desires both in a competitive (i.e. cache protection) and cooperative (i.e. food-sharing during courtship) context (Ostojic et al., 2014, 2016, 2017, 2013). Thus, while there is compelling evidence to indicate that Eurasian jays have such theory of mind-like abilities, Chapter 2 tentatively suggests that their abilities are limited, specifically with regard to the ability to attribute a false belief in others for which I found no evidence.

As discussed in Chapter 1, in animals (and infants, c.f., Heyes, 2014b), 'behaviour reading' is generally thought to be the alternative hypothesis to an ability to attribute mental states to explain their performance in theory of mind tasks (Heyes, 1998; Penn & Povinelli, 2007, 2013). According to the behaviour reading hypothesis, animals respond to behavioural and contextual cues and to how they are related. Both the cues and their relationships are learned about in previous encounters with conspecifics. In **Chapter 3** I investigated which behavioural cues birds could use when employing cache protection strategies. Specifically, I built on work by Ostojic and colleagues (2017) that shows that Eurasian jays and scrub-jays respond to the desire of a conspecific when protecting their caches, both when they know what caused the change in desire, and when they have no information about this cause but could only observe the effect of the change. This finding could indicate that the observing birds in Ostojic and colleagues' (2017) study might have changed their behaviour depending

on their desire. This behavioural change in turn could have been used by the cachers to protect their caches. In Chapter 3, to manipulate their desire, birds were first pre-fed on one of two types of food. Eating one type of food to satiety decreases the preference for that food for a certain amount of time (Balleine & Dickinson, 1998; Dickinson & Balleine, 1994). In Experiment 3.1, the jays then had the possibility to observe a human experimenter cache the food they currently desired or the food they had just eaten to satiety. The birds tended to attend more to the caching of the food they desired than to the food they did not desire. In contrast to this, Experiment 3.2, in which a conspecific cacher was used, the birds showed no clear pattern of overt behavioural changes in response to their desire: when birds had a desire for the food that was cached, only some of the birds tested spent more of their time in closer proximity to the cacher. Taken together, my results suggest that birds might exhibit certain cues related to their desire, such as increased attention to a caching event that involves their desired food. However, given that pilfering behaviour differs with social status and age (Bugnyar & Kotrschal, 2002b; Shaw & Clayton, 2012), not all individuals might consistently show the same behavioural changes (see also Shaw & Clayton, 2012). For example, a dominant observer might approach a cacher when being motivated to pilfer the caches, whereas a subordinate observer might be more secretive about an attempt to pilfer in order to avoid a confrontation.

The possibility that conspecifics ‘read’ each other’s behavior requires corvids to be especially tuned toward the behaviour of their conspecifics. One of the most reliably found cues that tune humans towards agents is the perception of biological motion patterns. Biological motion is arguably related to the development of social-cognitive abilities, such as theory of mind because it draws attention specifically to animate agents (e.g., Frith & Frith, 1999). Biological motion perception was thus investigated in **Chapter 4** in California scrub-jays using a looking time paradigm. Previous research has shown that scrub-jays prefer to observe events that are of interest for them (Grodzinski et al., 2012; Watanabe et al., 2014). Therefore, scrub-jays are an ideal species to test with such a looking time paradigm.

Biological motion patterns were presented as dot displays of a number of small dots moving in a biological way. Such a display creates in a human observer the automatic impression of a complete action, such as walking or jumping, rather than a percept of individual dots (Johansson, 1973). From a very young age, humans prefer to observe such a biological motion pattern over random motion (reviewed in Simion et al., 2013), and such a tendency has also been demonstrated in newly-hatched chicks (Vallortigara et al., 2005). In the first experiment, I demonstrated that the scrub-jays had a preference for observing a full-

detailed display of a social agent (a conspecific) over an inanimate object that was matched for size and colour (Experiment 4.1). The results of Experiment 4.1 also suggest that video playback can be used to present stimuli to corvids in a controlled manner: scrub-jays showed a preference for an agent over an object, in both the live as well as the video playback condition. This finding is in line with previous research showing that rooks respond to videos of their partner in a similar way to when the partner is presented live. In two subsequent experiments, the birds were allowed to observe random motion and two different types of biological motion pattern, namely biological motion of another scrub-jay (Experiment 4.2a) and that of a horse (Experiment 4.2b). In both Experiments 4.2 and 4.3, the scrub-jays did not prefer to observe the biological motion pattern compared to the random motion. Consequently, I concluded that scrub jays might not show a preference for biological motion pattern in the same way as humans do.

In order to read behaviour an individual should not only be sensitive to the motion of an agent, but also to which direction an agent is oriented to. Thus, it is conceivable that a cue that corvids should attend to is where a conspecific is looking – its direction of gaze. Attending to gaze offers a possibility to assess whether a conspecific is interested in her environment (Emery, 2000), for example, whether or not a conspecific is interested in a caching event, as suggested in Chapter 3 (see also Grodzinski et al., 2012). In the light of previous results showing that corvids can take into account the perspective of others (reviewed in e.g., Clayton et al., 2007) one would assume that the birds also respond to another's direction of gaze. For example, if a conspecific is not attending to a caching event because they are observing another conspecific, then they pose less of a threat to one's caches. The experiments reported in **Chapter 5** therefore tested whether or not California scrub-jays are sensitive to 1) the direction of gaze of a human experimenter and 2) the direction of gaze of a conspecific observer in a caching context. In Experiment 5.1, I demonstrated that scrub-jays were slower to approach and retrieve food that was placed in front of an experimenter looking in their direction, compared to an experimenter looking away from them. This result is in line with a large body of research on sensitivity to gaze in a range of different animals (for a review see Davidson et al., 2014; Emery, 2000). In Experiments 5.2 and 5.3 – based on the successful validation of video playback to present stimuli reported in Experiment 4.1 – I presented caching birds with a video of a conspecific either looking at them or away from them. However, the 'observer' presented on the video screen did not influence the cachers' behaviour: the birds did not protect their caches from a forward facing 'observer' by caching preferentially in a tray out of sight of the 'observer', and they did not re-cache caches that the

‘observer’ had had visual access to. Taken together, these results suggest that while the scrub-jays appear to be sensitive to the direction of gaze of a live human experimenter, they do not adjust their caching behaviour in response to the video playback of a conspecific and their gaze.

In addition to eyes, the whole face might present an important cue in a social context, for example to differentiate different social agents from each other. Specifically, corvids are known to differentiate between individuals in different contexts (Bird & Emery, 2008; Bugnyar, 2011; Dally, Emery, et al., 2006) and have been found to do so based on facial cues (Clucas et al., 2013). The specialised recognition of faces in humans seems to be configural (e.g., Bartlett & Searcy, 1993; Maurer, Grand, & Mondloch, 2002; Rhodes, Brake, & Atkinson, 1993), which can be impaired by inversion (Towler & Eimer, 2016). Thus, the face inversion effect has been largely seen as an indicator for specialised processing of faces in humans (R Diamond & Carey, 1986) and some great apes (Dahl, Rasch, Tomonaga, & Adachi, 2013b; Parr, 2011a, 2011b). In **Chapter 6**, I used a delayed matching-to-sample task to investigate the face inversion effect in carrion crows (Experiment 6.1). Carrion crows were used because they are able to recognise pictures (Veit & Nieder, 2013) and are known to differentiate between conspecifics (Braun, 2013) and humans (Clucas et al., 2013; Marzluff et al., 2010). Performance in recognising human and crow faces, presented upright or inverted, was compared to performance for matched non-social controls, presented upright or inverted. While overall performance for inverted pictures was worse than performance for upright pictures, there was no pronounced impairment for pictures of crow faces or human faces. This was in contrast to the clear face inversion effect for human faces that was found when human participants were tested with the same task and the same stimuli used for the crows (Experiment 6.2). Therefore, crows – unlike humans – might not process faces in a qualitatively different way than stimuli of other categories.

What are the limits of theory of mind in corvids?

