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Author contributions

Chapter 1: Introduction

I wrote the introduction

Chapter 2: Is caching the key to exclusion in corvids? The case of carrion crows (*Corvus corone corone*)

I designed this study with input from my co-authors. I collected and analysed the data and wrote the paper. The co-authors were involved in editing the paper.

Chapter 3: The influence of local enhancement on choice performances in African grey parrots (*Psittacus erithacus*) and jackdaws (*Corvus monedula*)

I designed this study with input from my co-authors. I collected and analysed the data and wrote the paper. The co-authors were involved in editing the paper.

Chapter 4: African grey parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food

I designed this study with input from my co-authors. I collected and analysed the data and wrote the paper. The co-authors were involved in editing the paper.

Chapter 5: Transitive inference in jackdaws (*Corvus monedula*)

I designed this study with input from my co-authors. I collected and analysed the data and wrote the paper. The co-authors were involved in editing the paper.

Chapter 6: Conclusion

I wrote the conclusion

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Summary

While the study of cognitive skills within the physical and social domains in primates is well established, much less is known about these abilities in birds. Recent studies on corvids and parrots discovered that they possess similar cognitive skills as primates. Based on this, it was the aim of my dissertation to contribute to a better understanding of the cognitive abilities of corvids and parrots.

Within the physical domain studies of animal cognition have focused on exclusion abilities. I tested carrion crows (*Corvus corone corone*) in a choice by exclusion experiment, in which a reward was hidden underneath one of two cups and the birds were only provided with visual information about the empty cup. One individual was able to choose correctly, while others showed local enhancement effects for the lifted but empty cup. A follow-up experiment controlling for the movement of the cups enabled more birds to exclude the wrong possibility.

Based on these findings I tested carrion crows, African grey parrots (*Psittacus erithacus*), and jackdaws (*Corvus monedula*) in a modified version of the cup lifting experiment, in which two rewards were used and always the full information about the food location was provided to the birds. All three species showed a strong local enhancement effect by preferring the only or last manipulated cup, irrespective of whether it was baited or not.

Additionally, I tested African grey parrots in an inference by exclusion task, in which the correct cup could only be inferred but not chosen by excluding an empty one. One individual was able to infer the food underneath the correct cup and is therefore the first bird in which this ability has been demonstrated.

Finally, I tested jackdaws in a transitive inference task on a computer touch screen. After having been trained to a hierarchically ordered sequence of five differently coloured squares, the birds were presented with an unknown pair of two non-adjacent colours. The

jackdaws were able to infer the relationship according to the previously learnt hierarchical order.

In summary, all three test species showed remarkable cognitive skills that are comparable to that of primates. However, there was no clear pattern with regard to different cognitive abilities of corvids and parrots, rather large individual differences appeared within each species.

Zusammenfassung

Während die kognitiven Fähigkeiten von Primaten sowohl im technischen als auch im sozialen Bereich bereits gut erforscht sind, ist noch relativ wenig über die Fähigkeiten von Vögeln bekannt. In letzter Zeit gab es einige Studien die zeigten, dass Vögel ähnliche kognitive Fähigkeiten wie Primaten besitzen. Aufgrund dessen, war es Ziel meiner Dissertation zum besseren Verständnis der kognitiven Fähigkeiten vor allem von Krähenvögeln und Papageien beizutragen.

Im Bereich der technischen Kognition steht oftmals die Fähigkeit Entscheidungen durch Ausschluss zu treffen, im Fokus von Untersuchungen. Ich testete Rabenkrähen (*Corvus corone corone*) in einem solchen Experiment, in dem eine Belohnung unter einem von zwei Bechern versteckt war und die Vögel nur visuelle Informationen darüber bekamen, welcher Becher leer war. Ein Individuum wählte korrekt, während andere den Effekt der lokalen Verstärkung zeigten, in dem sie den leeren, angehobenen Becher bevorzugten. In einem Folgeexperiment, in dem die Bewegung der Becher kontrolliert wurde, waren mehr Vögel im Stande die falsche Möglichkeit auszuschließen.

Basierend auf diesen Ergebnissen, testete ich Rabenkrähen, Graupapageien (*Psittacus erithacus*) und Dohlen (*Corvus monedula*) in einem modifizierten Experiment, in dem zwei Belohnungen verwendet wurden und die Vögel die volle Information über das Futterversteck bekamen. Alle drei Arten zeigten einen starken Effekt von lokaler Verstärkung, indem sie den einzigen oder zuletzt manipulierten Becher bevorzugten, unabhängig davon ob dieser Futter beeinhaltete oder nicht.

Zusätzlich testete ich Graupapageien in einem Versuch zur „Folgerung durch Ausschluss“, in dem der korrekte Becher nur durch Schlußfolgerung und nicht durch Vermeidung des leeren Bechers gewählt werden konnte. Ein Individuum war im Stande auf den korrekten Becher zu schließen und ist damit der erste Vogel, bei dem diese Fähigkeit nachgewiesen werden konnte.

Abschließend testete ich Dohlen an einem Computer mit berührungsempfindlichen Bildschirm auf die Fähigkeit hin transitive Schlussfolgerungen zu ziehen. Nachdem die Vögel eine hierarchische Folge von fünf unterschiedlich farbigen Quadraten gelernt hatten, wurden sie im Test mit zwei nicht benachbarten Farben konfrontiert. Die Dohlen waren im Stande die Beziehung gemäß der vorher gelernten Reihenfolge abzuleiten.

Zusammenfassend ist zu sagen, dass alle drei getesteten Arten bemerkenswerte kognitive Fähigkeiten zeigten ähnlich denen von Primaten. Allerdings gab es kein klares Muster im Bezug auf unterschiedliche kognitive Fähigkeiten von Krähenvögeln und Papageien, vielmehr traten interessanterweise große individuelle Unterschiede in allen Arten auf.

Chapter 1: Introduction

Animals that are fittest are those most likely to survive, reproduce, and pass on their genes (Darwin 1859). The fitness of many vertebrates is strongly influenced by their highly developed cognition and the ability to learn and adapt. Over the last decades different cognitive and learning mechanisms, relevant to the physical and social environment of an organism have been revealed (for a review see Kirkpatrick and Hall 2008).

One mechanism which builds on these learning mechanisms, and is sometimes considered the pinnacle of human intelligence, is the ability to reason. Reasoning offers high levels of flexibility but in turn creates costs due to its complexity. Therefore, the ability of animals to use reasoning and the adaptiveness of reasoning have been hotly debated (Bird and Emery 2009; Call 2004, 2006; Penn and Povinelli 2007a, b; Pepperberg 1999; Povinelli 2000; Visalberghi and Tomasello 1998). One point that appears to be certain, though, is that if any animal species were able to use reasoning, these would be amongst the most cognitively advanced families, such as primates, canids, cetaceans, corvids, or parrots. Therefore, the present dissertation aims at furthering the knowledge of the cognitive processes involved in causal reasoning of two highly cognitive bird families, corvids *Corvidae* and parrots *Psittacidae*.

First I will provide an overview of the learning mechanisms and types of reasoning used by animals in general and birds in specific. Next, an account will be given of the evidence showing physical compared to social cognition in corvids and parrots, followed by a theoretical framework of the cognitive abilities displayed by these two families. This chapter will conclude with an overview of the structure and intent of the present thesis.

Learning and reasoning

About a century ago the concept of animal intelligence was restricted to simple learning mechanisms, several of which have been identified in vertebrates. The simplest of these is usually considered to be habituation, which refers to the reduction or cessation of a reaction in response to a particular stimulus without the presence of a reward (Hinde 1970).

The effects of habituation diminish in a process called dishabituation when for an extended period of time the stimulus is no longer present (Kirkpatrick and Hall 2008).

A group of several learning mechanisms which are based on the receiving of rewards in response to certain situations or actions is referred to as associative learning. One such mechanism is classical conditioning which was first described by Pavlov (1903, 1927). Classical conditioning refers to learning based on the formation of associative connections between an innately positive stimulus and a neutral stimulus. When the neutral stimulus becomes associated with the positive stimulus by repeated simultaneous presentation, the reaction towards the neutral stimulus changes to match the reaction that was previously only shown towards the positive stimulus. Thus an association is formed between a stimulus and the receiving of a reward.

Another form of conditioning called operant or instrumental conditioning (Thorndike 1911) refers to the formation of associations between an action oneself performs and a reward, rather than between a stimulus and a reward. Here the timely presentation of a reward or punishment following an action leads to learning of positive or negative association respectively. Operant conditioning is often tested in a conditioning chamber or Skinner box (Skinner 1938) which automatically presents rewards following an action such as a lever press or peck on a pecking key or touchscreen.

If operant conditioning takes place outside a structured environment so that the solution that leads to the reward is encountered by chance, it is often referred to as trial and error learning. Here, the animal learns about the characteristics of the environment, may these be in the physical, social, or of any other domain, by coincidentally directly experiencing the effects of its own actions and classing the outcome as positive or negative. In Thorndike's (1911) classical experiment demonstrating operant conditioning, for example, he locked cats *Felis silvestris* in a puzzle-box. The cats managed to escape from the box by trial and error exploration. The positive outcome led the cats to repeat their previously discovered actions when repeatedly presented with the same situation. With time the actions leading to the escape were performed very quickly and efficiently demonstrating that the cats had learnt a solution to a problem which they had originally encountered by chance.

While these simple learning mechanisms are the basis for much of the behaviour changes we can observe in non-human animals as well as humans, later studies have shown a steadily increasing interest in more advanced cognition (Jolly 1966; McGonigle and Chalmers 1977; Premack 1976). One form of learning which is not founded on simple associative processes is said to be based on insight. Insight is defined as the solving of a novel problem without the opportunity to use trial and error learning and, thus, to solve the problem by purely internal reasoning and not by external exploration (Kirkpatrick and Hall 2008). When learning occurs based on solutions found through insight this is referred to as insightful learning (Reznikova 2007). For example, if a bird, through insight, understands that it can reach a reward by using a stick this discovery is likely to lead to the learning of the situation and with that to the immediate use of the stick in comparable future situation. In contrast, observational causal learning describes the opposite process (Meltzoff et al. 2012). Here, the observation of the causal relationships appearing in the world leads to understanding and insight. For example, if a bird observes that water in a tube is raised by falling stones it might at some point understand that it can use this principle to float up a reward which was previously unreachable.

Furthermore, insight can be considered a prerequisite for reasoning (Call 2004) which enables the animal to draw conclusions based on the available information. As such, insight is the moment of realization of an abstract principle, whereas reasoning is the mental process which uses insight. Given the many different situations in which reasoning can be applied there are several different types of reasoning. Causal reasoning, for example, explores cause and effect relationships (Emery and Clayton 2004; Visalberghi and Tomasello 1998) such as reasoning about the consequences of actions. A special form of causal reasoning is inference by exclusion which refers to the ability to deduce information about one unavailable entity from the available information of another entity (Call 2006). Similarly, analogical reasoning refers to the ability to make equivalence judgements between different sets of stimuli (Pearce 2008; Taylor et al. 2009) such as transferring the relationship of one pair of stimuli onto another pair.

Recent studies have provided evidence for the existence of both insight learning and observational causal learning by showing that learning might be a prerequisite for insight (Meltzoff et al. 2012; von Bayern et al. 2009) and that insight in turn can lead to learning (Bugnyar et al. 2007; Emery and Clayton 2001). As reasoning seems to be directly linked to insight, it appears somewhat arbitrary to draw a very clear line between the concepts of learning and reasoning and to view these as independent. The present thesis acknowledges the interconnection between the two concepts and does not attempt to present them as separate. When, hereafter, referring to reasoning, the internal logical thought process is meant and when referring to learning, a process of acquisition is meant, while always recognizing the relationship between the two processes.

Whether animals are generally able to use insight and reasoning or whether this ability is uniquely human has been hotly debated (Bird and Emery 2009; Call 2004, 2006; Penn and Povinelli 2007a, b; Pepperberg 1999; Povinelli 2000; Visalberghi and Tomasello 1998). However, before any debate about the presence or absence of insight can be initiated, it is necessary to exclude the possibility that a certain task has been affected by low-level mechanisms such as associative learning and local or stimulus enhancement. The strong effect that local enhancement can have on, for example, dogs *Canis familiaris* has been demonstrated by Erdöhegyi (2007). This study showed that low-level mechanisms can in fact be so strong that they can mask the cognitive performance that an animal might be able to show on a complex task. Therefore, the consideration of any possible low-level mechanisms is particularly important when interpreting negative results.

Nevertheless, the capability for reasoning was first suggested in Great apes (Call 2004, 2006; Premack and Premack 1994). Call (2004), for example, tested apes on a variety of cup-lifting and tin-shaking tasks. The apes were able to find the location of food based on information about a location that did not contain any food. Similarly, several studies claim that reasoning has also been shown in corvids (Bird and Emery 2009; Bugnyar 2007; Weir et al. 2002) and parrots (Pepperberg 1999, 2006a).

In all of the above studies the animals had some previous experience with the materials which were used in the task, even though these materials were never before combined and presented in the same way as they were during the task. Penn and Povinelli (2007a) claim that the separate behavioural components of this pre-experience could have been acquired through associative learning in all of the above studies. Based on this they state that the animals could have given the superficial impression of using insight by simply putting together components of information and skill that they have previously learnt by trial and error exploration. Furthermore, they claim that there is no evidence to date that shows a non-human animal using insight learning, and, on these grounds, reject the hypothesis that non-human animals are capable of operating on the basis of insight. Additionally, they state that causal reasoning is so entwined with analogical reasoning that it cannot be separated based on experimental approaches.

In support of this argument Epstein (1984) replicated a study by Köhler (1925). Köhler’s original data suggested insightful behaviour of chimpanzees *Pan troglodytes* as his subjects were able to push a box into the correct position to be able to reach a banana suspended from the ceiling. Training pigeons *Columba livia* to independently push a box and peck a banana for food and by later combining the two skills in a test, Epstein showed that what was interpreted as insight in the chimpanzees could be based on previous experience and associative learning. However, this does not necessarily mean that the chimpanzees did not use reasoning to solve the problem, but simply that it is also possible to solve the problem using methods other than reasoning. Given the available evidence, it is impossible to determine which mechanism was used by Köhler's chimpanzees.

Pre-experience with the relevant elements of this world, however, lays the grounds on which reasoning is built. Thus, carefully designed follow-up studies aimed at excluding the possibility that the pre-experience which was required for solving the tasks provided in the initial studies on animal reasoning was based on associative learning of the separate components of the tasks. Hanus and Call (2011) and Schrauf and Call (2011) lend support to the notion that reasoning is possible in non-human animals by showing that causal discriminations are achieved more easily than arbitrary ones. Both studies showed that Great apes were much more successful at identifying an opaque target container when the distinctive feature was weight rather than colour. According to Penn and Povinelli's (2007a) hypothesis that any potential insight shown in animals is based directly on previous associative learning, there should have been no difference in the speed of understanding weight discriminations compared to colour discriminations. Thus, Schrauf and Call (2011) and Hanus and Call's (2011) results suggest that the apes have an internal representation of the food and the fact that food has a certain weight. Similarly, Taylor et al. (2009) demonstrated both causal and analogical reasoning by showing that New Caledonian crows *Corvus moneduloides* were able to transfer knowledge learnt on a trap-tube task to a trap-table task. As the birds had no previous experience with any of the parts of the manipulations needed to solve the trap-table problem, the use of previous associative learning can be excluded.

To conclude, the topic of whether insight has as yet been demonstrated in animals is hotly debated. However, recent studies lend strong support to the idea that insight is indeed possible in non-human animals. Areas of cognition which are likely to benefit from the ability to reason are social and physical cognition. The next section of this chapter will introduce these concepts and explain how reasoning is helping birds in their interactions with their physical surroundings and their interactions with other members of their social group.

Reasoning in the physical and social domain

Within the broad field of comparative cognition there are different sub-domains, such as physical and social cognition. While some animals appear to be masters within one particular area, others tend to perform well on a whole range of tasks. To date it is not clear whether the performance within the separate domains is solely dependent on the immediate adaptive value for that particular species or whether a more general process is in operation. The existence of a general intelligence (g) has been suggested in a notion previously known from the human intelligence literature (Spearman 1904) and only recently adopted for an animal model (Banerjee et al. 2009; Galsworthy et al. 2002; Matzel et al. 2003; Plomin 2001; Reader et al. 2011). General intelligence defines the overall intelligence of individuals within a species across cognitive domains. Those species whose individuals have a high g-score should perform well on a whole range of cognitive tasks, including social and physical cognition tests. This should be relatively independent of the immediate ecological needs of the species.

One of these specific domains, physical cognition, refers to the knowledge of how the physical world works (Shettleworth 2010). It contains a common sense understanding of shapes, weight, movability of items, spatial locations, and so on. This type of knowledge is often referred to as ‘folk physics’ (Povinelli 2000) and was examined with physical cognition experiments testing food finding, tool use, means-end understanding, and spatial navigation abilities. When attempting to understand how the physical world works and how its parts interact with each other, the ability to reason logically is invaluable. It enables an animal to avoid lengthy trial and error learning every time a new but conceptually similar problem is encountered. In contrast, the animal would be able to jump straight to the logical solution without expending valuable energy or even risking health and safety in exploration. Therefore, it can be assumed that the ability to reason would be an advantageous and adaptive trait in the physical domain.