Chapter 2 tentatively suggests that Eurasian jays’ theory of mind-like abilities have a limit in that they do not encompass an understanding of others’ false beliefs. This null-result could be explained by a range of possible factors as discussed in Chapter 2, such as by the high cognitive load posed by the task. Prior research however suggests that the Eurasian jays do take into account what others can and cannot see (Legg & Clayton, 2014) and can and cannot hear (Shaw & Clayton, 2013), as well as what others desire (Ostojić et al., 2014, 2016, 2017, 2013). In this respect, their abilities appear similar to those of other corvids, notably California scrub-jays and ravens (e.g., Bugnyar, 2007; Clayton et al., 2007), and non-human

primates, for which there is primarily evidence for an ability to respond to the perspective (Hare et al., 2001, 2006) and the desires of a conspecific (Buttelmann, Call, & Tomasello, 2009). Recent findings, however, suggest that great apes might also be able to appreciate others' false beliefs. First, results of a looking-time study suggest that great apes seem to anticipate that a human experimenter will act according to her false belief (Krupenye et al., 2016). There are concerns with the interpretation of the results of this study; specifically, it is possible that the great apes used other mechanisms than false belief understanding, such as learning and memory (Heyes 2016). A second study investigated the behaviour of great apes when cooperating with a human experimenter who either had a true or a false belief (Buttelmann et al., 2017). However, it is not clear how the result that great apes respond to the false belief of the human experimenter fits with the difficulties reported previously when testing chimpanzees in a cooperative paradigm (e.g., Call & Tomasello, 1999; Povinelli & Eddy, 1996; Reaux, Theall, & Povinelli, 1999).

Testing full-blown theory of mind without imposing a high cognitive load, or without introducing a possible confound, is not a trivial task. In a false belief condition, there always has to be a switch of some kind that is not present in the true belief condition (or conversely, a switch that is present in the true belief but not in the false belief condition, as in Buttleman et al.'s, 2017, study) and the interactant has to leave the scene or turn around before later re-appearing. Such salient events have the potential to impair memory of the events prior to the false-belief induction due to their saliency (Heyes, 2014b).

A procedure that has the potential to show mental state attribution in such tasks is the 'goggles'-paradigm (first proposed by Novey, 1975; see Heyes, 1998, 2014a). The focal animal first receives experiences with two pairs of mirrored goggles each with a visibly distinct rim: one pair, with, say, a yellow rim, is see-through, whereas the other pair, with a green rim, is not. Importantly, the fact that one pair of goggles is see-through can only be determined when wearing them. The differentiation between the pairs thus has to be learned. Then, the animal is confronted with an interactant wearing one of the pairs of goggles. In case the interactant can see through the goggles, the focal animals, using their own experience wearing the goggles, should for example engage in cache protection strategies, or approach a food item more slowly. This goggles method would also allow rendering true and false belief conditions in a false belief task as similar as possible. An agent could observe the placement of an object in one of two boxes. Subsequently, the agent could put on the goggles while the object is transferred to the other location. In the true belief condition, the goggles are see-through; in the false belief condition they are opaque. Here, looking time could be used to

measure whether the subject is anticipating the agent to reach towards the box containing the object. If the subject understood false belief, the subject should do so only when the agent was wearing the see-through goggles; in the false belief condition with the opaque goggles, the subject should anticipate the agent to reach towards the now empty box.

The novelty of the experience (some goggles are see-through, some are opaque) is crucial to exclude the possibility that animals learned the effect of the goggles on the behaviour of a conspecific. Crucially, this method avoids the possibility that animals use some form of learned rule when solving a theory of mind task. It thus allows for a direct test of whether the animals' performance can best be explained in terms of mental state attribution. However, note that this goggles method has so far only been used with humans (e.g., Senju, Southgate, Snape, Leonard, & Csibra, 2011; Teufel, Alexis, Clayton, & Davis, 2010; Teufel, Clayton, & Russell, 2013) and, in a modified version, with primates where the goggles were replaced with screens (Karg, Schmelz, Call, & Tomasello, 2015)¹⁸. One reason for this is that using actual goggles potentially causes stress in animals. Furthermore, using a modified screen-version is methodological demanding: for example, it must be ensured that the subjects do not see another agent responding to the screens prior to the test trials, and it must be ensured that the subject sees an interactant behind the screen without the interactant being able to look over or under the screen (Heyes, 2014a). This last issue is especially tricky with birds that are able to fly.

In humans, the goggles method has been used to investigate whether or not informative pointing gestures of two year old children to request an item from their parent can be explained by an attribution of perceptual and knowledge states (Teufel et al., 2013). In such a paradigm, a child is presented with her parent having her eyes covered with her hands, or open while a sticker is being hidden in one of two boxes positioned in front of the parent and out of reach of the child (O'Neill, 1996). Subsequently, the child has the chance to request the sticker from their parent. Infants used informative pointing gestures to guide their parent when they parent could not see the placement of the sticker, and hence did not know its whereabouts – thus, it seems that the tested infants attributed knowledge to their parent (O'Neill, 1996). Note however that children likely had prior experience with people covering their eyes, and the effects of covered eyes on behaviour. To assess whether or not the children's performance was due to an attribution of perceptual and knowledge states as opposed to using past experience with regularities in behaviour, Teufel and colleagues (2013)

¹⁸ Note that Bugnyar et al. (2016) used a peephole procedure mirroring the goggles method; however, for reasons discussed in the introduction it is not entirely clear that focal animals did not see that there was no observer on the other side of the barrier.

used the goggles method described above. Teufel and colleagues (2013) had three manipulations of the parent ‘seeing’ the placement of the sticker. In a ‘natural’ situation, the parent was using her hands to cover her eyes in the same way as in the O’Neill (1996) study. In what I shall call ‘self-goggle’ situation, the parent was wearing opaque or see-through goggles. Importantly, prior to testing, children experienced the effect of goggles on their own vision. In a second goggles-condition, children learned only about the effect of the goggles on their parent’s behaviour: for example, children learned that one pair of goggles made their parent unresponsive and unable to play a game with them. Importantly, in this situation, they did not experience the goggles themselves (henceforth ‘other-goggle’ situation). Teufel and colleagues (2013) showed that, in the ‘natural’ situation, children correctly reported whether their parent could see and used informative pointing gestures when the parent could not see. In the ‘self-goggle’ situation, children reported correctly whether their parent could see, but did not use informative pointing gestures. In the ‘other-goggle’ situation, children were not able to correctly report whether or not their parent could see but they did use informative pointing gestures. These results suggest that first, informative pointing in O’Neill’s (1996) task might not necessarily imply that children understand the association between ‘seeing’ and ‘knowing’. Rather, children might use the behavioural cue ‘eyes covered’ to predict whether their parent needed information about the sticker’s whereabouts, but did not do so by attributing mental states. Furthermore, children did not seem to realise that their parent’s ‘clumsy and unresponsive’ behaviour in the ‘other-goggle’ situation was an indicator of the parent not being able to see. However, the children seemed to have noticed something in their parent’s behaviour was wrong, and that the parent might require help to find the sticker.

This finding demonstrates that the goggles method can be used to investigate whether someone is able to attribute mental states (in this case: the knowledge where the sticker is), or whether they are relying on regularities in someone else’s behaviour when interacting with them. Additionally, the findings show that some aspects of behaviour might be more difficult to ‘read’ than others: children were not able to use the cue ‘clumsy and unresponsive behaviour’ in the same way as they used the cue ‘eyes covered’ (Teufel et al., 2013).

Hence, the fact that behaviour might change as a function of changes in mental states does not always imply that an individual can easily ‘read’ this behaviour. Therefore, Teufel and colleagues’ (2013) results show that while it is crucial to put mentalistic explanations of performance in a theory of mind task to a test, it is equally important to assess the claim that an individual can ‘read behaviour’, or finds it easy to do so. Indeed, ‘behaviour reading’ has often been offered as a simpler and thus more parsimonious explanation for animal theory of

mind-like behaviour (e.g., Heyes, 1998; Penn & Povinelli, 2007; Schlinger, 2009; Shettleworth, 2010); however, so far there is no evidence that behaviour reading is indeed easier for an animal to do, and hence constitutes the ‘simpler’ mechanisms, compared to the presumably more complex attribution of mental states (c.f., Mikhalevich, 2015). Behaviour-reading explanations put forward in the literature have also been criticized because they are largely post-hoc (e.g., Halina, 2015), generating new rules animals should be aware of after performance in a new theory of mind task is reported. In order for them to be falsifiable, they need to make explicit testable predictions based in the literature (Heyes, 2014b).

A direct test of a behaviour reading explanation has been reported in a study conducted by Ostojić and colleagues (2017), who studied Eurasian and scrub-jays’ ability to respond to the desire of a conspecific observer during caching. Specifically, the authors predicted (and explicitly tested) that, if behavioural cues are sufficient, they should be able to respond to the desire of an observer even if they had not seen the cause of the desire (i.e., the pre-feeding). It was found that when the birds did not know what food an observer was sated on, they still responded to the observer’s desire. This finding suggests that birds indeed can ‘read behaviour’ in some circumstances. But which behaviour did they read? Chapter 3 suggests that certain behaviours might change with desire, but not all behaviours do in the same way across different individuals. If this is indeed the case, it raises the question how animals learn which relations between behaviours and contextual cues are good indicators of future behaviour and which are not (Penn & Povinelli, 2013), as well as which behaviour is a good indicator for future behaviour for which individual. Shaw and Clayton (2012), for example, demonstrate that dominance plays a role in the pilfering behaviour of conspecifics: a dominant pilferer will approach the caching faster, and might even interrupt the caching, compared to a subordinate pilferer, who might only approach a caching site once the cacher has left. Thus, in the context of Chapter 3, birds might have to learn that an observer that is more likely to pilfer the food they cache will approach them – but only if the observer is dominant. For a subordinate conspecific a cacher might have to be attentive to different cues. Importantly, a cacher might have seen a conspecific A interact with another conspecific B in a certain way – from this past experience the cacher can however not necessarily predict how A will behave towards herself. Therefore, a behaviour-reading animal should be sensitive towards specific social aspects of their environment, such as dominance hierarchies (something corvids have been found to be able to track, Bond, Kamil, & Balda, 2003; Massen et al., 2014; Paz-y-Miño, Bond, Kamil, & Balda, 2004), and how they relate to the behavioural repertoire of conspecifics. Additionally, these relations are fluid and can change

over time – a cacher’s ability to ‘read’ a conspecific’s behaviour is thus also reliant on a sensitivity to possible changes in themselves and in relation to others (c.f., Emery & Clayton, 2008). This then begs the question how the relevant relations between behaviour and conspecifics are recognised and remembered (see also Emery & Clayton, 2008).

What mechanisms could be the basis of corvids’ theory of mind-like abilities?

The ability to distinguish between inanimate and animate entities is important for animals that need to cooperate and compete with others. It is also an important pre-existing¹⁹ ability for theory of mind abilities in humans (C. D. Frith & Frith, 1999). The assumption should therefore be that inanimate-animate discrimination should be present in animals with socio-cognitive abilities. Furthermore, as Penn, Holyoak, and Povinelli (2008) noted, the results from corvid studies (e.g., Clayton et al., 2007; Dally, Emery, & Clayton, 2010; Grodzinski & Clayton, 2010a) demonstrate that corvids “are ... able to keep track of the social context of specific past events, as well as the what, when, and where information associated with those events” (p. 120), which in turn could allow them to ‘read behaviour’. In what follows, I will discuss the possible cues that could signal a social context for corvids. In order to attend specifically to social agents and their behaviour, it is first crucial to identify these agents.

The findings described in Chapter 4 are in line with this suggestion: the scrub-jays showed an increased interest in their (animate) conspecific compared to an (inanimate) object. Which cues indicates ‘animacy’ for scrub-jays? Chapter 4 suggests that biological motion is not among those cues. Note that I do not intend to imply that scrub-jays cannot *differentiate* between biological and random motion. They have, however, no *preference* for biological motion. At first glance, this finding is somewhat surprising; detecting agents is crucial for all animals, and biological motion should be an important indicator of animacy (e.g., Frith & Frith, 2012). However, it has been proposed that biological motion tuning might be closely link to a species’ ecology. For example, preference for biological motion over random motion found in chicks (Vallortigara et al., 2005) might be related to the need to imprint on their mother (Miura & Matsushima, 2016). Keeping in mind necessary caution when interpreting null-results, Chapter 4 tentatively supports the notion that biological motion perception in humans is not necessarily an evolutionarily old mechanism (Troje & Westhoff, 2006) and might therefore not present a pre-requisite upon which more complex social cognitive abilities build upon.

¹⁹ In the sense that it is found earlier in human development than an understanding of others’ minds can be demonstrated, not necessarily in the sense that it is an innate ability.

Consequently, if scrub-jays lack this ‘basis’ of theory of mind, their theory of mind-like abilities might actually be based on different mechanisms than human theory of mind. There are however a range of other motion stimuli that have been associated with animacy (Premack, 1990) that need to be addressed in further studies, such as a sensitivity for self-propelled and goal-directed motion. For example, recent work reports that chicks prefer objects that are moving in a self-propelled manner over objects whose movement has been physically caused (Mascalzoni, Regolin, & Vallortigara, 2010); however, it is again unclear whether the reported preference of chicks for self-propelled objects is associated with their particular need to imprint on their mothers (Miura & Matsushima, 2016). Therefore, it would be of interest to investigate whether corvids, representing altricial birds, are more interested in self-propelled objects, as opposed to objects moved by an external force. One possibility would be to present birds with sequences of objects moving in one of the two ways (‘agency induction’), and assess whether and how fast they approach food next to the self-propelled object after seeing the objects move / be moved in the agency induction. If birds perceive the self-propelled object as an agent, they might take longer to approach the food, because an agent could in principle move again on its own, and consequently might pose a threat, whereas an inanimate object is on its own harmless. Specifically, this procedure would also allow presenting the objects side by side after the ‘agency induction’ – such a comparison then requires the birds to decide which object to approach. Similar procedures have been used with New Caledonian crows (*Corvus moneduloides*) who spent more time inspecting a location from which a stick was moved by an agent, compared to when the stick seemingly moved on his own (Taylor, Miller, & Gray, 2012).

Such an approach could in principle also be used to investigate biological motion perception further. For example, an object A could be associated with the presentation of biological motion patterns, whereas object B could be associated with the presentation of random motion patterns. In a subsequent choice test, birds could then retrieve food next to object A or object B. However, here predictions are less clear: birds could also be more interested in biological motion, and not be fearful to approach the object that has been *associated* with agency as opposed to an object that *has* agency.