Furthermore, social cognition is concerned with all social interactions and relationships between individuals (Fitch et al. 2010; Shettleworth 2010). The importance of this is particularly obvious in group-living animals such as corvids or parrots. Birds that form large groups are likely to profit from social learning because it increases learning speed and efficiency, and reduces foraging risks. This means they benefit from learning based on the observation of conspecifics rather than attempting to learn everything by individual trial and error learning. Furthermore, a prerequisite for group living is an understanding about group dynamics, such as a hierarchical order of individuals.

The social intelligence hypothesis (Humphrey 1976; Jolly 1966) states that social cognition has developed as an adaptation for group living. Accordingly, social animals or those that have been social in their recent evolutionary past should be much better at using social cognition than solitary animals. However, to date there have been two studies (Fiorito and Scotto 1992; Wilkinson et al. 2010) that showed social learning in non-social species suggesting that social learning might be based on a general ability to learn rather than on an adaptation for group living. The social complexity hypothesis (Balda and Kamil 1989; de Waal and Tyack 2003) goes one step further by stating that the level of complexity within a social network should reflect the extent of the species’ cognitive abilities. There is evidence showing that species with highly complex social structures learn more efficiently and quickly than closely related species with a less complex social structure (Bond et al. 2003; Bond et al. 2010; Maclean et al. 2008). Despite the debate about its exclusivity, social learning is unquestionably a very useful and important tool for those species that do have close social bonds.

The ability to reason is likely to be of great advantage when dealing with social cognition problems. For example, animals need to understand and remember the hierarchy within their group. The ability to observe and understand the social relationships of other group members might enable an animal to infer its own position, particularly in relation to higher-ranking individuals, and to, thus avoid potentially harmful hierarchy fights. Inferences such as these are referred to as transitive inference (Bryant and Trabasso 1971).

Reasoning can be a useful tool not only in selected, artificial incidences but also in complex situations involving both manipulations of the physical world and interactions with social partners. Schmelz (2011), for example, showed that chimpanzees are able to infer that other chimpanzees know about the physical properties of their environment, in this case about food hidden under a slanted versus a flat board.

Reasoning has been proven to be a useful tool in interactions with both the physical and the social world. Accordingly, it seems like it might be a useful tool for those animals that are cognitively advanced, despite its cost and complexity. Two such bird families are corvids and parrots and the following section will elaborate on their cognitive abilities and their potential convergent evolution with Great apes.

Corvids and parrots

Some decades ago the opinion of bird intelligence was less than favourable. Their cognitive abilities were believed to be in no means comparable to those of mammals (Herrick 1924). However, nowadays this unfortunate misconception has been repeatedly and thoroughly disproven. One reason for the belief that birds were unequal to mammals might be the fact that the bird brain is structurally very different form the mammalian brain. Today, it is known that the cognitive abilities of birds are located in different brain regions than those of mammals but are qualitatively and quantitatively comparable (Emery 2006; Reiner et al. 2004).

Amongst the birds two families, corvids and parrots stand out with respect to their cognitive abilities (Emery and Clayton 2004). In fact, the abilities of the members of these two families have been shown to be very comparable, if not sometimes superior, to those of even the most cognitively advanced mammals, the Great apes (Emery 2006). The process in which these striking similarities are believed to have evolved in these distantly related species is referred to as convergent evolution. This means that comparable or equal cognitive abilities have developed in a parallel, analogue manner based on environmental demands without having a common route in a shared ancestor (Ryan 2008).

Support for the convergent evolution hypothesis and the immense cognitive abilities of birds has been found in the testing of numerous different paradigms and tasks in several different corvid species. Carrion crows *Corvus corone corone* have demonstrated impressive abilities such as refraining from immediate gratification in exchange for a later, more desired reward (Dufour et al. 2011; Wascher et al. 2012a) and distinguishing between individuals based on acoustic information (Wascher et al. 2012b). Jackdaws *Corvus monedula* have been proven to be sensitive to social information and show great capabilities in social learning (Scheid et al. 2007; Schwab et al. 2008). New Caledonian crows are known to have very strong tool use abilities (e.g. Hunt 1996; Weir et al. 2002; Weir and Kacelnik 2006) and have been shown to perform well in causal and analogical reasoning tasks (Taylor et al. 2009). Ravens *Corvus corax* have demonstrated competencies in a whole array of tasks involving social and physical cognition (Boeckle and Bugnyar 2012; Bugnyar 2011; Heinrich 1995; Schloegl et al. 2009). Bugnyar (2007) even claims to have found them capable of forming theory-of-mind-like concepts suggesting a very high level of insight.

Further striking evidence of the cognitive abilities of birds was derived from experiments testing different parrot species. Keas *Nestor notabilis*, for example, have shown great physical cognition abilities, mastering even very complex tasks innovatively using a large variety of actions such as twisting, pulling, pushing, and many more (Huber and Gajdon 2006; O'Hara et al. 2012). Furthermore, African grey parrots *Psittacus erithacus* have demonstrated extraordinary cognitive abilities in both the social and physical domain (Pepperberg 1999, 2008; Peron et al. 2011). To mention just one example, the pioneer of Grey parrot cognition research, Irene Pepperberg, showed that her famous parrot Alex has even developed numerical skills involving a zero-like concept (Pepperberg and Gordon 2005) and addition abilities (Pepperberg 2012). Alex showed the ability to form and reason about abstract representations of, for example, quantities being represented by both words and written letters (Pepperberg 2006a, b). This lends support to the hypothesis that African grey parrots are able to use reasoning.

To conclude, corvids and parrots have been shown to have very advanced cognitive skills. Several studies have even shown good indications that reasoning in animals might be possible. However, further studies are needed to extend these findings. The present thesis has aimed at making a significant contribution towards filling these gaps and extending the base of knowledge in this area. The following section will demonstrate why this is so by explaining the structure of the present dissertation and introducing the major study questions and hypotheses.

Aims and structure of this thesis

The present thesis focused on the study of reasoning in birds in general, and corvids and parrots in particular. After the present brief overview of the theoretical background of reasoning and insight, the study presented in Chapter 2 aimed at solidifying the foundation of knowledge underlying the study of reasoning in carrion crows. It, firstly, tested whether carrion crows are able to succeed in making exclusion judgements. Secondly, it explored the general effects of local enhancement and its effects on exclusion performance tasks in particular. One of the findings was that local enhancement had a striking effect on the performance of the crows.

Previous studies on ravens, jackdaws, keas and African grey parrots tested in a setup directly comparable to that described in Chapter 2 had shown different effects of local enhancement (Schloegl et al. 2009; Schloegl 2011; Schmidt et al. unpubl.). To determine the differential influence local enhancement may have on the cognitive performance of the different species, the study described in Chapter 3 extended the local enhancement test paradigm used with carrion crows in Chapter 2 to jackdaws and Grey parrots.

Chapter 4 aimed at clarifying which mechanism exactly was used by African grey parrots when attempting to solve an exclusion task. To date most studies testing exclusion performance in birds have not controlled for the possibility that the task might be solved by avoidance rather than causal reasoning. The study described in Chapter 4 was designed to avoid this shortcoming and to answer the question of whether Grey parrots are able to show inference by exclusion.

While those corvid species that cache food have been shown to be very proficient in physical cognition tasks (Schloegl et al. 2009), the jackdaw, a non-caching corvid species, has encountered difficulties in, for example, exclusion tasks (Schloegl 2011). However, as jackdaws are closely related to the other corvid species there is no reason to assume that their general cognitive abilities and reasoning skills are much lower than those found in their relatives. Jackdaws have been shown to be particularly sensitive to social information and to perform well in social learning tasks (Scheid et al. 2007; Schwab et al. 2008). Thus, the study described in Chapter 5 examined the reasoning skills of jackdaws in a task relevant for the social domain rather than the physical domain – transitive inference. As such, Chapter 5 aimed at taking the ecology of the test species into account when choosing the experimental test paradigm.

Finally, Chapter 6 presents a discussion of the main findings and conclusions drawn from the studies presented in Chapter 2 to 5, and embeds them in the theoretical framework. Implications of the current findings and future directions are discussed.

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Chapter 2: Is caching the key to exclusion in corvids?

The case of carrion crows (*Corvus corone corone*)

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Abstract

Recently, two corvid species, food-caching ravens and non-caching jackdaws, have been tested in an exclusion performance (EP) task. While the ravens chose by exclusion, the jackdaws did not. Thus, foraging behaviour may affect EP-abilities. To investigate this possibility, another food-caching corvid species, the carrion crow (*Corvus corone corone*), was tested in the same exclusion task. We hid food under one of two cups and subsequently lifted either both cups, or the baited or the un-baited cup. The crows were significantly above chance when both cups were lifted or when only the baited cup was lifted. When the empty cup was lifted, we found considerable inter-individual variation, with some birds having a significant preference for the un-baited but manipulated cup. In a follow-up task, we always provided the birds with the full information about the food location, but manipulated in which order they saw the hiding or the removal of food. Interestingly, they strongly preferred the cup which was manipulated last, even if it did not contain any food. Therefore we repeated the first experiment but controlled for the movement of the cups. In this case, more crows found the food reliably in the un-baited condition. We conclude that carrion crows are able to choose by exclusion, but local enhancement has a strong influence on their performance and may overshadow potential inferential abilities. However, these findings support the hypothesis that caching might be a key to exclusion in corvids.

Keywords

carrion crow; exclusion performance; local enhancement; two-choice task; reasoning

Introduction

Exclusion performance (EP) is defined as “selecting the correct alternative by logically excluding other potential alternatives” (Call 2006). To test for this ability, a two choice task is commonly used, in which the animal is confronted with two options, A and B. Then it is informed that one option, say B, is incorrect (i.e. un-baited). Two possible approaches can lead to the correct choice of A. Either the individual avoids the incorrect option and therefore, its choice is only based on knowledge about B (Aust et al. 2008), or it is aware that option A is correct *because* B is not, i.e. that the food is in cup A because B is empty. The latter mechanism has been labelled “inference by exclusion” (Call 2004, 2006) or “reasoning by exclusion” (Erdöhegyi et al. 2007) and is presumably cognitively more demanding than the first one.

Originally, EP has been discussed as a learning mechanism facilitating the acquisition of language in humans (Dixon 1977; Markman and Wachtel 1988) and therefore, many language-trained animals have been tested. Sea lions *Zalophus californianus* (Schustermann and Krieger 1984), bottlenose dolphins *Tursiops truncatus* (Hermann et al. 1984), dogs *Canis familiaris* (Kaminski et al. 2004; Pilley and Reid 2011) and an African grey parrot *Psittacus erithacus* (Pepperberg 2006) had been trained to associate various objects with verbal labels. When confronted with a set of familiar objects and one new object, they matched the new object with a new, unknown label. This suggests that their choice was based on the exclusion of the known objects. Interestingly, they could also memorize and learn the meaning of these new labels through exclusion (Bloom 2004; Markman and Abelev 2004; Fischer et al. 2004).

EP may not be restricted to vocal learning but may also facilitate the performance in forced discrimination tasks. For instance, in a matching-to-sample (MTS) task, animals are trained to match several objects as correct and others as incorrect. Finally, an already known incorrect object is matched with a new object, so that a correct choice of the new object would need to be based on exclusion. In such a task, chimpanzees *Pan troglodytes* (Beran and

Washburn 2002; Tomonaga 1993), sea lions (Kastak and Schustermann 2002), dogs (Aust et al. 2008) and pigeons *Columba livia* (Aust et al. 2008; Clement and Zentall 2003) were able to match a new object via exclusion; additionally pigeons also showed EP in a similar non-matching-to-sample task (Zentall et al. 1981).

In an influential study, Call (2004) devised a food-finding task to test for exclusion. This task cannot distinguish unequivocally between exclusion based on true inference about the correct option and exclusion based on avoidance of the incorrect option (Paukner et al. 2009); still, it provides an easy-to-use tool to compare various species in an ecologically more relevant context than the before-mentioned test designs. In this task, an experimenter hid a food reward in one of two boxes and then provided the subjects with different information by opening either one or both boxes. Hence, when only the content of the un-baited box was shown to the animals, they had to exclude this box and choose the opposite box to find the hidden food. The Great Apes (Call 2004) and several monkeys (capuchin monkeys *Cebus apella* (Paukner et al. 2006; Paukner et al. 2009; Sabbatini and Visalberghi 2008); Tonkean macaques *Macaca tonkeana* (Petit et al. 2005); and baboons *Papio hamadryas anubis* (Schmitt and Fischer 2009)) showed strong evidence for the ability to choose by exclusion, whereas dogs (Bräuer et al. 2006; Erdöhegyi et al. 2007) are only able to do so under very specific circumstances.

Taken together, a diverse range of species demonstrated EP in very different experiments, but it is not clear if they show EP in certain contexts only or if they can apply this ability broadly across various contexts (Schloegl et al. 2009a). The first case would be in line with the "adaptive specialisation hypothesis", which aims to explain the evolution of intelligence in general and suggests that each species evolved specific cognitive abilities in adaptation to their socio-ecology (de Kort and Clayton 2006; Kamil 1987); the second case would support the "general process view", which proposes a wider set of cognitive abilities as a consequence of the evolution of large brains (Bolhuis and Macphail 2001).

When Schloegl et al. (2009b) conducted the above mentioned food-finding task in birds, they found that ravens *Corvus corax*, but not keas, *Nestor notabilis*, were able to choose by exclusion. One might speculate that this finding represents a cognitive difference between two distantly related taxa (Hackett et al. 2008), but both groups are commonly assumed to possess advanced levels of cognitive abilities (Emery 2006). Alternatively, ecological differences may explain the differences between the two species, as ravens cache food and pilfer the caches of others (Heinrich 1989), whereas keas do not cache at all. It had been suggested that feeding ecology could affect the prevalence of EP in corvids (Schloegl et al. 2009b), as cachers are frequently confronted with pilfering, and consequently empty cache sites; thus, the sight of an empty food location may inform a cacher about the fate of food that had been present before, whereas the same may not be true for a non-caching species. This argument is supported not only by the finding that non-caching jackdaws *Corvus monedula* fail to show EP in the same test paradigm in which ravens had been successful (Schloegl 2011), but also from another, unrelated foraging task in which jackdaws used information about the absence of food differently than related, food caching jays (Gould-Beierle 2000).

Thus, the currently available data support the adaptive specialisation hypothesis to explain the prevalence of EP in corvids, but further studies on more species are clearly needed, as only one caching species has been tested so far. Carrion crows (*Corvus corone corone*) are closely related to ravens, possess a similar social organisation and do cache food, although a bit more seasonal than ravens (Goodwin 1986; dos Anjos et al. 2009). Therefore, this species is an ideal candidate for further studies and similar test set-ups to that used in ravens and jackdaws seem to be feasible. We here conducted a series of experiments to test the exclusion abilities of carrion crows. First, we replicated the previous studies of Schloegl and co-workers; this was followed by two follow-up experiments, in which we aimed to test and to control for the effect of local enhancement, as this had been shown to mask exclusion abilities in dogs (Erdöhegyi et al. 2007), We predicted that the crows would perform similar to ravens and choose by exclusion if caching may indeed be linked to EP in corvids.

Experiment 1: cup-lifting

Methods

Subjects

Seven hand-raised carrion crows (four males, three females, aged 0.5 - 20 years old), which were individually marked, participated in this study. They were housed in outdoor aviaries at the Konrad Lorenz Research Station in Grünau im Almtal, Austria. Two crows lived together as a pair in an aviary of approx. 14 m^2 with a height of 2.5 m and the other 5 lived together with 2 not tested individuals in an aviary of approx. 47 m^2 with an average height of 3 m. Both aviaries had natural vegetation like small bushes, grass and stones. Additionally, perches were affixed and naturally occurring obstacles and wooden walls provided hiding places. For testing, the crows were separated individually in one compartment of the aviary (12 and 10 m^2, respectively), which was open to all crows when not being tested. Although the test compartment was not visually isolated, none of the subjects was observed by other birds when being tested. The birds were fed once in the morning and tested in the late afternoon.

Material

A wooden platform (30 cm x 40 cm) was attached to the aviary’s outer wire mesh boundary in a height of 35 cm above ground; adjacent to it, another wooden platform (50 cm x 45 cm) was attached on the inner wire mesh boundary at the same height, on which the birds were able to sit during testing. Two identical plastic cups (6.5 cm in diameter and 7.5 cm in height) and a plastic platform (35 cm x 10 cm), which was free to move on the wooden platform, were used to present the setup (see Fig. 1). The reward was a piece of dried dog food, which is preferred by the crows but not available during normal feeding.