When investigating sensitivity to conspecifics’ direction of gaze presented as video playback in Chapter 5, I found that the birds neither adjusted their caching behaviour at the point of caching nor their re-caching behaviour when they had access to the caching tray in private. Importantly, the birds also did not show different caching behaviour when being presented with a conspecific, irrespective of her direction of gaze, compared to when being

presented with an empty cage. It is therefore possible that scrub-jays did not perceive the video playback as a threat to their caches because it lacked certain features. However, in human research even impoverished stimuli such as a line drawing of eyes seem to bring about robust changes in behaviour. For example, in humans, eyes placed in a simple line drawing of a face can serve as a very powerful attentional cue (reviewed in Langten et al., 2000). This has been famously demonstrated with a ‘Posner paradigm’, where participants have to respond as fast as possible to the occurrence of a target. The target can appear on both sides of the screen, and sometimes its appearance is preceded by an endogenous cue. This cue is either valid (the cue indicates the correct side of where the target will appear) or invalid (the cue indicates the wrong side). However, the cue does not predict the location of the target (Posner, 1980). In such a paradigm, using eye gaze as the cue has a facilitating effect on attention in valid trials, similar to non-social arrows (e.g., Driver et al., 1999; Friesen & Kingstone, 1998). Furthermore, when the direction of eye gaze is counter-predictive, that is, when the gazing to the left precedes a target on the right in the majority of cases, eye gaze cues are hard to ignore (Friesen & Kingstone, 1998; Ristic, Friesen, & Kingstone, 2002). By contrast, caching is a more deliberate behaviour (e.g., Grodzinski & Clayton, 2010a) than the automatic shift of attention in a Posner cueing paradigm. However, studies on the influence of eyes on more deliberate behaviours in humans reveal similar tendencies: the presence of eyes affects the willingness to cooperate or leads to a reduction of littering (Bateson, Callow, Holmes, Redmond Roche, & Nettle, 2013; Bateson, Nettle, & Roberts, 2006; Ernest-Jones, Nettle, & Bateson, 2011). Therefore, there seems to be an interesting divergence in how readily humans and scrub-jays respond to eye gaze.

This then raises the question of *which* features are relevant for a corvid, triggering cache-protection strategies. One possibility might be ‘interaction’ with the conspecific: the conspecific in the video did not respond to the cacher’s behaviour in any way in contrast to the dynamic relationship between a cacher and a live conspecific observer. This lack of interaction must have been an unusual situation for the birds being tested and might have led them to believe that their caches were safe, or at least that circumstances were not normal. Related to this, note that in a previous study, scrub jays treated a mirror present during caching as if they were in private, rather than as if the observed image in the mirror was a live observer. In other words, the ‘conspecific’ reflected by the mirror image was not sufficient to elicit cache protection strategies (Dally et al., 2010). Consequently, I suggest that it is the contingent responses from an interactant that could serve as a salient cue that the birds use in order to detect other agents. In this sense, the corvids do not seem to be tuned to the same

social cues that humans are tuned to, perhaps not surprisingly given how different and distantly related the two species are. My findings might be taken to suggest that the jays rely on the contingent interaction of a conspecific in order to perceive them as such. In Chapter 4, I presented findings for a special interest in conspecifics compared to objects, even though the conspecific on the video screen did not interact with the focal bird. However, the experiment mirrored the birds' usual housing situation. Consequently, they might not have expected the conspecific to respond to their behaviour, whereas they might have learned that conspecifics will respond to their caching behaviour, for example by coming closer to the caching site or by carefully monitoring the caching.

The possibility that corvids do not rely on the same social cues as humans might be also one potential explanation for the lack of a face inversion effect reported in Chapter 6. Conceptually, there are two possible reasons for a lack of face inversion effect in crows: firstly, crows could use and process different cues to recognise and discriminate between conspecifics. As discussed, it is possible that, for crows, the whole body is relevant. Such a finding could in turn be related to the relevance of interaction – if corvids are tuned towards the behaviour of a conspecific, they might show a body inversion effect. Future research is necessary to determine this possibility. Secondly, the face inversion effect might simply not be an indicator for specialised processing in birds. In this case, a different approach might be necessary to evaluate whether faces are processed differently to stimuli of other categories.

The primate literature has demonstrated that rhesus macaques have a brain area specifically dedicated to processing faces: the fusiform face area in the superior temporal sulcus (STS) (Allison, Puce, & McCarthy, 2000). Yet, robust evidence of a face inversion effect in monkeys is missing (Parr, 2011a). Therefore, specialised face processing might not manifest itself in a face inversion effect in all species. Furthermore, in humans, perceiving biological motion patterns is also associated with activation in the STS; thus, it might be of interest to investigate the processing of faces in corvids with other methods as well, such as neuroimaging techniques that would allow assessing whether corvids have brain areas dedicated to recognising faces.

Concluding remarks

The research conducted in this thesis tentatively suggests that corvids might not be able to respond to false beliefs of conspecifics despite their remarkable socio-cognitive abilities both in the realm of competitive caching and co-operative food-sharing behaviours. However, the findings highlight the need for a specification of how then corvids respond to others and their mental states. To begin to address this question, I investigated a range of

7: Discussion and Conclusion

possible indicators that corvids attend to social stimuli differently than to non-social stimuli. I demonstrated that corvids are interested in other agents – but also that they might not use the same cues to determine whether someone is an agent or not. They seem to be sensitive to direction of gaze; further research is needed, however, to widen our understanding of the relevance of eye gaze for corvids. These birds might be sensitive to how conspecifics are related to each other and to how they interact with each other and with objects in their environment. In sum, corvids do not seem to be sensitive to cues that, in humans, are generally thought to be crucial for the development of social cognitive abilities, suggesting that human theory of mind and corvid theory of mind-like abilities might rest on different mechanisms.

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Appendix A

Subjects, Set-up & Supplementary Material

Table A.1. Participating birds.

	Gender	Chapter	Previous caching and pilfering experience
Scrub-Jays			
13 ^a	F	Chapter 5	J.M. Dally, unpubl. data
31 ^b	M	Chapter 4	Ostojić et al. ¹
108	M	Chapter 5	Ostojić et al. ¹
202	F	Chapter 4, 5	Ostojić et al. ¹
203	M	Chapter 4, 5	Ostojić et al. ¹
207	F	Chapter 4, 5	J. Thom, unpubl. data
210 ^a	M	Chapter 5	Ostojić et al. ¹
215	F	Chapter 4, 5	Ostojić et al. ¹
220	M	Chapter 4, 5	Ostojić et al. ¹
222	M	Chapter 4, 5	Ostojić et al. ¹
223	F	Chapter 5	T & C ²
229	F	Chapter 4, 5	Ostojić et al. ¹
Eurasian Jays			
<i>Colony 1</i>			
Caracas	M	Chapter 2, 3	Ostojić et al. ¹
Wellington	F	Chapter 2, 3	Lj. Ostojić, unpubl. data
Lima	M	Chapter 2, 3	Ostojić et al. ¹
Jerusalem	F	Chapter 2, 3	Ostojić et al. ¹
Lisbon	M	Chapter 2, 3	Lj. Ostojić, unpubl. data
Rome	F	Chapter 2, 3	Ostojić et al. ¹
Dublin	M	Chapter 2, 3	Ostojić et al. ¹
Quito	F	Chapter 2, 3	Lj. Ostojić, unpubl. data
Washington	F	Chapter 2, 3	Ostojić et al. ¹
<i>Colony 2</i>			
Hoy	M	Chapter 2, 3	L & C ³ , S & C ⁴
Romero	M	Chapter 2, 3	L & C ³ , S & C ⁴
Pendleton	M	Chapter 2	L & C ³ , S & C ⁴
Adlington ^b	F	Chapter 2	L & C ³ , S & C ⁴
Ainsley ^b	M	Chapter 2	L & C ³ , S & C ⁴
Carrion Crows			
Hugo	M	Chapter 6	
Walt	M	Chapter 6	

Note. ^a birds were excluded from the study, ^b birds did only participate as non-focal bird
¹ Ostojić et al., 2017; ² Thom & Clayton, 2013; ³ Legg & Clayton, 2014; ⁴ Shaw & Clayton, 2013, 2014.

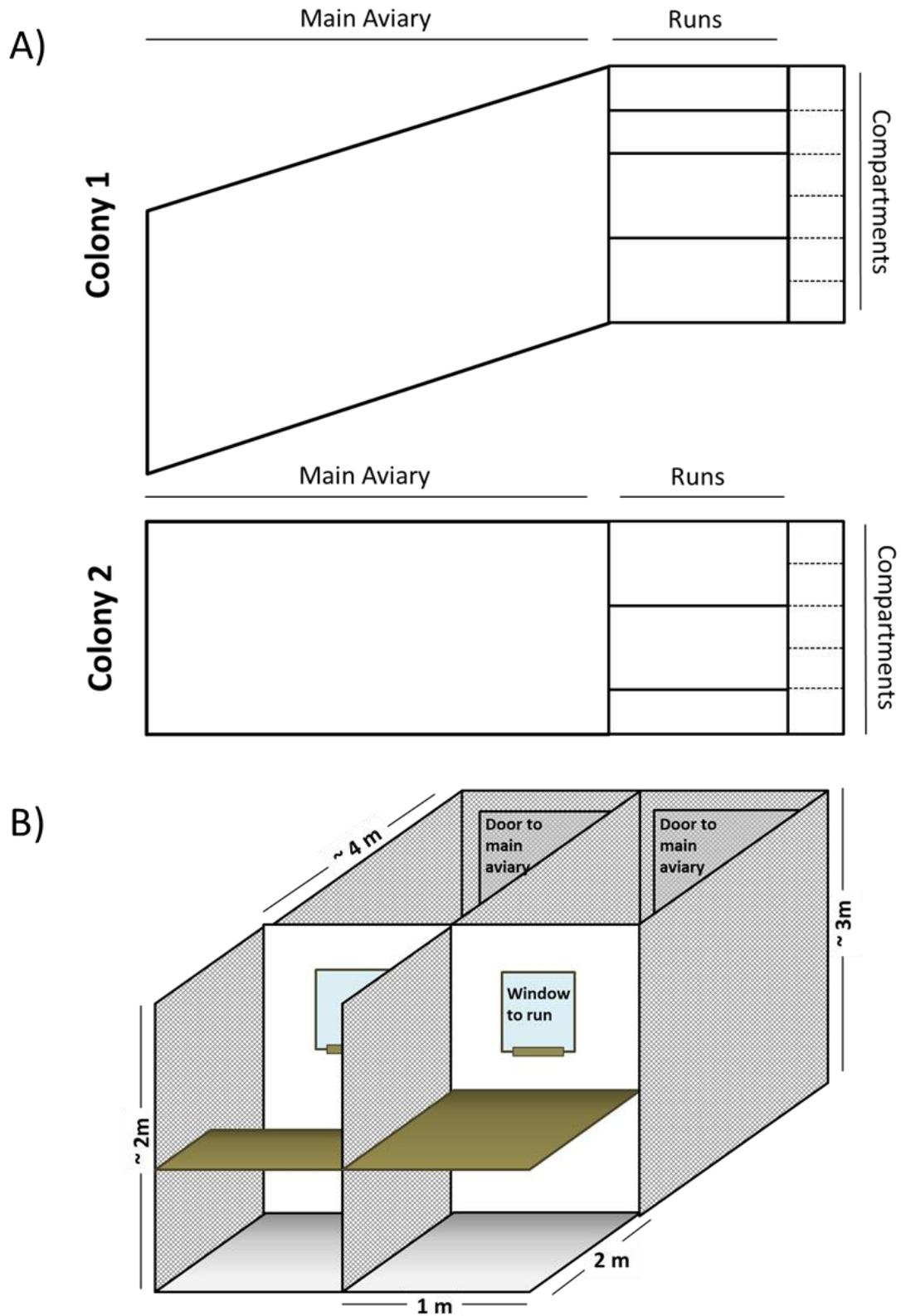


Figure A.1. Housing and testing compartment of Eurasian jays (Chapter 2 and 3). Panel A shows an aerial view of the aviaries of colony 1 and 2 (not to scale), and panel B a view of testing compartments.

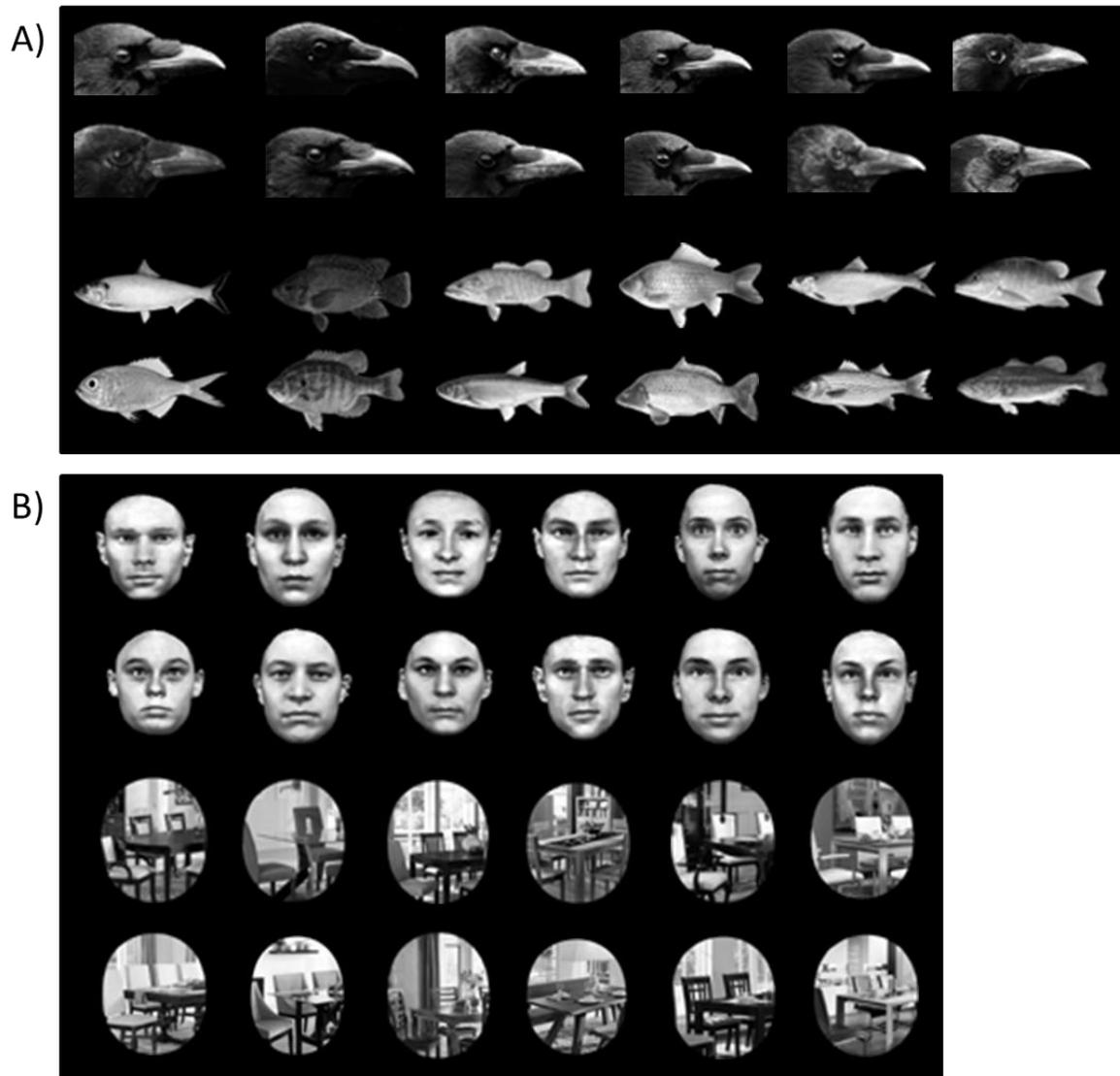


Figure A.2. Stimuli used in Experiment 6.1 and 6.2. Panel A shows crow profiles and the corresponding non-face controls (fish). Panel B shows human faces and the corresponding non-face controls (house interior)

Appendix B

Supplementary Raw Data

Table B.1. Chapter 2, Step II. Table shows the number of pots checked and the number of searches in the ‘inaccessible’ and the ‘accessible’ trays, as well as whether the accessible tray was approached first and the number of pots checked before the first switch.