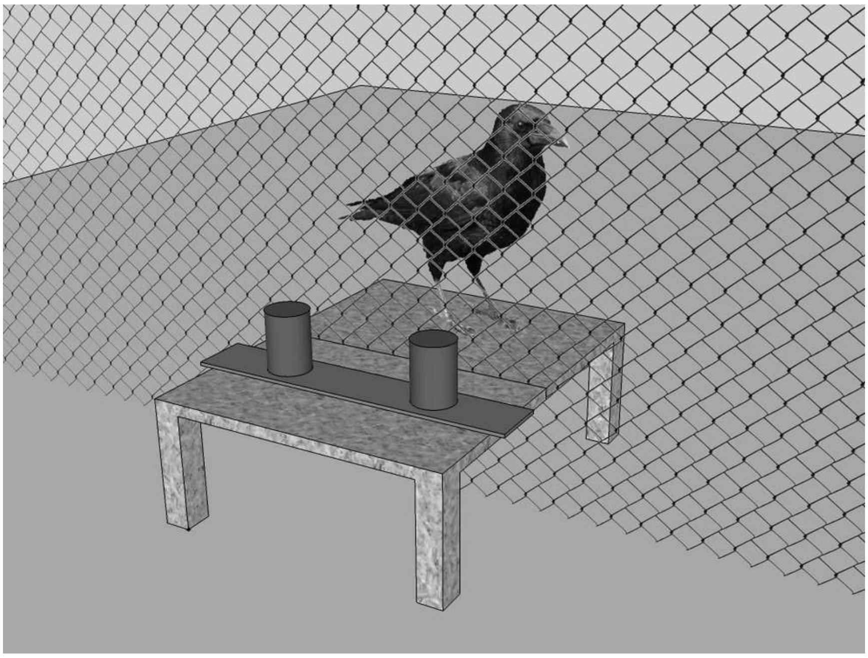

Figure 1: Basic test-set-up for all three experiments

Procedure and design

All experiments were conducted between May and September 2009. The crows were habituated to the apparatus before testing to avoid neophobic reactions during training and testing.

Prior to testing all crows received a training phase to ensure that they reliably choose the baited cup when having seen were the reward was hidden. Here, the plastic platform was positioned on the outer wooden platform, approx. 10 cm away from the wire mesh. The experimenter (E; S.M.) visibly placed a reward on it and then simultaneously positioned the two cups on the platform in approx. 20 cm distance from each other, with one cup covering the reward. The plastic platform was pushed to the wire mesh to allow the crow to make a choice by touching a cup with its beak. The chosen cup was lifted by E and the crow was allowed to take the reward by itself or to see the empty cup. The position of the reward (left / right) was semi-randomized, with the food on the same side for not more than two consecutive trials. The next trial started after 10-20 seconds when E had prepared the cups again. The crows received daily sessions consisting of ten trials each. They had to choose the baited cup in at least eight out of ten trials in two consecutive sessions to advance to the test phase.

In the test phase, the reward was hidden underneath one of the two cups below the wooden platform and out of view of the birds. The food was positioned randomly on the left or on the right, with the exception that it was not placed on the same side in more than two consecutive trials. The plastic platform with the two cups was then placed on the wooden platform in view but out of reach of the birds, approx. 10 cm away from the wire mesh. Then, one of the following conditions was conducted:

Both E touched both cups with her hands simultaneously, lifted them to a height of approx. 20 cm above the platform and then returned the cups to the starting position.

Baited E touched both cups but lifted the baited cup only so that the food could be seen on the platform. During the presentation, E continued to touch the un-baited cup.

Un-baited As before, but now the empty cup was lifted.

Control No cup was lifted but both cups were touched by E.

Each cue lasted for 5 seconds and E looked straight ahead throughout the trial to avoid unintentional cueing. Then, E pushed forward the plastic platform towards the wire mesh to allow the crow to make a choice; if it chose correctly, it received the reward; if it chose incorrectly, the empty cup was lifted. Following this procedure, E removed the plastic platform and the two cups from the wooden board without lifting the non-chosen cup, and the next trial began. The crows received 12 sessions, with 8 trials per session, consisting of two trials of each condition in randomized order.

Data analysis

All sessions were videotaped and later analysed from tape. Per trial, we measured whether the bird chose the baited or the un-baited cup. As the choice of a cup was unambiguous in any case, we did not calculate an inter-observer reliability. If the data were not normally distributed, we applied non-parametric statistics. We tested for differences in percentage of correct choices between the conditions using a Friedman test. For post-hoc analysis we used the Student-Newman-Keuls (SNK) method. The performance in the first half and in the second half of the experiment was compared using paired t-tests or Wilcoxon tests, as appropriate. To assess if the birds' success rates differed from chance we used a Binomial test. All tests were conducted two-tailed and alpha was set to 0.05. Data analysis was conducted using Sigma Plot 11.0 and SPSS 11.5 for Windows.

Results

The crows received 40.0 ± 19.3 ($\bar{x} \pm SD$; range: 20 - 65) training-trials until they reached the criterion. In the test phase, the birds' performance differed between the conditions (Friedman: N = 7, $\chi^2 = 17.294$, df = 3, $P < 0.001$). Post-hoc analyses revealed no significant difference between the both and the baited condition (SNK: both vs. baited: $P > 0.05$; Fig. 2), but the birds were significantly better in these two conditions than in the control and in the un-baited condition (SNK: all comparisons: $P < 0.05$; Fig. 2). In contrast, the control condition and the un-baited condition did not differ significantly from each other (SNK: un-baited vs. control: $P > 0.05$; Fig. 2). There was no significant improvement or decline over the course of the experiment in any condition (both: Wilcoxon: N = 7, $T^+ = 3.0$, P = 1.0; all other comparisons: paired t-test: $P \geq 0.172$).

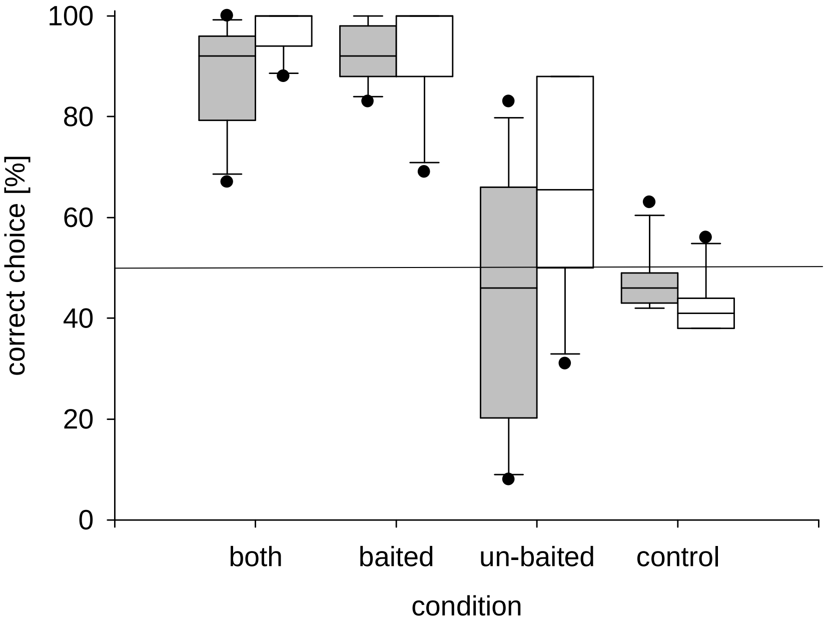

Figure 2: Percentage of correct choices in experiment 1 and 3. The grey bars show the performance of the crows in experiment 1 and the white bars show their performance in experiment 3. The horizontal line indicates the chance level. The box plot shows the median and quartile. The whiskers represent 10% and 90% range, dots indicate 5% and 95% range.

On an individual level, all birds selected the baited cup on the majority of the trials in the baited and in the both condition, with six of seven birds being significant in the both condition (Binomial-test: for these six birds, all $P < 0.023$, the seventh bird, $P = 0.152$); all birds significantly preferred the baited cup in the baited condition (Binomial-test: all $P < 0.002$). In the un-baited condition, one bird significantly preferred the baited cup (Binomial-test: $P = 0.002$), whereas two crows had a significant preference for the un-baited cup (Binomial-test: both birds: $P < 0.001$). The other four birds were on chance level (Binomial-test: all $P > 0.152$). In the control condition, all birds were on chance level (Binomial-test: all $P > 0.307$; Tab.1).

Table 1: Individual performances of the crows in experiment 1 and 3, given in percentage correct choices. Significant performances (according to a Binomial-test) are highlighted in bold.

individual	both		baited		un-baited		control	
	Exp. 1	Exp. 3	Exp. 1	Exp. 3	Exp. 1	Exp. 3	Exp. 1	Exp. 3
Baerchen	**95.8**	**100.0**	**91.7**	**100.0**	**83.3**	**87.5**	62.5	56.3
Peter	66.7	**100.0**	**91.7**	**87.5**	62.5	50.0	45.8	37.5
Hugo	**91.7**	**93.8**	**87.5**	**100.0**	45.8	31.3	45.8	43.8
Gabi	**75.0**	**87.5**	**83.3**	68.8	41.7	56.3	50.0	37.5
Klaus	**100.0**	**100.0**	**100.0**	**100.0**	**12.5**	75.0	45.8	37.5
Toeffel	**95.8**	**100.0**	**100.0**	**100.0**	**8.3**	**87.5**	41.7	43.8
Mate	**91.7**	**-**	**87.5**	**-**	66.7	**-**	41.7	-

Discussion

When the birds saw the food underneath one of the cups in the both and in the baited condition, nearly all of them performed above chance level. When only the un-baited cup was lifted, however, only one bird chose the baited cup significantly above chance. Thus, against our predictions the crows performed worse than the ravens. While four birds performed at chance in the un-baited condition, the two remaining birds had a significant preference for the manipulated, but un-baited cup. However, we found no improvement or decline over the course of the experiment. A similar preference for the lifted, but un-baited cup was found in dogs (Erdöhegyi et al. 2007). Apparently, local enhancement through the movement of a cup was a more salient cue for the dogs than the sight of the empty cup. The influence of human social cues or local enhancement on animals' performances in choice tasks is well known. Apart from dogs, gorillas *Gorilla gorilla* (Peignot and Anderson 1999), chimpanzees (Itakura et al. 1999), wolves *Canis lupus* (Viranyi et al. 2008), horses *Equus caballus* (Krueger et al. 2011) and goats *Capra hircus* (Kaminski et al. 2005) and at least two bird species, ravens

(Schloegl et al. 2008a) and Clark's nutcrackers *Nucifraga columbiana* (Tornick et al. 2010), use touch cues or local enhancement to find hidden food in object-choice tasks.

The question arising is whether the susceptibility to enhancement in our experiment is a result of the complexity of the EP task and the presumed advanced cognitive abilities required to solve it, or whether enhancement in general has such an impact on carrion crows. To answer this question, we ran a second experiment in which a reward was placed visibly under both cups and then different manipulations were performed in full view of the birds. Here, the reward was shown to them again and then either lay back under the cup or taken away. Additionally, a combination of both manipulations was performed with one of the rewards shown to the bird and the other reward taken away, or vice versa. We predict that under these circumstances, in which always the full information about the food location is provided, the birds would be less distracted by local enhancement and would be able to choose the baited cup in all conditions.

Experiment 2: object manipulation

Methods

Subjects

The seven birds from experiment 1 participated in this test.

Material

The same setup as in experiment 1 was used.

Procedure

This test was conducted in direct succession of the first experiment and without further training trials. Now, two rewards were placed on the board visibly and were then covered with the cups. Thus, both cups were now baited. Then, one of the following manipulations was performed in full view of the birds:

Show (S) With one hand E lifted one of the cups to a height of approx. 20 cm and with the other hand she took the reward between her fingertips and clearly showed it to the bird. After this, she laid the reward back on the same position as before and covered it with the cup.

Take (T) As above, with the exception that the reward was taken away and put in E’s pocket after having been shown to the bird.

Show & Take (ST) Now, both cups were lifted sequentially. The reward underneath the first cup was shown to the bird (identical to “Show” manipulation), and the reward underneath the second cup was lifted and put in E’s pocket (identical to “Take” manipulation).

Take & Show (TS) As above, but the two manipulations were conducted in reversed order.

Each manipulation was performed slowly (approx. 5 sec) and E assured that the bird watched the whole time. Then, the plastic platform was pushed forward and the bird was allowed to make a choice. After the bird had made its choice, the plastic platform and the cups remained on the board and a possibly remaining reward was removed in full view of the bird. The crows received nine sessions, with eight trials per session, consisting of two trials of each condition in randomized order. The cup (left or right) and the order of manipulations (left or right first) were randomly manipulated.

Note that in the condition S, both cups were baited, but we were interested in how often the birds would choose the cup that had been manipulated. Therefore, in the S condition we scored whether the birds chose the manipulated cup, whereas in the other conditions we scored if they chose the baited cup.

Data analysis

The birds' choice was defined in the same way as in the first experiment. As the data were normally distributed, we used a one-way repeated measures ANOVA to test for differences between conditions. For post-hoc analysis we used the Student-Newman-Keuls (SNK) method. To look for preferences for the manipulation of the cups we used a paired t-test.

Results

The performance of the birds differed between conditions (one-way repeated measures ANOVA: $F_{6, 27} = 8.379$, $P = 0.001$, Fig.3a). In condition S, where the food was shown again, the birds most frequently chose the manipulated cup, even though both cups contained food. In condition T the birds again preferentially chose the manipulated cup, even though it did not contain food. Consequently, they obtained food significantly more often in condition S than in condition T (SNK: $P < 0.05$). Similarly, they preferred the cup that was manipulated last when two manipulations were performed, even when they had seen the food being removed from underneath the second cup. This resulted in the birds choosing the baited cup significantly more often in the TS condition than in the ST condition (SNK: $P < 0.05$). Consequently, as the last manipulation appeared to be crucial, no significant difference was found between condition S and TS (SNK: $P > 0.05$) and between T and ST (SNK: $P > 0.05$). Furthermore, the birds' performance was significantly better in the S condition than in the ST condition (SNK: $P < 0.05$) and significantly worse in the T than in the TS condition (SNK: $P < 0.05$).

When combining the data of all four conditions, the crows chose the last (or only) handled cup significantly more often than the first (or untouched) cup (paired t-test: $N = 7$, $t = 3.395$, $df = 6$, $P = 0.015$, Fig.3b).

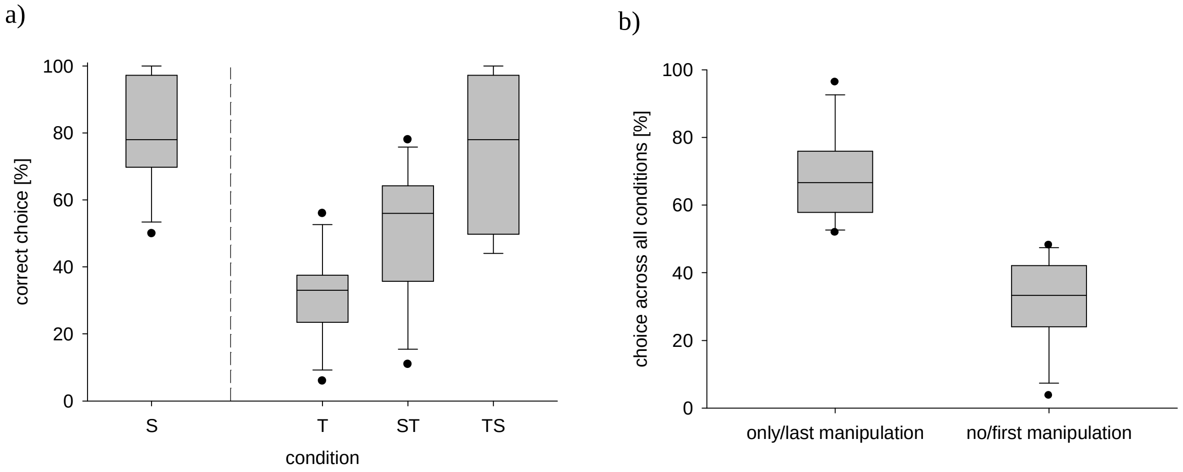

Figure 3: Preference for the manipulated cup in experiment 2. a) Percentage of correct choices in the four conditions of experiment 2. In the S condition we plotted the choice of the manipulated cup (note that the choice of both cups would have been correct), whereas in the other conditions we plotted the choice of the baited cup. b) Percentage of choices of the only or last manipulated cup and for the not or the first manipulated cup across all four conditions. The box plots show the median and quartile. The whiskers represent 10% and 90% range, dots indicate 5% and 95% range.

Discussion

In contrast to our predictions, the birds did not choose the baited cup reliably in all conditions. They were highly affected by the manipulation through the experimenter, and preferred the last (or only) handled cup even if the food had been removed from there. This preference for the ultimate object manipulated in a sequence of manipulations is known as recency effect (Pineno and Miller 2005) and has been found, among others, in monkeys (Wright et al. 1985), pigeons (Wright et al. 1985) as well as humans (Knoedler 1999). Although experiment 2 was easier to solve than the previous experiment, as the location of the food was never concealed, the impulse to choose the last manipulated cup was stronger than the knowledge about the food location itself. Interestingly, all individuals were equally affected and not only those two individuals who had shown a strong effect of local enhancement in experiment 1.