Subject	‘Accessible’ tray		‘Inaccessible’ tray		1 st approach to ‘accessible’ tray	Pots checked before first switch
	Searches	Pots checked	Searches	Pots checked		
Hoy	13	8	3	2	Yes	5
Romero	19	13	35	15	No	10
Pendleton	14	9	3	3	Yes	9
Caracas	13	12	39	13	No	26
Dublin	0	0	0	0	Yes	NA
Lima	45	15	35	15	Yes	15
Lisbon	7	6	1	1	Yes	6
Quito	1	1	0	0	Yes	1
Jerusalem ^a	17	1	1	1	Yes	1
Washington	9	0	0	0	Yes	4

Table B.2. Chapter 2, Step III. Table shows caches made in successful training trials.

Subject	Caches made	
	Tray without lid	Tray with lid
Pendleton	3	1
Hoy	2	4
Romero	6	3
Jerusalem ^a	0	0
Washington	4.5	11
Caracas	11	27
Lima	15	5
Lisbon ^a	0	0
Quito	6	19
Dublin ^a	0	0

Note. ^a Birds did not finish training and did not commence to the false belief task because they stopped caching.

Appendix B

Table B.3. Chapter 2, False and True Belief Task. Table shows caches made in the ‘accessible’ and ‘inaccessible’ tray in the both the social and non-social conditions of the false and true belief task.

Subject	False Belief				True Belief			
	Social		Non-Social		Social		Non-Social	
	No Access	Access	No Access	Access	No Access	Access	No Access	Access
Caracas	2	15	0	4	2	2	3	7
Washington	3	5	4	5	2	2	3	7
Lima	2	1	0	10	-	-	-	-
Quito	0	3	0	3	-	-	-	-
Pendleton	1	0	1	2	-	-	-	-
Romero	4	6	3	1	1	2	4	3
Hoy ^a	3	5	3	1	-	-	-	-

Table B.4. Chapter 3, Experiment 3.1. Looking time in seconds during the test phase and during the food-only phase when the cached food was different (conflicting condition) and the same (matching condition) as the pre-fed food.

Subject	Test phase		‘Food-only’ phase	
	Matching Condition	Conflicting Condition	Matching Condition	Conflicting Condition
Lima	9.84s	19.2s	2.36s	6.64s
Caracas	2.44s	0s	1.16s	0.28s
Rome ^a	1.92s	17.16s	0s	0s
Quito ^a	5.16s	8.52s	0s	0s
Wellington	0s	0.88s	5.92s	10.47s
Romero	0s	3.12s	0s	3.84s
Washington	1.54s	0s	3.58s	21.42s
Lisbon ^b	0s	0s	7.72s	1.56s
Hoy ^c	0s	0s	0s	0s
Jerusalem ^c	0s	0s	0s	0s
Dublin ^c	0s	0s	0s	0s

Note. ^a Birds excluded from analysis of looking time in ‘food only’ phase, ^b Bird excluded analysis of looking time in test phase, ^c birds excluded from all analyses.

Appendix B

Table B.5. Chapter 3, Experiment 3.2. Total time spent (in seconds) in section 1, in section 1 while the cacher was present, and in the different parts of section 1 ('near' to and 'far' from the window allowing access to the cacher) depending on pre-feeding (matching or conflicting).

Subject	Conflicting Pre-feeding				Matching Pre-feeding			
	Section 1	Sec 1 with cacher	Sec 1: 'far'	Sec 1: 'near'	Section 1	Sec 1 with cacher	Sec 1: 'far'	Sec 1: 'near'
Caracas	279.6s	88.4s	7.4s	246s	235.8s	76.4s	136.6s	118.8s
Washington		15.6s	63.6s	10.6s	76.2s	34.8s	21.6s	41.6s
Lisbon	561.4s	50.6s	217.8s	343.6s	17.6s	3.8s	4.2s	13.4s
Quito	34.2s	6.4s	28.2	6s	5.2s	0s	0s	5.2s
Dublin	41s	36s	7.4s	11.4s	171.8s	90.4s	26.6s	122s
Rome	241.4s	193.6s	195.2s	53.6s	26.4s	9.4s	8s	18s
Wellington	453.2s	200.8s	409.2s	100.4s	875.4s	382s	875.4s	0s

Table B.6. Chapter 4, Experiment 4.1. Looking time in seconds at the agent and the object for both the live and video presentation.

Subject	Live Presentation				Video Presentation			
	Object Condition		Agent Condition		Object Condition		Agent Condition	
	Object	Object	Agent	Object	Object	Object	Agent	Object
202	0	0	1.64	2.22	0	4.25	4.34	18.01
203	12.03	40.23	1.39	128.22	2.33	0.75	0	139.4
207	24.01	41.93	6.4	224.9	3.13	20.27	10.76	57.45
215	19.37	32.23	25.71	40	0	3.01	0	3.4
222	15.83	45.1	24.35	65.91	4.94	4.94	8.81	13.99
229	33.06	40.59	13.31	208.26	2.96	8.85	8.81	13.99
223 ^a	13.5	17.47	23.42	34.3	-	-	-	-
220 ^a	20.26	3.87	54.36	62.91	-	-	-	-

Note. ^a Bird died after participation in the live presentation.

Table B.7. Chapter 4, Experiment 4.2a and 4.2b. Looking time in seconds at the different motion patterns on day 1 and 2.

Subject	Experiment 4.2a				Experiment 4.2b			
	Conspecific		Random		Heterospecific		Random	
	Day 1	Day 2	Day 1	Day 2	Day 1	Day 2	Day 1	Day 2
203	4.47	0	3.82	0.63	0.16	1.48	12.80	1.19
207	32.55	10.78	9.68	12.50	0	0.73	3.64	0
215	11.42	3.89	2.12	4.66	0	2.10	0	6.44
222	15.83	45.10	24.35	65.91	2.44	1.40	3.07	3.37
229	5.10	0	0	4.89	0	2.07	0	3.10

Appendix B

Table B.8. Chapter 5, Experiment 5.1. Latency to approach food in seconds when a human experimenter was facing towards the subject or away from the subject.

Subject	Condition	
	Facing Forward	Facing Away
203	600s	102.08s
207	83.64s	22.2s
215	426.8s	3.92s
222	17.52s	12.56s
229	600s	17.18s

Table B.9. Chapter 5, Experiment 5.2. Items cached when being presented with an empty cage, a rope, a conspecific facing away or a conspecific facing forward.

Subject	In-view tray				Out-of-view tray			
	Empty Cage	Rope*	Facing Forward	Facing Away	Empty Cage	Rope*	Facing Forward	Facing Away
108	22.5	5.5	0	7.5	17	16	7	11
215	4.5	3.5	2.5	3.5	1	5	4.5	4.5
207	0	9	3.5	5.5	3.5	0	0	0.5
203	13	6	17	19	8	8	7.5	4
202	8	10	2	6	5	9	4	4
220	1.5	1	0	0	0	2.5	1	1
222	9	8	22	12	11	0	8	4
223	1	1.5	1	2	0	0	0	5
229	11.75	8.5	3.75	6	8	9	1	1

Note. *As an additional non-social control, the rope condition was run to ascertain that a difference between the social conditions (Facing Forward and Facing Away) and the empty compartment would not be due to movement on the screen. As there was no significant difference between the conditions Empty Compartment and Rope (one-tailed permutation test, $Z = 0.56, p = .31$), this condition is not included in the main report of the experiments in Chapter 5.

Table B.10. Chapter 5, Experiment 5.3. Items re-cached when being presented with an empty cage, a rope, a conspecific facing away or facing forward.

Subject	Cached				Re-Cached			
	Empty Cage	Rope*	Facing Forward	Facing Away	Empty Cage	Rope*	Facing Forward	Facing Away
108	22.5	11.5	21	14	22.5	11.5	7	5
215	4	2	-	-	2	1	-	-
207	4	2.5	3	2.5	3	1	1	0.5
203	3	1.5	13	2	1	1.5	4	0
202	23	21.5	24	27	8	4	10	11
220	8.5	7.5	5	7	2	3	3	6
222	11	12	14	27	5	8	8	11
223	1.5	4.5	10.5	1	1.5	3.5	6.5	1
229	15	38	13	5.5	4.25	11	6	1

Note. *As an additional non-social control, the rope condition was run to ascertain that a difference between the social conditions (Facing Forward and Facing Away) and the empty compartment would not be due to movement on the screen. As there was no significant difference between the conditions Empty Compartment and Rope (one-tailed permutation test, $Z = -0.14, p = .55$), this condition is not included in the main report of the experiments in Chapter 5.

Table B11. Chapter 6, Experiment 6.1. Mean accuracy in % for all stimuli classes tested in the matching-to-sample task for all sessions.

Session Nr.	Hugo												Walt											
	Fish			House interior			Crow profile			Human face			Fish			House interior			Crow profile			Human face		
	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}
1	75.0	54.5	20.5	80.0	85.7	-5.7	92.3	92.3	0.0	66.7	77.4	-10.8	82.8	64.9	17.9	72.7	68.6	4.2	77.4	63.2	14.3	63.2	54.5	8.6
2	82.8	64.9	17.9	92.3	80.0	12.3	80.0	96.0	-16.0	82.8	75.0	7.8	61.5	64.9	-3.3	88.9	68.6	20.3	82.8	51.1	31.7	63.2	52.2	11.0
3	80.0	70.6	9.4	100.0	72.7	27.3	92.3	85.7	6.6	75.0	75.0	0.0	66.7	64.9	1.8	82.8	61.5	21.2	60.0	72.7	-12.7	60.0	82.8	-22.8
4	77.4	72.7	4.7	80.0	58.5	21.5	75.0	85.7	-10.7	75.0	50.0	25.0	70.6	72.7	-2.1	77.4	80.0	-2.6	57.1	72.7	-15.6	82.8	58.5	24.2
5	80.0	72.7	7.3	92.3	70.6	21.7	75.0	77.4	-2.4	72.7	75.0	-2.3	88.9	66.7	22.2	75.0	80.0	-5.0	63.2	75.0	-11.8	57.1	63.2	-6.0
6	92.3	77.4	14.9	85.7	77.4	8.3	92.3	70.6	21.7	72.7	85.7	-13.0	77.4	66.7	10.8	68.6	75.0	-6.4	72.7	70.6	2.1	70.6	70.6	0.0
7	85.7	77.4	8.3	88.9	72.7	16.2	92.3	72.7	19.6	88.9	75.0	13.9	85.7	77.4	8.3	70.6	75.0	-4.4	85.7	60.0	25.7	68.6	68.6	0.0
8	85.7	77.4	8.3	92.3	80.0	12.3	75.0	80.0	-5.0	68.6	70.6	-2.0	68.6	70.6	-2.0	75.0	58.5	16.5	80.0	70.6	9.4	68.6	58.5	10.0
9	80.0	88.9	-8.9	92.3	77.4	14.9	92.3	60.0	32.3	66.7	75.0	-8.3	70.6	70.6	0.0	61.5	66.7	-5.1	70.6	66.7	3.9	70.6	64.9	5.7
10	88.9	72.7	16.2	85.7	68.6	17.1	88.9	85.7	3.2	77.4	66.7	10.8	72.7	68.6	4.2	72.7	60.0	12.7	70.6	72.7	-2.1	63.2	52.2	11.0
11	88.9	63.2	25.7	88.9	77.4	11.5	63.2	85.7	-22.6	61.5	77.4	-15.9	77.4	77.4	0.0	70.6	82.8	-12.2	85.7	61.5	24.2	80.0	70.6	9.4
12	82.8	77.4	5.3	72.7	85.7	-13.0	77.4	80.0	-2.6	57.1	60.0	-2.9	63.2	70.6	-7.4	70.6	64.9	5.7	80.0	82.8	-2.8	70.6	61.5	9.0
13	88.9	82.8	6.1	80.0	70.6	9.4	82.8	80.0	2.8	72.7	60.0	12.7	75.0	68.6	6.4	66.7	75.0	-8.3	57.1	70.6	-13.4	75.0	60.0	15.0
14	75.0	85.7	-10.7	85.7	61.5	24.2	82.8	75.0	7.8	80.0	70.6	9.4	80.0	72.7	7.3	63.2	58.5	4.6	85.7	77.4	8.3	66.7	68.6	-1.9
15	77.4	72.7	4.7	72.7	82.8	-10.0	85.7	82.8	3.0	66.7	68.6	-1.9	80.0	70.6	9.4	68.6	68.6	0.0	85.7	58.5	27.2	60.0	55.8	4.2
16	70.6	75.0	-4.4	82.8	77.4	5.3	80.0	85.7	-5.7	75.0	53.3	21.7	92.3	72.7	19.6	80.0	82.8	-2.8	80.0	68.6	11.4	75.0	92.3	-17.3
17	82.8	82.8	0.0	75.0	85.7	-10.7	88.9	77.4	11.5	72.7	75.0	-2.3	57.1	58.5	-1.4	77.4	72.7	4.7	58.5	60.0	-1.5	82.8	61.5	21.2
18	88.9	77.4	11.5	82.8	77.4	5.3	100.0	85.7	14.3	60.0	57.1	2.9	70.6	77.4	-6.8	82.8	77.4	5.3	85.7	72.7	13.0	66.7	72.7	-6.1
19	85.7	85.7	0.0	85.7	77.4	8.3	96.0	96.0	0.0	70.6	63.2	7.4	70.6	85.7	-15.1	75.0	75.0	0.0	88.9	92.3	-3.4	61.5	75.0	-13.5
20	92.3	88.9	3.4	100.0	80.0	20.0	96.0	70.6	25.4	72.7	70.6	2.1	68.6	82.8	-14.2	92.3	75.0	17.3	92.3	85.7	6.6	64.9	66.7	-1.8
21	80.0	80.0	0.0	77.4	82.8	-5.3	92.3	82.8	9.5	70.6	75.0	-4.4	70.6	72.7	-2.1	82.8	88.9	-6.1	75.0	92.3	-17.3	75.0	68.6	6.4
22	75.0	77.4	-2.4	77.4	88.9	-11.5	85.7	70.6	15.1	66.7	72.7	-6.1	70.6	77.4	-6.8	77.4	80.0	-2.6	72.7	80.0	-7.3	70.6	54.5	16.0

Table B.11 cont. Chapter 6, Experiment 6.1. Mean accuracy in % for all stimuli classes tested in the matching-to-sample task for all sessions.