Since enhancement had such a strong effect in experiment 2, we suggest that enhancement cues may have prevented the birds from choosing by exclusion in the first experiment, i.e. in experiment 1 the birds may have experienced a conflict between making a choice according to the observed action (enhancement) or the observed absence of the food (exclusion); such a masking effect has been described previously for dogs in a very similar experiment (Erdöhegyi et al. 2007). These authors tried to control for the movement of the cups in a follow-up experiment, in which they positioned a smaller, opaque cup covering the food underneath one of the cups. Thereby, both external cups could be lifted while the food remained hidden. In this case, the dogs chose the correct cup when they had the choice between nothing (underneath the empty cup) and the internal cup (with the food underneath). However, this setup does not exclude that the dogs may have chosen the cup itself (i.e., as a toy) rather than because it contained the food. Also jackdaws showed a strong susceptibility to local enhancement in a similar setup; to control for a possible preference for the cup (as in the study on dogs), here two internal cups (one transparent, one opaque) were used (Schloegl 2011). Therefore in our next experiment, we replicated this experiment to control for the movement of the cups. In detail, two additional smaller cups, transparent and opaque, were used underneath the normal cups. Then, always both external cups were lifted and the amount of information available in each condition was constructed through the combination (opaque or transparent) of the smaller cups. We predicted that the crows should base their choice on exclusion, if their failure in experiment 1 had indeed been due to a masking effect.

Experiment 3: cup-lifting with inner cups

Methods

Subjects

Six out of seven birds from experiment 1 and 2 participated in this task. One bird, Mate, refused to complete this task and was therefore excluded from the analyses.

Material

The birds were tested in the same test compartment and with the same test platform as in experiment 1 and 2. In addition to the two cups from experiment 1 (external cups), four smaller plastic cups (4 cm in diameter and 4 cm in height), two of them laminated with dark tape to make them opaque, were used in this test.

Procedure

The third experiment was conducted in direct succession of experiment 2 again without any further training trials. The procedure was the same as in the first experiment with the exception that under the external cups always two smaller cups were placed and that both external cups were lifted (and returned to the board) in each condition. The information about the food location was given to the bird through the combination of the smaller cups used in each condition. According to experiment 1, conditions were performed as follows:

Both Two small transparent cups were used with a reward placed under one of them.

Baited A small transparent and a small opaque cup were used, with a reward placed under the transparent cup.

Un-baited As before, but with the exception that the reward was hidden underneath the small opaque cup.

Control Two small opaque cups were used with a reward hidden underneath one of them.

The crows received eight sessions with eight trials per session, consisting of two trials of each condition in randomized order; we reduced the number of trials per condition because we were interested in a spontaneous change in choice behaviour.

Data analysis

The birds' choice was defined in the same way as in the previous experiments. To test for differences between conditions we used a one-way repeated measures ANOVA. For post-hoc analysis we used the Student-Newman-Keuls (SNK) method. To compare the performances in experiments 1 and 3, we used a two-way repeated measures ANOVA (excluding the subject that participated in experiment 1 only) and Holm-Sidak tests (HS) for post-hoc analyses.

Results

The performance differed between the conditions (one-way repeated measures ANOVA: $F_{5,23} = 28.529$; $P < 0.001$). Post-hoc analyses showed that as in experiment 1, the birds chose the baited cup significantly more often in the both and in the baited condition than in the control condition. (SNK: both vs. control: $P < 0.05$; baited vs. control: $P < 0.05$). Importantly and in contrast to experiment 1, the birds also selected the correct cup significantly more often in the un-baited condition than in the control condition (SNK: un-baited vs. control: $P < 0.05$; Fig. 2). We found no significant difference between the both and the baited condition (SNK: both vs. baited: $P > 0.05$), but the birds were more successful in the baited and in the both condition than in the un-baited condition (SNK: both vs. un-baited: $P < 0.05$; baited vs. un-baited: $P < 0.05$). Overall, there was no change detectable in the birds' performance over the course of the experiment in any condition (comparison of first and second half of the experiment: both and baited-condition: Wilcoxon: $P = 0.371$; un-baited and control: paired t-test: $P \geq 0.638$).

On an individual level all crows had a significant preference for the baited cup in the both condition (Binomial-test: $P < 0.004$) and five out of six birds had this preference also in the baited condition (Binomial-test: for these five birds, all $P < 0.004$, the sixth bird, $P = 0.210$). The crow with a significant preference for the baited cup in the un-baited condition in experiment 1 kept its preference in experiment 3 (Binomial-test: $P = 0.004$). Those two crows with a significant preference for the un-baited cup in the un-baited condition of experiment 1 now switched to a preference for the baited cup (Binomial-test: $P = 0.004$ and $P = 0.077$, respectively), whereas those crows that where on chance level in experiment 1 continued to do so in experiment 3 (Binomial-test: $P > 0.210$). All crows performed on chance level in the control condition (Binomial-test: all: $P > 0.454$; Tab.1).

To compare the performance of the birds between experiment 1 and 3, a two-way repeated measures ANOVA was conducted. A significant difference between the conditions ($F_{5,47} = 45.447$; $P < 0.001$), but neither between experiment 1 and 3 ($F_{5,47} = 3.154$, $P = 0.136$) nor an interaction of both factors ($F_{5,47} = 1.747$, $P = 0.200$) could be found. Post-hoc analyses (Holm-Sidak tests) revealed similar results as found in experiment 1, with no significant difference between the both and the baited condition (HS: both vs. baited: $P = 0.950$; Fig. 2), but these two conditions differed significantly from the control and the un-baited condition (HS: both vs. control: $P < 0.001$; both vs. un-baited: $P < 0.001$; baited vs. control: $P < 0.001$; baited vs. un-baited: $P < 0.001$; Fig. 2). In contrast, the control condition and the un-baited condition did not differ significantly (HS: un-baited vs. control: $P > 0.163$; Fig. 2).

Discussion

In this third experiment, the birds again performed at a high level in the both and in the baited condition. Although we found no significant difference between experiment 1 and 3, the birds’ performance in the un-baited condition increased. This is mostly due to the improvement of those two birds that had been influenced the most by local enhancement in the first experiment. Now, these two birds chose the baited cup when the food was hidden underneath the opaque cup and only the empty transparent cup was visible. Additionally, we could show that the improvement in the un-baited condition was most likely not influenced by learning, as we could not find a change between the first and the second half of the experiment. Though, it seems as if local enhancement had overshadowed the crows’ ability to choose by exclusion in experiment 1. In comparison to the ravens, the carrion crows showed a similar ability to choose by exclusion, but seemed to be more sensitive to local enhancement.

General discussion

We here show that similar to ravens, jackdaws and keas, also carrion crows easily find hidden food in a two-choice task if they had seen it before they made their choice (Schloegl et al. 2009b; Schloegl 2011). When only the information about the empty cup was provided and subjects would have to choose by exclusion, only one bird went for the baited cup spontaneously. This is in contrast to our findings in ravens (Schloegl et al. 2009b), and in contrast to our predictions. However, two other birds showed a preference for the lifted, un-baited cup; when we controlled for the movement of the cups in experiment 3 they reversed their preference and chose the correct, baited cup. This allowed the birds as a group to be successful in the un-baited condition of experiment 3. Such a reversal was not found in a previous study in jackdaws (Schloegl 2011); this indicates that jackdaws and carrion crows were both distracted by the manipulations, but that exclusion abilities were masked in crows only. While absence of evidence should not be mistaken for evidence of absence, it is nevertheless striking that the jackdaws did not solve the identical tasks that ravens and crows mastered. At the very least this suggests that jackdaws – if capable of exclusion – rely less on this ability than the other two, closely related, species.

Surprisingly, the strong enhancement effect was even more pronounced in experiment 2, in which most birds were unable to inhibit their impulse to choose the cup handled last or only, even if they had seen that nothing was underneath. This strong effect of the manipulation of the cups in experiment 2 is most likely to be explained by local enhancement or an associative strategy: instead of associating a cup with the presence or the absence of food, they may have associated the number of presentations of food with a cup. For instance, in the T condition, the food was seen once underneath the correct cup, whereas it was seen twice (at first presentation and at removal) at the incorrect cup (Russell and Thompson 2003). However, while this may explain the performance in the S and the T condition, it fails to explain the performance in the ST and TS conditions.

Interestingly, the ravens’ susceptibility to the manipulation of the cups was less strong than that of the crows (Schloegl et al. 2009b), which may be due to their prior experimental experience. For the crows, the experiments described here were the first in which they were directly tested by an experimenter in a two-choice task. In contrast, the ravens have participated in a number of such choice tasks (Schloegl et al. 2008a, b) and were therefore more experienced than the crows. For African grey parrots *Psittacus erithacus* it is known that the experimental history of an individual could affect its performance in a subsequent experiment (Pepperberg 2007). Thus, different experimental histories of crows and ravens may have resulted in a stronger effect of the cup manipulation in the crows than in the ravens.

Until recently inference was believed to be the mechanism underlying the ability to choose by exclusion. However, Paukner et al. (2009) and Schmitt and Fischer (2009) showed that other explanations are feasible. While it is indeed possible that animals have a mental representation of the food underneath the baited cup, they could also use a lower level cognitive function by simply avoiding the empty cup without knowing anything about the other cup. We cannot resolve which mechanisms the crows relied on to solve the task, but the high susceptible to low-level enhancement effects suggests that the birds may have been guided by low-level perceptual mechanisms, thus making avoidance the most likely explanation for the successful solution of the task. Furthermore, although we did not find a significant learning effect in the un-baited condition, it was notable that most of the errors occurred in the first half of the experiments. Thus, we cannot exclude a rapidly learned avoidance of the empty cup.

Nevertheless, we can clearly demonstrate that carrion crows are capable of EP and even though their performance was somewhat weaker than those of ravens and more strongly influenced by local enhancement, they performed better than the keas and jackdaws. Taking all these findings in consideration (Schloegl et al. 2009b; Schloegl 2011), our results are in line with the "adaptive specialisation hypothesis" (de Kort and Clayton 2006; Kamil 1987), suggesting that different feeding ecologies may have shaped the different performances in the EP task. In contrast to jackdaws and keas, ravens and crows are regularly faced with social interactions related to caching including pilfering and re-caching (Bugnyar and Kotrschal 2002). This could also have led to an increased motivational and attentional state during food-finding experiments. Similarly, it has been proposed that caching and non-caching species may value and interpret information about the absence of food differently and non-cachers may be more inclined to return to empty cache sites to see if the food had been replenished (Gould-Beierle 2000). Thus, it appears likely that feeding ecology plays an important role for the ability to choose by exclusion and more precisely, caching might be a key for EP in corvids.

However, another possible explanation for EP in crows is the close phylogenetic relationship to ravens. Exclusion abilities may have emerged in corvids first after the split of the ancestor of present day jackdaws from the ancestor of present-day ravens and crows. To shed light on this issue, future studies need to investigate EP in other caching corvid species that are more distantly related to crows and ravens and, in particular, of the only other non-caching species beside jackdaws, the white-throated magpie-jay *Calocitta formosa* (de Kort and Clayton 2006). Furthermore, future studies may incorporate additional parrot species to elucidate whether the performance of keas is representative for parrots.

We should keep in mind that apart from food-caching corvids, also some non-caching mammals like chimpanzees (Call 2004), dolphins (Hermann et al. 1984) and sea lions (Kastak and Schustermann 2002) are able to use exclusion. Thus, there need to be alternative explanations why these animals possess these cognitive skills. Therefore caching as a key for exclusion could only be conceivable in corvids so far.

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Conflict of interest:

The authors declare that they have no conflict of interest.

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Chapter 3: The influence of local enhancement on choice performances in African grey parrots (*Psittacus erithacus*) and jackdaws (C*orvus monedula*)

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Abstract

Being attentive to the behaviour of others may be advantageous to gain important information e.g., on the location of food. Often, this is achieved through simple local enhancement. However, this is not always beneficial, as it may override cognitive abilities, with negative consequences. Grey parrots and ravens have already succeed in exclusion tasks, but carrion crows do so only when controlling for local enhancement, and jackdaws fail entirely. Presently, we tested whether jackdaws would still be influenced by local enhancement in a simple choice-task. We compared their performance with those of Grey parrots. Since these birds did not respond to enhancement in the exclusion task, we expected them also to be less susceptible to enhancement here. In our tasks, two pieces of food were visibly hidden under two cups. Then one cup was lifted, the reward was shown to the bird and was either laid back underneath the cup or was removed. Alternatively, both manipulations were combined with the first reward being shown to the bird and the second one being removed or vice versa. Surprisingly, both species had a preference for the last handled cup, irrespective of whether it contained food or not. However, if the birds had to wait for ten seconds after the presentation, the jackdaws performed better than the Grey parrots. Additionally, the delay improved the performance of both species in conditions in which the reward was removed last and deteriorated their performance in conditions in which the item was shown last.

Keywords

African grey parrots, jackdaws, local enhancement, two-choice task, delay

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* This abstract has been used for the application of various scientific conferences and might be published in the internet and/or the abstract book of the respective conferences.

Introduction

The term “enhancement” is commonly used to describe an animal’s attention to a site or an object elicited by the presence of a conspecific at this site or the manipulation of an object by a demonstrator (Heyes et al. 2000). In the case of local enhancement the animal is attracted only to the object contacted by the demonstrator (Terkel 1995) whereas in the case of stimulus enhancement attention is directed to all objects of the same physical appearance (Fritz et al. 2000). Enhancement is a powerful, yet simple social learning mechanism and may facilitate the access to food resources (e.g.,Fritz and Kotrschal 1999; Krueger et al. 2011; Coleman and Mellgren 1997). This effect has been illustrated repeatedly in studies on rats in different contexts; Terkel (1995) found that young black rats *Rattus rattus* learned to feed on pine cones through local enhancement, as the young rats followed adults and continue to gnaw on half- stripped cones that had been left by them. Similarly, Norway rats *Rattus norvegicus* preferred food sites at which conspecifics had eaten previously (Laland and Plotkin 1991). Noteworthy, the enhanced attractiveness of a specific location due to the activity of a model is not restricted to intra-specific interactions; for instance, several studies showed that in a two-way object-choice task animals used the experimenter’s touch of an object as a reliable hint to choose that particular object (Itakura and Tanaka 1998; Byrnit 2004; McKinley and Sambrook 2000; Tornick et al. 2010).

However, local enhancement may not always be beneficial, as it may overshadow advanced cognitive abilities. Such a masking effect had been detected in an exclusion performance experiment conducted with dogs *Canis familiaris* (Erdöhegyi et al. 2007) and carrion crows *Corvus corone corone* (Mikolasch et al. 2012): Here, food was hidden in one of two boxes and the animals had to choose the baited box after an experimenter had lifted the other box to show that it is empty. Surprisingly, the dogs and a subset of the crows preferentially chose the manipulated but un-baited box. However, when controlling for the manipulation of the boxes in a follow-up experiment the animals were able to choose by exclusion. Erdöhegyi et al. argued that a set of hierarchically ordered choice rules described the dogs' behaviour best, suggesting that reasoning by exclusion is a lower-ranking strategy than responding to the social cue (touching of the box); similarly, we had suggested that local enhancement had masked the crows' ability to choose by exclusion.

In contrast to crows and dogs, jackdaws *Corvus monedula* were not able to choose by exclusion even under controlled test conditions, but were similarly susceptible to the manipulation of a cup (Schloegl 2011). In contrast, other species did not show a local enhancement effect in similar exclusion performance experiments (chimpanzees *Pan troglodytes* (Call 2004; Hill et al. 2011), bonobos *Pan paniscus*, Bornean orang-utans *Pongo pygmaeus* (Call 2004), Sumatran orang-utans *Pongo abelii* (Hill et al. 2011), capuchin monkeys *Cebus apella* (Heimbauer et al. 2012; Paukner et al. 2009; Sabbatini and Visalberghi 2008), olive baboons *Papio hamadryas anubis* (Schmitt and Fischer 2009), ravens *Corvus corax*, keas *Nestor notabilis* (Schloegl et al. 2009), African grey parrots *Psittacus erithacus* (Schmidt et al. unpubl. data) and children *Homo sapiens* (Hill et al. 2012)).

In the crow study mentioned above (Mikolasch et al. 2012), we also investigated if their reliance on local enhancement was a consequence of the cognitive burdens associated with the exclusion performance task. To do so, we conducted a simple "object manipulation" task in which the birds always received full information about the location of the food; we argued that if the crows had switched to an enhancement response because the task was (too) complicated, they should now rely on the visually available information about the presence of the food instead. Here two cups were baited in full view of the birds; after the initial baiting, one or both cups were manipulated by the experimenter with one manipulation consisting of again showing the food reward to the bird and laying it back under the cup and the other manipulation consisting of showing the reward to the bird and taking it away. Surprisingly, not only those individuals that were affected by the manipulation in the exclusion performance test were influenced by local enhancement, but all individuals preferred the only or last handled cup, even if they had witnessed the removal of the reward from this cup. Thus, in this simple “object manipulation” task in which the full information about the food location was always provided, it was even more difficult for the birds to inhibit the impulse to choose the last manipulated cup.

Due to the surprising performance of the crows in this task, we were interested how jackdaws, which were not able to solve the exclusion performance task and showed a strong preference for the manipulated cup, and Grey parrots, which evidently did not succumb to local enhancement, would fare in the “object manipulation” task. In a follow-up experiment we tested if the insertion of a time delay between cue presentation and choice would have an influence on the bird’s performance. This idea is based on the observation that a delay between stimulus presentation and choice induced pigeons *Columba livia*, rhesus monkeys *Macaca mulatta* and humans to switch from remembering the last item in a serial list best to remembering the first item in the list best (Wright et al. 1985). In consequence, a delay may help our subjects in a similar way to inhibit an initial impulse to respond to the last object manipulated.

Based on the results of the exclusion performance tasks and the findings from the crow study (Mikolasch et al., 2012), we predicted that the most likely outcome of our first experiment would be that, similar to their performances in the exclusion performance tasks, the jackdaws, but not the Grey parrots, would be susceptible to the manipulation of the cups. Alternatively, the Grey parrots may perform similar to the carrion crows and will - independent of their behaviour in the exclusion performance task and like the jackdaws - succumb to the manipulation of the cups. For the second experiment, we predicted that the incorporation of a delay between cup manipulation and choice would allow the birds to overcome their enhancement bias.

Experiment 1: object manipulation

Methods

Subjects

Five hand-raised jackdaws (three males, two females) at the age of two years participated in this experiment. All birds had participated in the exclusion performance experiment of Schloegl (2011), in which the majority of them showed a high susceptibility to local enhancement. They were housed in a 60 m^2 outdoor aviary at the Konrad Lorenz Research Station in Grünau im Almtal, Austria. The aviary consisted of two outdoor sections and five smaller testing compartments, in which the subjects could be tested in visual isolation from the other birds. Except for testing, the birds were free to enter all sections of the aviary. The two outdoor compartments contained natural grass vegetation, feeding platforms, nest boxes and some perches. The indoor section had a gravel ground and was equipped with some perches. The main indoor compartment (approx. 3 x 2 m) and one of the smaller neighbouring compartments (approx. 1.5m x 1m) were both equipped with wooden platforms (approx. 40 x 70 cm and 30 x 60 cm, respectively; 1.5 m above ground), on which the tests took place. Both platforms were adjacent to each other and connected through a wire sliding door (open during the entire experiment). When being tested, the bird was sitting on the test platform in the main compartment whereas the experimenter (E; S.M.) was standing in the neighbouring compartment presenting the test on the corresponding platform. The birds were fed in the morning and in the afternoon with various kinds of fruits, grain, milk products and vegetables. The jackdaws were tested in September 2009.

Additionally, seven Grey parrots (four males, three females), with different and often not fully known histories and between approx. 7 and 25 years old, were tested. Previously, three of the birds had participated in a exclusion performance task, in which they showed no susceptibility to local enhancement (Schmidt et al. unpubl. data). They were all housed in an indoor-outdoor aviary (3 x 5 m each) at a parrot rescue centre in Vienna, Austria. The aviary was enriched with several perches, platforms and toys. The birds were fed with fruits in the morning and seeds in the afternoon. For testing, the birds were separated in a test compartment (120 x 70 cm with 210 cm height) within the aviary, in which the subjects were visually isolated from the other birds through opaque curtains. In this compartment they could sit on a wooden platform (60 x 35 cm at a height of 130 cm) in front of a movable, wooden platform (40 x 23 cm), which was hanging from the ceiling at the same height. The test setup was presented on the movable platform. The Grey parrots were tested between March and June 2010.

Training

To ensure that the birds were aware that they have to make a choice we placed one piece of food (in case of the jackdaws a piece of dry cat food; for the Grey parrots a piece of walnut or a seed) visibly on the test platform (left/right randomized). Then two identical opaque plastic cups (Grey parrots: 9 cm height and 8 cm diameter; jackdaws: 7.5 cm height and 6.5 cm diameter) were placed simultaneously on the platform (approx. 20 cm away from each other) with one cup covering the reward. In the jackdaws, the bird was allowed to approach the cups as soon as E had removed her hands from the cups; the birds themselves turned the cups and retrieved the food. In the Grey parrots the movable platform was pushed forward to allow the bird to touch one cup with its beak, which was then lifted by E so that the bird was able to eat the food if choosing correctly. If a bird chose incorrectly, it was prevented from approaching the second cup and the remaining food item was removed in view of the bird. The cups remained on the board the whole time and the next trial was conducted in direct succession of the previous one. All birds received one session per day with 10 trials each; to reach the test phase they had to choose the baited cup in at least 8 trials in each of two consecutive sessions.

Testing procedure

Two rewards were placed visibly and simultaneously on the wooden test platform and were covered with the two opaque cups, so that each cup was baited. Then, one of the following manipulations was performed, which were identical to those described in Mikolasch et al.(2012):

Show With one hand E lifted one of the cups to a height of approx. 20 cm and with the other hand she took the reward between her fingertips and clearly showed it to the bird. After this, she returned the reward back to the same position as before and covered it with the cup.

Take As above, with the exception that the reward was taken away and put in E's pocket after having been shown to the bird.

Show & Take Now, both cups were lifted sequentially. The reward underneath the first cup was shown to the bird (identical to *Show* manipulation), and the reward underneath the second cup was lifted and put in E's pocket (identical to *Take* manipulation).

Take & Show As above, but the two manipulations were conducted in reversed order. Each manipulation was performed slowly (approx. 5 sec.) and E made sure that the bird was attentive from the start of the manipulation and throughout the procedure, meaning that the bird looked at the set-up and the manipulations. The choice procedure of the cups was identical to the procedure in the training phase and the location (left or right) and the order of the manipulations were randomized. Each bird received only one session per day. In the jackdaws each session consisted of six trials and a total of nine sessions were given to the birds. Initially, we expected different responses to *Take* trials, *Show* trials and trials in which both presentations would be presented. However, we did not expect different responses to *Take & Show* and *Show & Take* trials. Thus, we designed the task originally as consisting of three conditions, and presented *Take & Show* and *Show & Take* trials to randomize the order of manipulations within one condition. However, as we found significant differences between the *Take & Show* and *Show & Take* trials (see below) in our initial tests with jackdaws, we changed the setup for the subsequent testing of the Grey parrots. Thus, the Grey parrots received nine sessions consisting of eight trials and with each of the four conditions being presented twice.

Analysis

All tests were videotaped for behaviour coding later on. Given that in the *Show* condition both cups were baited and therefore both cups would have been correct, we scored whether the birds chose the manipulated cup. In all other conditions we scored if the birds chose the baited cup. A second observer, who was blind to the purpose of the study, coded 10% of all trials to calculate an inter-observer reliability using Cohen's kappa. Both coders agreed in 100% of the trials (Cohen's $\kappa = 1.0$). As the data of the training phase did not meet the requirements for parametric testing we used a Mann-Whitney-U test to check for differences between the species. Test performance data (i.e. choice of the manipulated or baited cup, respectively) were normally distributed and we compared the performance in the different conditions and in the two species by running a two-way repeated measures ANOVA, using *condition* as within-subject factor and *species* as between-subject factor. For post hoc analyses we used the Holm-Sidak test. For each condition we tested the performance against the hypothetical chance level of 50% using a one-sample t-test. To see how often the birds chose the only or last manipulated cup compared to the not or first manipulated one, we combined the data of all four conditions and calculated another one-sample t-test. All tests were conducted two-tailed with $\alpha = .05$.

Results

The jackdaws needed an average of 21.7 trials (*SD* = 4.5; range = 20 to 30) and the Grey parrots an average of 30.0 trials (*SD* = 15.3; range = 20 to 60) to reach the training criterion, which is not significant different from each other, Mann-Whitney test, U(7, 5) = 27.5, *p* = .432.

In the test phase, the jackdaws chose the manipulated cup in condition *Show*, *t*(4) = 12.67, *p* < .001, and the baited cup in condition *Take & Show*, *t*(4) = 16.74, *p* < .001, significantly more often than expected by chance, whereas in condition *Take* they chose the un-baited cup significantly above chance, *t*(4) = -2.92, *p* = .043, and in condition *Show & Take* they did not prefer any cup, *t*(4) = -1.47, *p* = .216, (Figure 1). Similarly, the Grey parrots also preferred the manipulated or the baited cup in the conditions *Show*, *t*(6) = 10.84, *p* < .001, and *Take & Show*, *t*(6) = 16.97, *p* < .001; again like the jackdaws, they did not have a preference for any cup in condition *Show & Take*, *t*(6) = -0.81, *p* = .448, but in contrast to them, their preference for the un-baited cup in condition *Take* failed to reach significance, *t*(6) = -2.06, *p* = .085, (see supplementary Table 1 for individual performance).

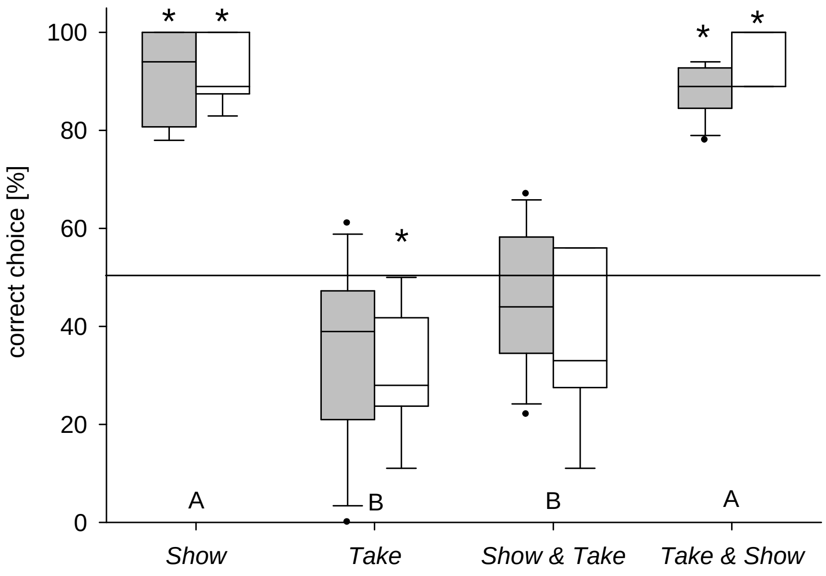

Figure 1: Performance in percentage of correct choices in experiment 1 across all four conditions. Grey bars indicate the performance of the Grey parrots and white bars the performance of the jackdaws. Note that both cups were baited in the *Show* condition and we therefore plotted the choice of the manipulated cup, whereas in all other conditions we plotted the choice of the baited cup. Significant differences between the conditions (data for both species pooled) are indicated by different letters below the bars (post hoc Holm-Sidak analysis). Asterisks above the bars indicate a significant difference from chance level (illustrated by the horizontal line) according to a one-sample t-test. The box plots show the median and quartile. The whiskers represent 10% and 90% range; dots indicate 5% and 95% range.

A two-way repeated measures ANOVA found a significant difference between the *conditions*, *F* (3,30) = 65.10, *p* < .001 (Figure 1, Table 1), but not between the two *species*, *F* (1,30) = 0.016, *p* = .903, nor an interaction of both factors, *F* (3,30) = 0.65, *p* = .592. Post-hoc analyses showed that because of their preference for the manipulated cup in the *Take* condition, the birds chose the reward in condition *Take* less frequently than in condition *Show* (*p* < .001), even though in both conditions they had seen where food was available. When two manipulations were performed (*Take & Show* and *Show & Take*) the birds preferred the cup that was manipulated last, resulting in a significantly better performance in the *Take & Show* condition, in which the last action was showing the food, than in the *Show & Take* condition, in which the food was taken away from the second cup ($p < .001$). As a consequence, the birds also obtained a reward less frequently in the condition *Show & Take* than in the condition *Show* ($p < .001$) and they were significantly better in the *Take & Show* than in the *Take* condition ($p < .001$). However, we found no significant differences between conditions *Take* and *Show & Take* ($p = .122$) and between the conditions *Show* and *Take & Show* ($p = .989$). When combining the data of all four conditions, we found that the jackdaws, $t(4) = 8.38$, $p = .001$, as well as the Grey parrots, $t(6) = 9.22$, $p < .001$, chose the only or last manipulated cup significantly more often than the first or untouched cup (Figure 2).

Table 1: Effect sizes and confidence interval for statistical comparisons of experiment 1

		95% CI	
	Effect size *r*	LL	UL
Show – Take	0.91	43.71	73.87
Show – Show & Take	0.88	35.46	63.62
Show – Take & Show	0.02	-6.34	7.27
Take – Show & Take	0.26	-18.57	0.70
Take – Take & Show	0.86	-70.03	-46.62
Show & Take – Take & Show	0.83	-61.48	-36.67

Note: CI = confidence interval; LL = lower limit; UL = upper limit

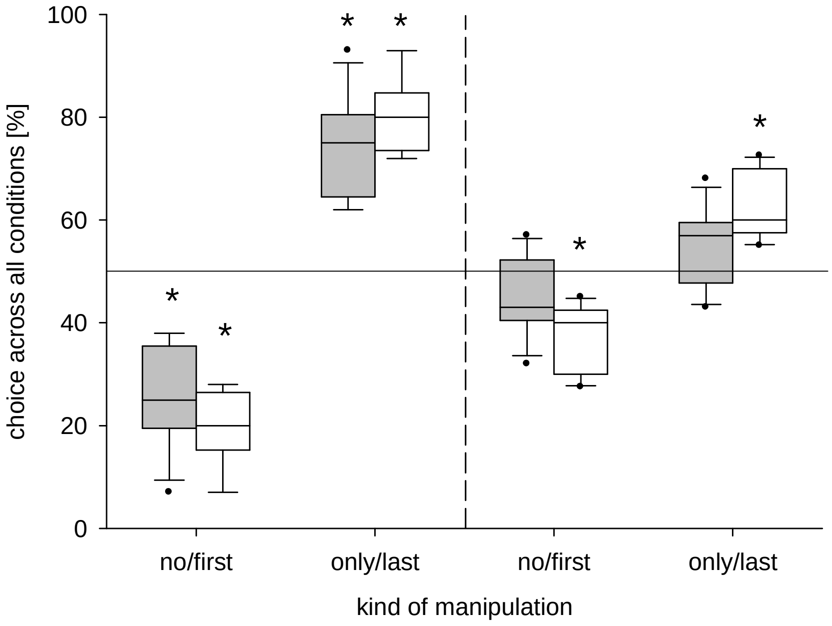

Figure 2: Percentage of choices for the only or last manipulated cup or the not or first manipulated cup across all four conditions in experiment 1 (left panel) and experiment 2 (right panel). The grey bars show the performance of the Grey parrots and the white bars the performance of the jackdaws. Asterisks above the bars indicate a significant difference from chance level (illustrated by the horizontal line) according to a one-sample t-test. The box plots show the median and quartile. The whiskers represent 10% and 90% range; dots indicate 5% and 95% range.

Discussion

Both species were highly susceptible to the manipulation of the cups, and we found no clear performance differences between Grey parrots and jackdaws. Moreover, our results match those found in carrion crows, which also preferred the manipulated cup, even if it did not contain any food (Mikolasch et al. 2012). In sum, even in our presumably simple discriminatory task, local enhancement seems to be a very potent trigger, so that the birds were not able to abstain from choosing the manipulated cup. Therefore, it seems as if their inhibitory control, which is the capability to suppress an immediate response in order to permit a later response (Anderson 2003), was weaker than the impulse to choose the manipulated cup. Whereas such a bias was expected in the jackdaws, it is surprising to find a strong susceptibility in the Grey parrots.

Whereas the preference for the manipulated cup in the conditions *Show* and *Take* can be explained by local enhancement alone, this is insufficient to explain the birds’ choices in the *Take & Show* and *Show & Take* condition, given that here both cups were manipulated. However, the preference for the cup that had been manipulated last is in accordance with a recency effect (Pineno and Miller 2005) as found in studies of list learning (Shettleworth 2010). Here, subjects are most accurate in remembering the last item of a list if they have to recall the list shortly after its initial presentation. This effect, however, disappears after longer intervals between presentation and recall and may even turn into a primacy effect, i.e. a most accurate performance in remembering the first item of the list. Such effects have been found in humans (Cornell and Bergstrom 1983; Knoedler 1999; Wright et al. 1985), rhesus monkeys and pigeons (Wright et al. 1985).

The time delay required to shift away from a recency effect differed between the species and ranged from ten seconds in pigeons to 30 seconds in monkeys and 100 seconds in humans (Wright et al. 1985). Thus, we reasoned that a time delay between the end of presentation and time of choice could allow the birds to overcome the recency effect and may even strengthen their inhibitory control to increase their choice accuracy. To test this, we conducted a second experiment in which the manipulations were identical to those of the first experiment, but we added a time delay before the birds were allowed to choose a cup. Based on a previous study demonstrating relatively short attention spans in jackdaws (Scheid et al. 2007), we opted to use a ten second delay, which is the same that had been used for pigeons. To make the test comparable, we used the same delay for the Grey parrots.

Experiment 2: object manipulation with delay

Methods

Subjects

Four jackdaws from experiment 1 participated. While the fifth jackdaw refused to work, two other individuals, which had not participated in the first task but were equally hand-raised and two years old, started to work in this experiment (for detailed information see supplementary material Table 1). Therefore, six jackdaws (three males, three females) were tested in this second experiment. The same seven Grey parrots from experiment 1 participated.

Training

Only the two jackdaws that had not participated in experiment 1 were trained to choose between the two cups; the training procedure was identical to the procedure used in experiment 1.

Testing procedure

The procedure and conditions were the same as in the first experiment with the exception that after the manipulations had been executed, E continued to touch both cups for ten seconds while looking straight ahead. After this delay E removed her hands and the birds were again allowed to choose one cup.