Session Nr.	Hugo												Walt											
	Fish			House interior			Crow profile			Human face			Fish			House interior			Crow profile			Human face		
	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}	up	inv.	D _{U-I}
23	96.0	88.9	7.1	92.3	82.8	9.5	72.7	72.7	0.0	82.8	68.6	14.2	82.8	75.0	7.8	96.0	88.9	7.1	80.0	82.8	-2.8	70.6	61.5	9.0
24	64.9	72.7	-7.9	96.0	75.0	21.0	75.0	60.0	15.0	60.0	68.6	-8.6	85.7	82.8	3.0	85.7	77.4	8.3	92.3	88.9	3.4	75.0	80.0	-5.0
25	85.7	80.0	5.7	77.4	80.0	-2.6	77.4	77.4	0.0	64.9	72.7	-7.9	66.7	64.9	1.8	82.8	80.0	2.8	75.0	80.0	-5.0	77.4	72.7	4.7
26	85.7	72.7	13.0	100.0	85.7	14.3	77.4	80.0	-2.6	82.8	66.7	16.1	80.0	85.7	-5.7	77.4	80.0	-2.6	80.0	82.8	-2.8	66.7	72.7	-6.1
27	92.3	82.8	9.5	88.9	77.4	11.5	96.0	96.0	0.0	63.2	68.6	-5.4	92.3	80.0	12.3	96.0	80.0	16.0	72.7	80.0	-7.3	82.8	68.6	14.2
28	100.0	88.9	11.1	88.9	77.4	11.5	100.0	96.0	4.0	77.4	68.6	8.8	72.7	82.8	-10.0	82.8	82.8	0.0	82.8	85.7	-3.0	63.2	58.5	4.6
29	88.9	92.3	-3.4	92.3	75.0	17.3	96.0	85.7	10.3	96.0	66.7	29.3	80.0	72.7	7.3	92.3	82.8	9.5	85.7	72.7	13.0	82.8	75.0	7.8
30	96.0	75.0	21.0	96.0	88.9	7.1	88.9	85.7	3.2	72.7	80.0	-7.3	77.4	77.4	0.0	85.7	72.7	13.0	77.4	70.6	6.8	61.5	64.9	-3.3
31	96.0	82.8	13.2	96.0	82.8	13.2	92.3	88.9	3.4	88.9	70.6	18.3	82.8	82.8	0.0	75.0	82.8	-7.8	80.0	85.7	-5.7	68.6	75.0	-6.4
32	85.7	100.0	-14.3	92.3	85.7	6.6	100.0	88.9	11.1	66.7	77.4	-10.8	82.8	77.4	5.3	75.0	77.4	-2.4	82.8	85.7	-3.0	63.2	52.2	11.0
33	88.9	77.4	11.5	92.3	80.0	12.3	80.0	96.0	-16.0	70.6	66.7	3.9	96.0	96.0	0.0	72.7	85.7	-13.0	75.0	80.0	-5.0	82.8	80.0	2.8
34	88.9	96.0	-7.1	85.7	92.3	-6.6	96.0	88.9	7.1	75.0	64.9	10.1	88.9	88.9	0.0	92.3	82.8	9.5	100.0	75.0	25.0	80.0	68.6	11.4
35	88.9	77.4	11.5	82.8	80.0	2.8	92.3	82.8	9.5	70.6	58.5	12.1	82.8	70.6	12.2	92.3	80.0	12.3	75.0	64.9	10.1	68.6	77.4	-8.8
36	85.7	82.8	3.0	92.3	88.9	3.4	96.0	92.3	3.7	85.7	75.0	10.7	77.4	85.7	-8.3	85.7	85.7	0.0	68.6	85.7	-17.1	77.4	63.2	14.3
37	92.3	82.8	9.5	96.0	82.8	13.2	82.8	85.7	-3.0	80.0	82.8	-2.8	80.0	82.8	-2.8	92.3	80.0	12.3	85.7	75.0	10.7	82.8	75.0	7.8
38	96.0	85.7	10.3	92.3	77.4	14.9	92.3	88.9	3.4	85.7	80.0	5.7	-	-	-	-	-	-	-	-	-	-	-	-
39	92.3	85.7	6.6	100.0	88.9	11.1	85.7	100.0	-14.3	82.8	61.5	21.2	-	-	-	-	-	-	-	-	-	-	-	-

Table B.12. Chapter 6, Experiment 6.2. Mean accuracy for each stimuli class for all participants tested.

Participant	Fish			House interior			Crow profile			Human face		
	upright	inverted	D _{U-I}	upright	inverted	D _{U-I}	upright	inverted	D _{U-I}	upright	inverted	D _{U-I}
1	100.0	87.5	12.5	100.0	95.8	4.2	79.2	83.3	-4.2	83.3	91.7	-8.3
2	95.8	100.0	-4.2	95.8	100.0	-4.2	66.7	75.0	-8.3	95.8	91.7	4.2
3	91.7	75.0	16.7	91.7	95.8	-4.2	70.8	33.3	37.5	87.5	79.2	8.3
4	87.5	62.5	25.0	100.0	100.0	0.0	54.2	66.7	-12.5	87.5	79.2	8.3
5	95.8	83.3	12.5	83.3	75.0	8.3	62.5	79.2	-16.7	87.5	50.0	37.5
6	95.8	95.8	0.0	100.0	83.3	16.7	75.0	75.0	0.0	91.7	58.3	33.3
7	91.7	100.0	-8.3	91.7	100.0	-8.3	58.3	62.5	-4.2	100.0	83.3	16.7
8	95.8	91.7	4.2	87.5	87.5	0.0	79.2	54.2	25.0	83.3	58.3	25.0
9	95.8	83.3	12.5	91.7	70.8	20.8	50.0	79.2	-29.2	79.2	37.5	41.7
10	83.3	87.5	-4.2	87.5	87.5	0.0	75.0	37.5	37.5	58.3	45.8	12.5
11	95.8	95.8	0.0	95.8	100.0	-4.2	91.7	79.2	12.5	91.7	91.7	0.0
12	95.8	87.5	8.3	100.0	87.5	12.5	79.2	75.0	4.2	87.5	79.2	8.3
13	91.7	91.7	0.0	87.5	100.0	-12.5	83.3	29.2	54.2	95.8	79.2	16.7
14	100.0	87.5	12.5	95.8	91.7	4.2	95.8	91.7	4.2	95.8	95.8	0.0
15	95.8	91.7	4.2	100.0	100.0	0.0	87.5	50.0	37.5	100.0	87.5	12.5
16	95.8	91.7	4.2	95.8	100.0	-4.2	83.3	91.7	-8.3	91.7	58.3	33.3
17	70.8	95.8	-25.0	91.7	100.0	-8.3	83.3	95.8	-12.5	91.7	83.3	8.3
18	100.0	91.7	8.3	91.7	95.8	-4.2	87.5	70.8	16.7	91.7	62.5	29.2
19	91.7	95.8	-4.2	91.7	95.8	-4.2	95.8	91.7	4.2	91.7	95.8	-4.2
20	87.5	91.7	-4.2	100.0	95.8	4.2	91.7	83.3	8.3	79.2	87.5	-8.3

Appendix C

Supplementary Data analysis

Chapter 4, Experiment 4.2

Analysis

A Bayes Factor (BF) with a Bayesian one sample t -test (test value $> .5$) was calculated using JASP Version 0.7.5.5 (JASP Team, 2016), with the default prior. The BF is the factor by which prior beliefs about a hypothesis were updated by the data. Importantly, the BF is a relative measure of evidence: it pits the predictions of two models against each other and thereby quantifies the relative strength of evidence for one hypothesis compared to a second, rivaling hypothesis (Dienes, 2011, 2014). For a BF above 1, the higher the BF , the more evidence supports the hypothesis in the nominator, compared to the hypothesis in the denominator, usually the alternative hypothesis, and the reverse is true for a BF below 1. As a rule of thumb, BF s above 3 are regarded to provide substantial evidence in favour of the alternative hypothesis (Jeffreys, 1961). Values lower than 0.33 instead favour the null hypothesis. Here, a default prior was used, reflecting the lack of knowledge about biological motion perception in scrub-jays: a Cauchy distribution on effect size that is centred around zero with a scale parameter of $r = .707$.

Results

The Bayesian one sample t -test, with the null hypothesis being that the birds would look 50% at the biological motion, and an alternative hypothesis being that the birds spend more time looking at the biological motion than would be expected by chance (Test value $> .5$), yielded a BF_{10} of 0.314 (error % = $0.3840 e^{-7}$). Hence, I found positive evidence to support the null-hypothesis, that is, that the birds did not look more than 50% of the time at the biological motion. Thus, the data suggest that the scrub-jays did not prefer looking at a biological motion pattern depicting a conspecific over a random motion pattern (see Figure 4.5). Similarly to Experiment 2a, in Experiment 2b the Bayesian one sample t -test, with the alternative hypothesis that the birds would look more than 50% of the time at the biological motion (Test value $< .5$), yielded a BF_{10} of 0.306 (error % = $5.755e^{-7}$). This again supported

the null hypothesis, namely that scrub-jays showed no preference for biological motion pattern.

Using wider priors, which assign a higher probability to an effect size bigger than zero, increased the relative evidence for the null hypothesis (i.e., there is no difference in looking time). Thus, the choice of prior did not influence the conclusions that birds did not spend more time looking at the biological motion than the random motion pattern.