Analysis

The inter-observer reliability of two coders for 10% of the trials was again at 100% agreement (Cohen's κ = 1.0). The principal analysis was identical to experiment 1. In addition and to compare the performances in the first and in the second experiment, we fitted a GLMM using the GENLINMIXED procedure in SPSS 19™. The model was constructed with the binomial variable *choice* as the response variate and identity of the subject as random term to account for repeated measurements. It contained *condition*, *species* and *delay* as fixed terms. Additionally, we incorporated all possible two-way interactions and a three way *species* × *condition* × *delay* interaction. According to standard stepwise model reduction procedures, we sequentially deleted fixed terms in order of decreasing significance, whereby the least significant term was determined after each removal step (Galwey 2006; Garamszegi et al. 2009). Deletion of fixed terms continued until only terms with a significance value below .1 remained. This was then considered the final model. Excluded terms were re-entered one by one into the final model to confirm that they did not explain a significant part of the variation. For each factor remaining in the final model, we calculated pairwise post-hoc comparisons using the sequential Sidak-procedure; terms were only regarded as being significant if $p < .05$.

Results

Experiment 2

The two new jackdaws both needed the minimum of two sessions (20 trials) only to reach the training criterion. Their test performance did not deviate from the other birds (see supplementary material Table 1 for individual performance data), arguing against carry-over or learning effects from experiment 1. Therefore, we pooled their data with those of the other birds for the subsequent analysis.

As in the test phase of experiment 1, the jackdaws chose the manipulated cup in condition *Show*, $t(5) = 6.33$, $p < .001$, and the baited cup in condition *Take & Show*, $t(5) = 7.68$, $p < .001$, significantly more often than expected by chance. In contrast to experiment 1, the jackdaws now chose the baited cup significantly above chance in condition *Show & Take*, $t(5) = 2.70$, $p = .043$, and they chose at chance level in condition *Take*, $t(5) = 1.17$, $p = 0.296$, (Figure 3). The Grey parrots showed a pattern similar to the jackdaws and were significantly above chance in the conditions *Show*, $t(6) = 3.65$, $p = .011$, *Take & Show*, $t(6) = 4.36$, $p = .005$, and *Show & Take*, $t(6) = 4.80$, $p = .003$, (Figure 3), and they were at chance level in the condition *Take* $t(6) = 0.11$, $p = .916$, (see supplementary Table 1 for individual performances).

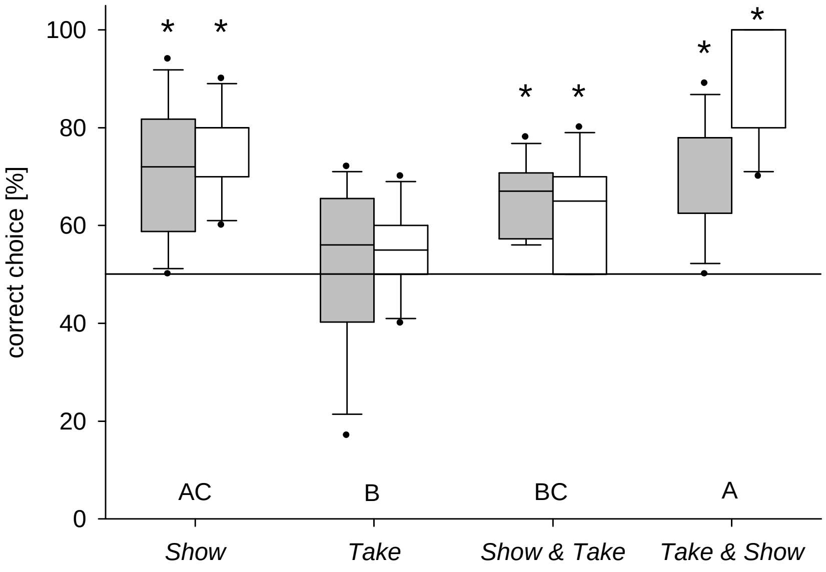

Figure 3: Performance in percentage of correct choices in experiment 2 across all four conditions. Grey bars indicate the performance of the Grey parrots and white bars the performance of the jackdaws. Note that both cups were baited in the *Show* condition and we therefore plotted the choice of the manipulated cup, whereas in all other conditions we plotted the choice of the baited cup. Significant differences between the conditions (data for both species pooled) are indicated by different letters below the bars (post hoc Holm-Sidak analysis). Asterisks above the bars indicate a significant difference from chance level (illustrated by the horizontal line) according to a one-sample t-test. The box plots show the median and quartile. The whiskers represent 10% and 90% range; dots indicate 5% and 95% range.

As in experiment 1, a two-way repeated measures ANOVA revealed significant differences between the *conditions*, F (3,33) = 10.17, $p < .001$, but now also between the two *species*, with the jackdaws outperforming the Grey parrots, F (1,33) = 5.35, $p = .041$ (Figure 3, Table 2). The interaction between both factors was non-significant, F (3,33) = 1.44, $p = .248$. Post hoc analyses revealed that the birds chose the manipulated cup in condition *Show* significantly more often than the baited cup in condition *Take* ($p < .001$), but there was no difference compared to the conditions *Show & Take* ($p = .083$) and *Take & Show* ($p = .182$).

Additionally, the birds chose the baited cup significantly more often in the condition *Take & Show* than in the conditions *Take* (*p* < .001) and *Show & Take* (*p* = .003). Due to the adjustment for multiple testing no difference was detectable between condition *Take* and *Show & Take* (*p* = .048). When combining the data of all four conditions, we again found a significant preference for the only or last manipulated cup in the jackdaws, *t*(5) = 4.33, *p* < .007, but not in the Grey parrots, *t*(6) = 1.53, *p* = .172, (Figure 2).

Table 2: Effect sizes and confidence interval for statistical comparisons of experiment 2

		95% CI	
	Effect size *r*	LL	UL
Show – Take	0.60	7.88	34.34
Show – Show & Take	0.38	0.46	19.58
Show – Take & Show	0.23	-17.15	3.29
Take – Show & Take	0.41	-25.06	1.96
Take – Take & Show	0.66	-42.06	-14.01
Show & Take – Take & Show	0.52	-27.94	-5.05

Note: CI = confidence interval; LL = lower limit; UL = upper limit

Comparison between experiment 1 and 2

The final model of the GLMM contained *condition*, *species* as well as a *condition* × *delay* and a *condition* × *species* interaction (Table 3). The post-hoc analysis for the factor *condition* revealed that no performance difference was detectable between the conditions *Show* and *Take & Show* (*p* = .092), but the birds were more successful in these conditions than in the conditions *Take* and *Show & Take* (all *ps* < .001); the lowest success rate was detectable in the condition *Take*, in which the birds were even less successful than in the condition *Show &*

Take (*p* = .023). The jackdaws were more successful than the Grey parrots, even though the factor *species* marginally failed to reach significance. As the post-hoc analysis of the *condition* × *species* interaction revealed, the superiority of the jackdaws is mainly based on their higher success rate in the condition *Take & Show* (*p* < .001), whereas no species difference could be found in any of the other conditions (all *ps* ≥ .403). It seems that the introduction of the delay did not alter the performance of the birds (non-significance of the factor *delay*), but the significant *condition* × *delay* interaction and subsequent post-hoc analysis show that a change in performance occurred, even though not uniformly in all conditions; the delay improved the performance of both species in the conditions *Show & Take* and *Take* (both *ps* < .001), but decreased the performance in the conditions *Show* (*p* < .001) and *Take & Show* (*p* = .001), and this decline in the condition *Take & Show* was particularly pronounced in the Grey parrots (Figure 3). Even though the *delay* × *species* interaction was dropped from the final model, it seems worth to mention that the introduction of the delay led to a drop in the overall success rate of the Grey parrots from 71% in the first experiment to 65% in the second experiment; in contrast, the jackdaws' performance remained relatively stable (74% and 75%, respectively).

Table 3: Full and final model of the GLMM to illustrate the performance differences in experiment 1 and 2.

Fixed terms	df	F	p
Full model			
Delay	1	0.383	0.536
Condition	3	58.509	< 0.001
Species	1	2.880	0.090
Condition × delay	3	16.032	< 0.001
Condition × species	3	2.801	0.039
Delay × species	1	0.913	0.340
Condition × delay × species	3	0.006	0.999
Final model			
Condition	3	61.095	< 0.001
Species	1	3.810	0.051
Condition × delay	3	15.832	< 0.001
Condition × species	3	3.597	0.013

Discussion

In this experiment we found a difference between the two species, with the jackdaws outperforming the Grey parrots. On the first view this is surprising given that the jackdaws are still biased towards choosing the last manipulated cup, whereas this bias disappeared in the Grey parrots. However, the jackdaws were in particular more successful than the Grey parrots in choosing the baited cup in the condition *Take & Show*, which led to the higher overall success rate of the jackdaws.

Importantly, even though the jackdaws were more successful than the Grey parrots, this was not due to a performance increase after the introduction of the delay on side of the jackdaws, but to a marginal performance drop after the delay in the Grey parrots. Furthermore, it becomes evident that the introduction of the ten second delay led to a decrease of the strength of the recency effect, which is evidenced by the finding that the success rate increased in those conditions in which the last seen manipulation was a removal of the food (conditions *Take* and *Show & Take*). However, at the same time, the birds' preference for the only or last manipulated cup dropped in those conditions in which the reward was only shown or in which showing was the last manipulation seen (condition *Show* and *Take & Show*).

General discussion

Even in our cognitively less demanding task, in which the full information about the food location was always available, the birds were only able to choose the baited cup reliably in some conditions. These findings support the results of Mikolasch et al. (2012), who found a similar pattern in carrion crows, and the report of Schloegl (2011), who found that jackdaws are highly susceptible to local enhancement. Against our prediction, we found a similar influence of local enhancement in African grey parrots. In previous studies, Grey parrots solved exclusion performance tasks without being distracted by the manipulation of the cups (Schmidt et al. unpubl. data; Mikolasch et al. 2011), and thus, we expected them to be more successful than the jackdaws in the present task.

Additionally, we found a decline in the birds' performance in our second experiment when a ten second delay was introduced, but interestingly this effect was not equally distributed across the conditions. While the birds were more likely to choose the not or first manipulated cup in the conditions *Show* and *Take & Show*, which led to a worse performance in the latter condition, their performances in the conditions *Take* and *Show & Take* significantly increased in the second experiment. Presumably, the delay strengthened the birds’ inhibitory control and thereby also choice accuracy, even though the jackdaws still remained susceptible to local enhancement. The idea of strengthened inhibitory control facilitating the birds to choose the baited cup is in accordance not only with the results of the *Take* and the *Show & Take* condition, but also with the decreased preference for the manipulated cup in the *Show* condition after the introduction of the delay; note that in this particular condition, both cups were baited and a choice of the non-manipulated cup did not have negative consequences. Furthermore, a simultaneous increase in distraction may have played a role, which may also explain why the performance decreased in the *Take & Show* condition, particularly in the Grey parrots. We could observe that in contrast to the jackdaws, which remained focused on the cups during the delay, some of the Grey parrots apparently lost attention and began to manipulate the wooden platform or one of the separation curtains. Other birds tried to grab the correct, but still out of reach cup during the delay, but then chose the other cup once they were allowed to choose. This is in line with recent findings from a delay-of-gratification task, in which Grey parrots did not wait for up to five seconds to gain a larger reward (Vick et al. 2010), but opted for a smaller, immediately available reward. An alternative explanation for the birds’ change in performance whether for the better or for the worse, would be a weakened memory of the last action produced by the experimenter. This may either be due to the delay itself or due to the touching of both cups by the experimenter during the delay. However, to achieve their increased success in the *Take* and *Show & Take* conditions, the birds had to rely on the information they obtained during the manipulations (i.e. the removal of the food). Thus, to apply the argument of a weakened memory, one needs to assume that the birds remembered where the food remained and where not, but forgot the order in which the experimenter’s actions occurred. Taken together and given that Grey parrots possess advanced cognitive abilities (Pepperberg 1999, 2006; Mikolasch et al. 2011) and reach stage 5 – object permanence (Pepperberg et al. 1997), it seems unlikely that their relatively weak performance in experiment 2 was based on an incapability to solve the task, but rather on decreasing interest or attention due to the delay.

Interestingly, the influence of local enhancement on the Grey parrots was more pronounced in this presumably cognitively less demanding task than in the previous exclusion performance tests (Schmidt et al. unpubl. data). The main difference between the tasks is the visibility of the food during the cup-manipulation. In the exclusion performance test, the food was hidden out of sight and the birds had not seen the food at all (when confronted with an empty cup) or had seen it only once before they made their choice. Here, however, they saw the food twice in each condition (during hiding and at the second presentation). From an associative point of view, it may be more difficult to inhibit the choice of a pilfered cup than to inhibit the choice of a cup that had always been empty. This is because the pilfered cup had been associated with food before, whereas no such association had been formed for the empty cup. For instance, Russell and Thompson (2003) found that 14-17 month old children, who witnessed two toys being placed in two boxes, were more likely to choose the box where an experimenter removed the toy afterwards, instead of the box that still contained a toy. Additionally, this preference weakened over time, as their performance was significantly better when they were asked to find the toy after 24 hours. The authors argued that this may be due to an associative strategy, in which the child associated the box from which the toy was removed with the availability of toys.

Taken all these findings together, we suggest that both species, jackdaws and Grey parrots, were highly susceptible to the manipulation of the cups. Similar to carrion crows (Mikolasch et al. 2012), they chose the cup that had been manipulated last, even if the food had been removed from there. In contrast to the exclusion performance tasks, which were solved successfully only by the Grey parrots and not by the jackdaws (Schmidt et al. unpubl. data; Schloegl 2011), we found only minor differences between both species in our object manipulation task. However, we found that jackdaws performed better than the Grey parrots when they had to wait for ten seconds before choosing one cup, which is mostly due to their better performance in the condition *Take & Show*. Based on our observations of the Grey parrots' behaviour during the delay (see above), we think that this difference is mainly attributable to a decrease in interest or attention of the Grey parrots.

From a comparative point of view, it is interesting to note that the carrion crows (Mikolasch et al. 2012) and the Grey parrots both succumbed to local enhancement in the object manipulation task, whereas only the carrion crows were similarly distracted by such cues in the exclusion performance task (Mikolasch et al. 2012; Schmidt et al. unpubl. data). Thus, in the exclusion performance task, bottom-up processes influenced the choices of Grey parrots and carrion crows differently. In consequence, low-level, bottom-up interferences may have a larger impact on cognitive tests than previously considered.

In summary, our study provides evidence for strong and unexpected effects of presumably cognitively simple mechanisms on test performance even in large-brained, cognitively advanced species and highlights the importance of considering low-level mechanisms during experimental planning and analysis. Being attentive to this, negative results in cognitive tasks, that are not due to an incapability of a species but to its enhancement to local stimuli, may be avoided.

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Supplementary material:

Table 1: Individual performances in percentage of correct choices in experiment 1 and 2 of jackdaws and Grey parrots (j = jackdaw; gp = Grey parrot; m = male; f = female).

Individual	Species	Sex	Show		Take		Show & Take		Take & Show	
			Exp.1	Exp.2	Exp.1	Exp.2	Exp.1	Exp.2	Exp.1	Exp.2
Hollo	j	f	100.0	80.0	27.8	60.0	55.6	80.0	100.0	100.0
Leechmilk	j	m	83.3	80.0	27.8	50.0	33.3	70.0	100.0	70.0
Collins	j	m	88.9	60.0	50.0	70.0	33.3	70.0	100.0	100.0
Bengi	j	m	88.9	80.0	38.9	40.0	55.6	50.0	88.9	100.0
Udo	j	f	100.0	-	11.1	-	11.1	-	88.9	-
Ahab	j	f	-	70.0	-	60.0	-	50.0	-	80.0
Nincs	j	f	-	90.0	-	50.0	-	60.0	-	100.0
Awisa	gp	f	100.0	66.7	16.7	44.4	44.4	72.2	83.3	66.7
Kasi	gp	f	100.0	77.8	0.0	16.7	22.2	77.8	94.4	88.9
Rocky	gp	m	77.8	50.0	38.9	61.1	66.7	55.6	77.8	77.8
Leo	gp	m	88.9	94.4	38.9	72.2	38.9	55.6	88.9	77.8
Cocohan	gp	m	94.4	72.2	33.3	38.9	33.3	61.1	88.9	61.1
Moritz	gp	m	77.8	55.6	61.1	66.7	61.1	66.7	94.4	50.0
Maja	gp	f	100.0	83.3	50.0	55.6	50.0	66.7	88.9	77.8

Chapter 4: African grey parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food

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Abstract

Exclusion allows the detection of hidden food when confronted with the choice between an empty and a potentially baited food location. However, exclusion may be based on avoidance of the empty location without drawing inferences about the presence of the food in the baited location. So far, such inferences have been demonstrated in the Great Apes only: after seeing an experimenter eating one of two food types, which both had been hidden previously in two boxes, the apes were able to choose the box that still contained the other food type. African grey parrots are capable of exclusion, and we here assessed if they are capable of inference by exclusion. In our task, two different but equally preferred food items were hidden in full view of the bird under two opaque cups. Then, an experimenter secretly removed one food type and showed it to the bird. Similarly to the apes, one out of seven parrots significantly preferred the baited cup; control conditions rule out that its choice was based on associative learning or the use of olfactory cues. Thus, we conclude that – like the apes – some grey parrots are able to infer the location of a hidden food reward.

Keywords

African grey parrots, inference by exclusion, reasoning

Introduction

Choice by exclusion is defined as “the ability to base the choice of a target on the rejection of potential alternatives” (Schloegl 2011); for instance, apes (Call 2004), monkeys (Hill et al. 2011; Sabbatini and Visalberghi 2008; Schmitt and Fischer 2009; Petit et al. 2005), dogs (Aust et al. 2008; Bräuer et al. 2006; Erdöhegyi et al. 2007) and ravens (Schloegl et al. 2009) selected the baited box in a two-choice procedure with two opaque boxes after they received information about the empty box only. However, this task can be solved by an avoidance of the empty box rather than an inference about the reward in the baited box. Only in a chimpanzee study by Premack and Premack (1994) was it possible to rule out avoidance of the incorrect alternative. First, the experimenter hid an apple and a banana in two different boxes in full view of the ape; subsequently the chimpanzee was allowed to witness the experimenter eating one of the fruits, which had been removed secretly, and was thereupon allowed to choose one box. Only one out of five individuals was reliably able to choose the still-baited box. This task was then replicated with all great ape species by Call (2006), who found a similar degree of inter-individual differences. Thus, in general, great apes are able to draw inferences by exclusion, but it seems to be a demanding, not easy-to-solve task. Nothing is known about “true” inferential reasoning in such a food-finding task beyond the great apes, as it has never been replicated with a non-ape species. Recent data indicate that African grey parrots (*Psittacus erithacus*), who are well-known for their advanced cognitive abilities (Pepperberg 1999), are able to choose by exclusion in the visible as well as in the acoustic domain (Schmidt et al.). Therefore, we here tested whether African grey parrots are capable of ape-like true inferential reasoning, which will be important for our understanding of the cognitive evolution of mammals and birds.

Material and methods

The subjects were seven grey parrots (four males), housed in a parrot rescue centre in Vienna, Austria. The birds were of different and often not fully known history and were between approx. 7 and 25 years old. They were housed together with other not tested individuals in an indoor – outdoor aviary (3 m x 5 m each) that was enriched with several perches and toys. Birds were fed with fruits in the morning and seeds in the evening. Testing was conducted between 9:00 and 13:00 h and each bird was tested in visual isolation (testing compartment: 120 cm x 70 cm and 210 cm height) on a fixed platform (60 cm x 35 cm at a height of 130 cm). The experimental setup consisted of two identical opaque cups (9 cm height and 8 cm diameter) on a wooden, movable platform (40 cm x 23 cm) hanging from the ceiling at the same height but 15 cm away from the fixed platform (see Figure S1 in supplementary material). Therefore, while the birds were positioned on the fixed platform, the experimenter could present the setup out of their reach on the movable platform and could push it within their reach to allow them to choose.

Pre-tests

Choice training

This test was introduced to ensure that the birds were aware that they would have to make a choice. One piece of food (e.g. a seed or a piece of walnut, depending on known preferences of the birds) was placed on the movable platform and covered with an opaque cup. Simultaneously, the second cup was placed on the same platform at a distance of approx. 20 cm. Then, the platform was pushed forward to allow the bird to make a choice by touching a cup with its beak and retrieve a food item if correct. One session consisted of ten trials; the training criterion to reach the next step was set to be correct on at least eight trials in two consecutive sessions.

Preference test

This test was introduced to ensure that the test performance would not be influenced by food preferences. We visibly placed two different food items (the same as in the training) simultaneously on the movable platform and covered them with the two cups. Then, the bird was allowed to choose and retrieve one food item. The position of the food types was semi-randomized with the stipulation that the same food type was not placed on the same side for more than three consecutive trials. Two sessions were conducted, each consisting of ten trials. Birds were advanced to the test if they did not show a preference for one food type, i.e. did not select one item more than 13 times over the two sessions.

Tests

In the test phase these two equally preferred food items were then placed simultaneously on the movable platform and covered with the two cups:

Visible condition

Standing equidistantly between the cups and in full view of the subjects, the experimenter looked straight ahead, lifted the left cup, manipulated the food, returned the cup, lifted the right cup, manipulated the food and returned the cup. One manipulation consisted of taking the food, showing it to the bird and putting it back on the board. The other manipulation consisted of taking the food, showing it to the bird and removing it. The order of manipulations was randomized, but no food type was removed more than three times in a row and no side remained baited in more than three consecutive trials. Afterwards the bird was allowed to make a choice and received the reward if correct or saw the empty cup if not.

Invisible condition

This condition was identical to the visible condition, with the exception that after covering the rewards with the cups an opaque barrier was placed between the bird and the cups and the two manipulations were performed behind this barrier. Then, the barrier was removed and the experimenter showed the item she had taken away and put it into her pocket. The birds first received either the visible or the invisible condition. If the birds showed a significant preference for the baited cup in the invisible condition, two control conditions were conducted.

Olfaction control

Behind the barrier, the experimenter hid one piece of food (per trial one of the two food types) underneath one of the cups. Without any information about the food location the bird was then allowed to choose one cup.

Association control

To test if the birds used the associative rule "always choose the cup with the food type not having been shown" we visibly placed the two food items on the board, covered them with the cups and then took – in full view of the subject - one piece of food (of the same type as one of the food items being hidden) out of the experimenters' pocket, showed it to the bird and put it back in the pocket. Afterwards the bird was allowed to choose. In all conditions, the birds received three sessions with ten trials per session for a total of thirty trials in each condition. Birds received only one session per day. If a bird left the testing area during testing, the session was continued on the following day (see supplementary material).

Results

The parrots received 22.9 ± 4.9 ($\bar{x} \pm SD$, range 20-30) trials of choice training. In the preference test, no bird chose one food type more than 12 times (Binomial-tests: $P \geq 0.503$). In the test, the birds significantly preferred the baited cup in the visible (One-Sample t-test: N = 7, df = 6, t = 7.772, $P < 0.001$), but not in the invisible condition (t = 1.430, P = 0.203; Figure 1).

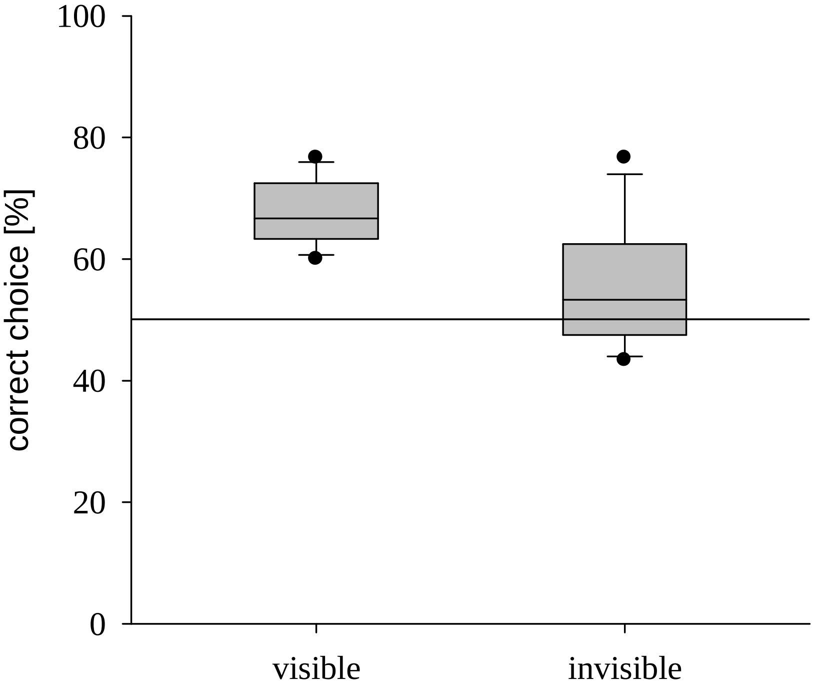

Figure 1: Percentage of correct choices in the visible and invisible condition. The horizontal line indicates the chance level. The box plot shows median and quartiles. The whiskers represent 10% and 90% range, dots indicates 5% and 95% range.

On an individual level, all birds selected the baited cup in the majority of the trials in the visible condition and three birds were significantly above chance level ($P \leq 0.043$; Table 1 and supplementary results). In the invisible condition one out of seven birds was significantly above chance (Binomial-test: P = 0.005; all others: $P \geq 0.200$; Table 1). The successful bird (a female of approx. 13 years) chose at chance level in the olfaction and in the association control (Binomial-test: P = 0.856 in both cases). When comparing her performance in the first and last fifteen trials, we found no difference in the visible condition (McNemar-Test: N = 15, P > 0.999) or in the olfaction (P = 0.625) and association control (P = 0.508), but a significant improvement in the invisible condition (P = 0.016).

Table 1: Individual performances given as percentage of correct choices. Significant performances (according to a Binomial-test) are highlighted in bold (f = female; m = male).

individual	sex	visible	invisible	olfaction	association
Awisa	f	**70.0**	**76.7**	46.7	56.7
Cocohan	m	63.3	50.0	-	-
Kasi	f	63.3	60.0	-	-
Leo	m	60.0	53.3	-	-
Maja	f	**76.7**	46.7	-	-
Moritz	m	**73.3**	63.3	-	-
Rocky	m	66.7	43.3	-	-

Discussion

Our study shows that African grey parrots can use partial information about the removed food item not only to choose by exclusion based on avoidance, but that they are capable of true inferential reasoning. However, whereas several subjects solved the task when they could see the experimenter’s actions, only one individual was able to solve the task when it had to infer the outcome of the experimenter’s actions; still, these findings are in line with the inter-individual differences found in the great apes (Call 2004; Premack and Premack 1994). The birds were clearly motivated to obtain the reward, even though side biases occurred (see supplementary data). As they were highly attentive and never refrained from making a choice, we are confident that the success of only a single bird in the invisible condition is not due to motivational issues; rather, it supports the assumption that these inference tasks are not trivial but cognitively demanding. Again, this result demonstrates substantial inter-individual differences in grey parrot cognitive performance (Pepperberg 2007) and that the level of performance depends on subtle differences between tasks (Pepperberg 1999; Giret et al. 2010).

Importantly, the successful bird significantly improved her performance only within the invisible condition. This improvement does not necessarily point to associative learning, as the bird performed at chance level in the association control. We suggest that the improvement is due to the fact that the bird did not comprehend the relevance of the food presentation in the beginning of the test. This is plausible in particular because this bird was first tested in the invisible condition. Probably, the bird needed a few trials to become acquainted with the test. Thus, we suggest that this bird's performance was not based on learning *instead* of reasoning, but rather that the bird *learned to reason* about the experimenter's action to solve the task.

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Supplementary material:

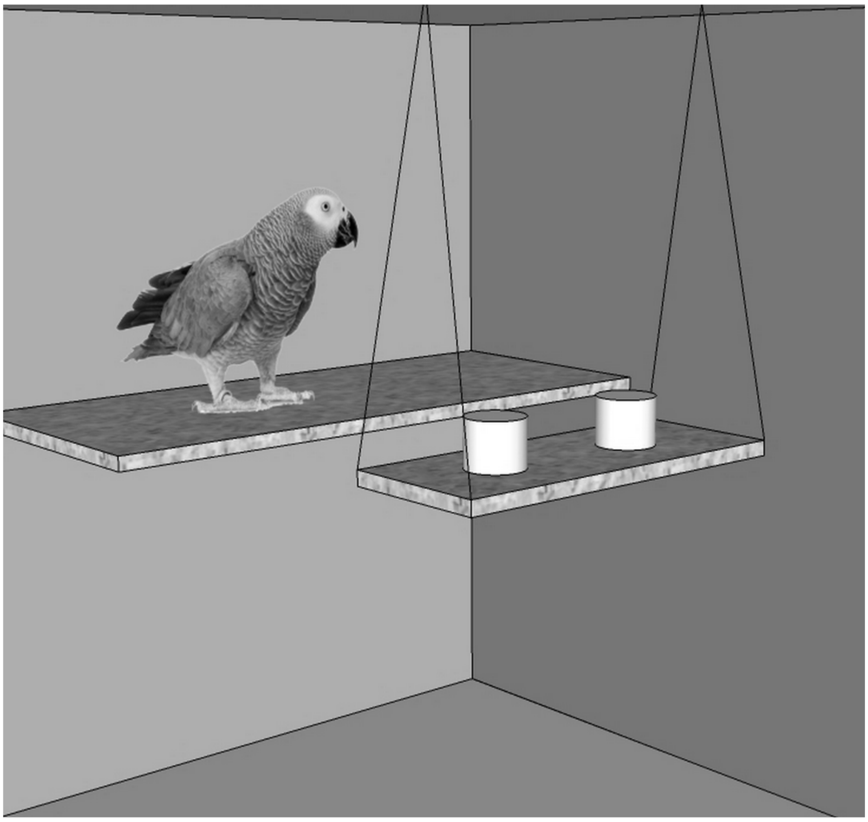

Figure S1: Test-set-up

Material and methods

Subjects

Three of the birds (Awisa, Kasi and Leo) had participated previously in a visible and acoustic exclusion task, in which only indirect information about the location of a food reward was provided.

Procedure

The experiment was conducted between September 8th, 2010 and December 9th, 2010 and the birds were tested five days a week (from Monday to Friday), but not each bird participated on each day.

During testing, the birds were free to leave the experimental area at any time. If a bird did so, the session was terminated and continued on a following day. However, this occurred only in two sessions with two birds.

During testing, the birds first received either the visible or the invisible condition first, and the other condition second. The order in which each bird received these conditions is shown in Table S1. The control conditions were conducted last.

Table S1: Order of test conditions for each subject

individual	first condition	second condition
Awisa	invisible	visible
Cocohan	invisible	visible
Kasi	invisible	visible
Leo	visible	invisible
Maja	visible	invisible
Moritz	invisible	visible
Rocky	visible	invisible

Results

The performance of the birds in the visible and the invisible condition cannot be explained by a newly developed preference for any of the two food types as none of the birds chose one of the two food types significantly above chance (Table S2). However, two of the seven birds showed a significant side bias in the visible condition and four of the seven birds showed a significant bias in the invisible condition (Table S3).

Table S2: Preference for one of the two food types in the two test conditions in percentage.

individual	visible condition	invisible condition
Awisa	60,0	46,7
Cocohan	53,3	50,0
Kasi	60,0	50,0
Leo	56,7	63,3
Maja	46,7	53,3
Moritz	46,7	50,0
Rocky	63,3	60,0

Table S3: Percentage of trials each bird chose the left cup (from the experimenters' point of view) in the two test conditions. Significant biases (according to a Binomial-test) are highlighted in bold.

individual	**visible condition**	**invisible condition**
Awisa	40,0	66,7
Cocohan	40,0	**6,7**
Kasi	**80,0**	**83,3**
Leo	**90,0**	56,7
Maja	60,0	**90,0**
Moritz	50,0	**73,3**
Rocky	56,7	46,7

Chapter 5: Transitive inference in jackdaws (C*orvus monedula*)

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Abstract

Transitive inference (TI) refers to the cognitive ability to derive a hierarchical relationship between items that have never been presented together before. TI could be a useful tool for individuals living in large social groups, as these are confronted with an increasing number of possible dyadic relationships between group members. Through TI, one could potentially infer rank relationships between group members and thereby avoid costly direct agonistic interactions. Jackdaws seem ideal candidates to test for the ability of TI as they live in relatively complex groups, in which such skills could be useful. We presently report the results of jackdaws in a touch screen experiment. Three individuals were trained to memorise an hierarchically ordered sequence of five differently coloured squares (A-E), which were presented in four pairs consisting of two adjacent colours each (A/B, B/C, C/D, D/E). After reaching the pre-defined criteria in each single colour pair in a time comparable to other species, they were confronted with an unknown pair of two non-adjacent colours (e.g. B/D). The birds were able to infer the relationship according to the previously learnt hierarchical order by preferring B over D.

Keywords

corvids; hierarchy; jackdaws; touch screen; transitive inference

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* This abstract has been used for the application of various scientific conferences and might be published in the internet and/or the abstract book of the respective conferences.

Introduction

Transitive inference (TI) refers to the ability to derive a hierarchical relationship between items that have never been presented together before (Lazareva and Wasserman 2006). For instance, after learning that A is faster than B and B is faster than C, transitivity would be demonstrated by inferring that A is faster than C. This ability was regarded as a hallmark of human cognition (Vasconcelos 2008), and had been suggested to be based on logical deductions (i.e. reasoning); furthermore it had been argued that language may be a necessary requirement for TI. This changed when Bryant and Trabasso (1971) discovered that children under the age of seven are capable of TI in a non-verbal test, whereas previous results of verbal tests had indicated that TI develops at around the age of seven (Riley and Trabasso 1974). This suggests that language does not seem to be a necessary requirement for TI. This view was supported when McGonigle and Chalmers (1977) first showed TI in a non-human animals, the squirrel monkeys *Saimiri sciureus*. Further studies indicated that TI may be based on simpler mechanisms than logical reasoning (e.g. associative strength models, for a review see: Vasconcelos 2008). Today, two generally different types of models are used to explain TI. Relational models postulate that subjects form a spatial array in which each item has his own ordinal position (D'Amato 1991) and TI is based on a comparison of the positions of the stimuli. In contrast, associative models postulate that TI is based on a comparison of the associative strengths of each of the two stimuli to be compared (Terrace and McGonigle 1994; Wynne 1995). These associative strengths are acquired when learning the hierarchy.

In non-verbal testing procedures, subjects are usually trained to a set of at least four simultaneous discriminations presented as follows: A>B, B>C, C>D and D>E, where X>Y means that when both stimuli appear together X is rewarded while Y is not. After having learned the different pairs, even when presented in mixed order, subjects are given a choice between a novel pair B/D, which is then labelled as TI pair (Shettleworth 2010). Since the inaugural study on squirrel monkeys, various other socially living species, such as rhesus monkeys *Macaca mulatta* (Treichler and Van Tilburg 1996), chimpanzees *Pan troglodytes* (Gillan 1981), ring-tailed lemurs *Lemur catta*, mongoose lemurs *Eulemur mongoz* (Maclean, Merritt, and Brannon 2008), rats *Rattus norvegicus* (Davis 1992; Roberts and Phelps 1994), pigeons *Columba livia* (Lazareva and Wasserman 2006; Steirn, Weaver, and Zentall 1995; von Fersen, Wynne, and Delius 1991; Wynne 1997; Zorina, Kalinina, and Markina 1996), hooded crows *Corvus cornix* (Lazareva et al. 2004; Zorina, Kalinina, and Markina 1996), pinyon jays *Gymnorhinus cyanocephalus* (Bond, Kamil, and Balda 2003; Bond, Wei, and Kamil 2010; Paz-y-Mino et al. 2004), western scrub jays *Aphelocoma californica* (Bond, Kamil, and Balda 2003; Bond, Wei, and Kamil 2010), Clark's nutcrackers *Nucifraga columbiana*, azure-winged magpies *Cyanopica cyanus* (Bond, Wei, and Kamil 2010), greylag geese *Anser anser* (Weiß, Kehmeier, and Schloegl 2010), domestic chick *Gallus gallus* (Daisley, Vallortigara, and Regolin 2010) and cichlid fish *Astatotilapia burtoni* (Grosenick, Clement, and Fernald 2007) were shown to be able of TI. However, whereas a large number of species is actually capable of TI, there are differences in how fast they learn a linear hierarchy and how complex (i.e. how many items it contains) the hierarchy may be (for a review see Vasconcelos 2008).

TI may be a crucial cognitive tool for socially living species. This idea is expressed in the "social complexity hypothesis", which predicts that living in large, social groups favours the evolution of cognitive abilities (de Waal and Tyack 2003; Jolly 1966; Balda and Kamil 1989). Animals that live in such societies are faced with a variety of information about others (e.g. about age, reproductive status, dominance rank), which may change over time and needs frequent updates. For determining one's own place in a social network, an individual can directly interact with all other members of the group or just observe interactions among others and draw conclusions from this and its own experience with a few of these individuals, allowing to infer ones' own position to others instead of being forced to explore it repeatedly. This may be achieved through TI (Seyfarth and Cheney 2003; Bond, Kamil, and Balda 2003).

Paz-y-Mino and co-workers (2004) showed that pinyon jays use TI to predict their social rank in relation to opponents after having observed interactions between these individuals only. Similarly, cichlid fish are able to learn the rank of five neighbour fish (A-E) by only observing encounters between them (Grosenick, Clement, and Fernald 2007). Due to the proposed linkage between TI and sociality, Bond and colleagues (2003) compared pinyon jays, which are highly social, with relatively non-social western scrub jays. Although both species showed the capability of TI, the pinyon jays learned dyadic relationships more rapidly and more accurately and showed a more robust mechanism of TI than the scrub jays. Similarly, Maclean and colleagues (2008) found that highly social ring-tailed lemurs outperformed the less social mongoose lemurs in TI tasks.

The jackdaw *Corvus monedula* is one of the most social corvid species, which lives in colonies throughout their whole life and establish long-term pair bonds (Röell 1978; Henderson, Hart, and Burke 2000). However, flock size varies seasonally and is mostly dependent on food availability and quality (Röell 1978). Therefore, jackdaws live within a dynamic fission-fusion social system, where individuals may leave or join a group. Thus, TI should be of high value for jackdaws, making them ideal candidates for such tests.

To do so, we decided to use a computerized touch screen procedure and trained the birds to a hierarchical sequence of five differently coloured stimuli (A-E), similar to the training procedure used by Lazareva and Wasserman (2006). As test pair we used B/D, because this is the only pair of non-adjacent stimuli in which both stimuli have been equally rewarded and not rewarded during training. Using pairs involving the first and last item in the series (e.g. A and E in the current example) would not be informative about TI, as these stimuli have always or never been rewarded during training and therefore could easily be solved by the total number of responses ("end-anchor effect" Bryant and Trabasso 1971). Based on the knowledge about TI in other non-human animals and the fact that it seems to be linked to sociality, we would expect the jackdaws, which are known as highly social, to master this task and to be able to transitively infer the relationship between the two stimuli according to their position in the previously learned order. Additionally, we expect the jackdaws to learn the hierarchical list in a comparable time to other socially living species that were tested under similar training conditions.

Methods

Subjects

Three hand-raised, female jackdaws (named Bruce, Udo and Pronto) participated in this experiment. At the beginning of testing, the birds were between one and two years old and lived together with 15 other jackdaws at the Konrad Lorenz Research Station in Grünau im Almtal, Austria. Originally, ten jackdaws took part in the experiment, but seven of them stopped to participate during the course of the study. All jackdaws were housed in a 60 m^2 outdoor aviary consisting of two outdoor sections and five smaller indoor compartments, which could be isolated visually from the other parts. The outdoor parts had natural grass vegetation, nest boxes, feeding platforms and perches, whereas the indoor sections had gravel stones on the ground and some perches. In the main indoor compartment (approx. 3 x 2 m) the computer (*Schneider A4F®* minicomputer) was located and hidden behind a wall so that only the screen (15” infrared touch monitor: 30.5 x 23 cm) was accessible for the birds. They could sit on a perch (54 cm long at a height of 30 cm) in a distance of approximately 10 cm to the touch screen; dried cat food was used as rewards, which were gained from a small bowl situated below the screen, between the perch and the screen so that the birds had to lower their heads to reach the reward.

Each bird received one session per day which lasted between approximately three and 15 minutes depending on the bird’s motivation. Birds were tested in the morning before they were fed with various kinds of fruits, grain, milk products and vegetables. Water was available ad libitum. The experiment was conducted between September 2008 and October

2010. For logistical reasons, the three test birds and three not tested birds were relocated to a new aviary (3 m x 5 m) at the University of Vienna, Austria in October 2009. The other jackdaws were released to the wild. Test conditions in the new aviary, including the computer box and touch screen, were comparable to the setup in Grünau. Testing in Vienna was resumed four months after the relocation and full habituation to the new environment.

Procedure

Initially, the birds were trained in groups of several individuals to approach the touch screen and peck once at the correct position on the screen to gain a food reward. When a bird was reliably pecking on the screen, further training and testing procedures took place in visual isolation from the other individuals: after an individual was separated in the main indoor compartment, the experimenter (E; S.M.) started the program at the computer and moved back to the rearmost corner of the compartment to allow the test subject to approach the touch screen. The bird was free to stop working on the touch screen at any time and to roam freely in the compartment. When the bird did not touch the screen for five minutes the session was terminated, the bird was released to the others and a new session was started the next day. When a bird had finished its session the screen turned black and the bird was also released to the group. In the beginning of the experiment, a session consisted of 32 trials. During the breeding seasons in 2009 and 2010, the birds lost their motivation nearly completely and testing was paused for a few weeks. After the breeding season 2009, we started with sessions of only eight trials to avoid over-taxing the birds, but already after two weeks we increased the number to 16 trials. As this number of trials seems to be optimal for the jackdaws we kept this session length until the end of testing.

For the analysis, we always plotted 16 trials as a block, independent of the number of trials within a session, to analyse whether the birds reached the predefined criteria (see below). When a session was terminated by the bird within the first few trials, we assumed that the birds are not motivated and the scores were discarded; performance data was included in the analysis only if at least eight trials had been completed.

Training

In the training phase the birds were trained to a hierarchical sequence of five different coloured squares (A-E) (for a comparable testing procedure, see Lazareva & Wasserman 2006). For this purpose, two squares (each 6 cm x 6 cm) were presented simultaneously as a pair (e.g. A/B, B/C, C/D, D/E) on the screen. One square was located on the left side of the screen (from the left lower corner: 10 cm to the right and 11 cm to the upper edge) and the other one on the right side (from the left lower corner: 20 cm to the right and 11 cm to the upper edge) of the screen so that the two squares were 6 cm apart. As colours we chose blue (RGB:0;0;255), red (RGB:255;0;0), green (RGB:0;255;0), cyan (RGB:0;255;255), magenta (RGB:255;0;255), yellow (RGB:255;255;0) and grey (RGB:165;165;165) to have a maximal discrimination for the human eye. To avoid an influence of the sequence of colours, we assigned a unique colour sequence to each individual. The training was separated into four different phases. In the first phase the individuals were confronted with the first pair (A/B) only. Pecking A would be rewarded automatically and after an inter trial interval (ITI) of three seconds the next trial begun. When the incorrect stimulus B was pecked the screen turned black, and the bird had to wait for three seconds before a correction trial begun. The correction trials were repeated as long as the bird continued to peck the wrong stimulus. When it pecked the correct one, the bird was again rewarded and the next trial begun. In July 2009 the ITI for incorrect trials was extended to six seconds and an acoustic feedback was introduced in order to alleviate the training. The location of the correct stimulus (left / right) was randomized. Only in a correction trial the stimuli were presented on the same side until the bird chose correct. The bird had to be correct in at least 13/16 trials without requiring a correction trial over four consecutive blocks to ensure that the bird reliably pecked the correct stimulus. Then the bird was transferred to the next phase in which two pairs (A/B; B/C) were then presented equally often and in a randomized order, with no pair being presented more than three times in a row. This randomization was also adopted in the following phases. In the second phase, the bird had to learn that stimulus B, which was incorrect when presented together with A, was correct when presented together with C. Again the criterion to reach the next training step was to be correct in 13/16 trials over four consecutive blocks with the addition that the birds needed to be correct in 13/16 trials within each pair over the last two blocks, to ensure that not all errors occurred in only one pair. In the third phase the third pair was added, so that a block consisted of pairs of A/B, B/C and C/D. Criteria to reach the next phase remained the same as in phase two. In the last phase, the fourth pair was added and the birds were confronted with four different pairs (A/B, B/C, C/D, D/E) within each block. Again, the choice accuracy criterion was set to 13/16 across four consecutive blocks and 13/16 within each single colour pair across the blocks.

Correction training

As new pairs were not trained separately but were added to the already trained repertoire, we introduced correction training (CT) from the second phase onwards to simplify learning. A bird was given CT when its choice accuracy in one block of the training was less than 50% correct within a pair. A block of CT consisted of 16 trials; in phase II and III, 75% (12 trials) of the trials presented the low-performance pair; in phase IV, 81.25% (13 trials) consisted of this pair. The remaining 25% (4 trials) in phase II and III and 18.75% (3 trials) in phase IV presented the other pairs. From phase III on, the not over-represented pairs were equally often presented in one block. A bird returned to the normal training procedure when its performance in the low-performance pair was at least 80% correct across two consecutive blocks (phase II and III: 19/24; phase IV: 21/26). The CT was not considered for reaching the criteria to advance to the next phase.

Pre-test

When the birds mastered the criterion of training phase IV they were advanced to the pre-test phase. This phase was conducted to acquaint the birds with unrewarded trials, which became necessary in the test (see below), and avoid a drop in performance. Therefore, the birds received blocks of 16 trials in which four trials, one of each colour pair, were not rewarded when pecking correctly. The required choice accuracy to advance to the test was set to 75% (12/16) correct over five consecutive blocks. Additionally, the birds needed to be correct in 15/20 trials (75%) within each single colour pair across the last five blocks. When not reaching these criteria, the birds received further pre-testing.

Test

After passing the criteria of the pre-test the birds were advanced to the test phase. Here, the birds received eight blocks of 16 trials, which consisted of 14 training trials and two test trials. Training trials consisted of the four training pairs (A/B, B/C, C/D, D/E), which were equally distributed across the eight test blocks. Randomization and feedback was the same as in the training. The two test trials consisted of the test pair (B/D) and were presented with at least four and at most ten training pairs in between. In contrast to the training trials the test trials were unrewarded regardless of the birds' choice. There was neither a positive nor a negative feedback for those trials.

Analysis

On an individual level, we first tested for differences between the different training phases by using chi square tests; for each colour pair, we used Binomial tests to test for deviations from chance level. As the data were normally distributed, we used one-sample t-tests to test if the birds as a group deviated in their performance from chance. To assess if the birds' performance changed during testing, we ran a Pearson correlation. To evaluate the relative associative strength of the stimuli B and D we calculated the reward/non-reward ratio R_x by dividing the number of trials a stimulus was rewarded (N_r) through the number of trials a stimulus was non-rewarded (N_n), including all correction trials, correction training and the pre-test (Lazareva and Wasserman 2006). All tests were conducted two-tailed and alpha was set to 0.05. Data analysis was conducted using Sigma Plot 11.0.

Results

Training

The birds needed a mean of 7.33 ± 2.52 training blocks ($\bar{x} \pm SD$, range 5-10) to reach the criterion in phase I, 20.33 ± 6.35 blocks ($\bar{x} \pm SD$, range 13-24) in phase II, 61.67 ± 51.87 blocks ($\bar{x} \pm SD$, range 18-119) in phase III and 56.00 ± 28.58 blocks ($\bar{x} \pm SD$, range 39-89) in phase IV. A Chi-square test revealed a significant difference between the four phases for each individual (Bruce: $\chi^2 = 148.792$, df = 3, $P < 0.001$; Udo: $\chi^2 = 113.977$, df = 3, $P < 0.001$; Pronto: $\chi^2 = 25.562$, df = 3, $P < 0.001$, Fig. 1). There was no consistent pattern in the number of blocks the three birds needed to reach the criterion in the different phases. All three birds at least tended to learn the second pair slower than the first pair (χ^2 tests: $P \leq 0.059$). In phase III Bruce and Udo needed significantly longer than in phase II to reach the criterion (χ^2 tests: $P \leq 0.001$), while there was no difference for Pronto between the two phases (χ^2 test: $P = 0.355$). In phase IV finally, it was Udo and Pronto, which needed significantly more blocks than in phase III to reach the criterion (χ^2 tests: $P \leq 0.004$), whereas Bruce needed significantly less blocks in phase IV than in phase III (χ^2 test: $P < 0.001$, Fig. 1).

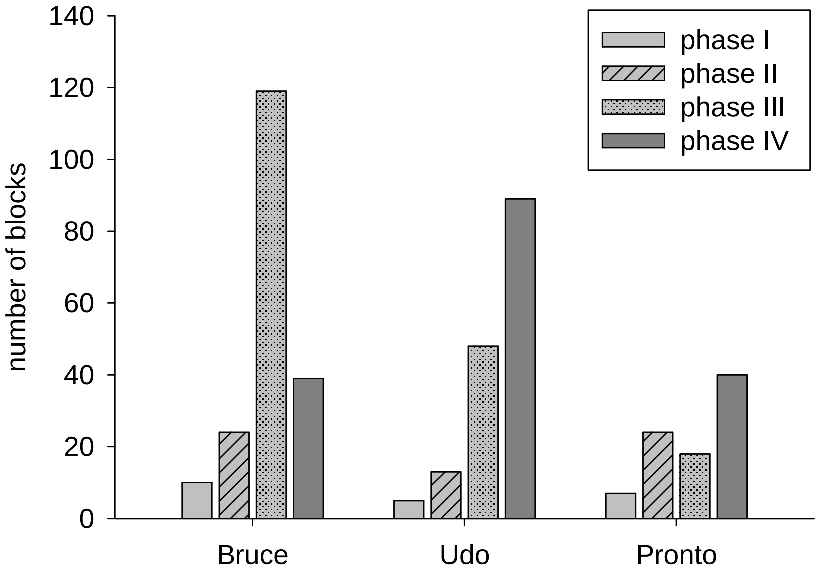

Figure 1: The number of blocks needed per bird to reach criterion in each training phase.

Correction training

Within phase II only Pronto needed a correction training of seven blocks, while in phase III all three birds received a CT (Bruce: 14 blocks; Udo: 35 blocks; Pronto: 31 blocks). In phase IV again Udo and Pronto needed additional training of the new pair (Udo: 15 blocks; Pronto: 7 blocks).

Pre-test

All three jackdaws needed only the minimum of five blocks to reach the criterion for the pre-test phase. Within each block and in each colour pair across all blocks they were correct in at least 75% of the trials (range: blocks: 12-16 trials (out of 16); colour pairs: 15-19 trials (out of 20)).

Test

All three birds chose colour B significantly more often than colour D in the test phase (Binomial test: Bruce: $P < 0.021$; Udo: $P < 0.004$; Pronto: $P < 0.001$, Fig. 2) so that the birds' choice within the TI pair differed significantly from chance (one-sample t-test: $t = 7.201$, $df = 2$, $P = 0.019$). Pronto was correct on all 16 test trials, while Bruce made an error each in block 1, 2 and 7, and Udo made an error each in block 6 and 8. In the non-transitive pairs, the birds were significantly above chance in the end-anchor training pairs across all eight test blocks (one-sample t-test: A/B: $t = 12.873$, $df = 2$, $P = 0.006$; D/E: $t = 7.133$, $df = 2$, $P = 0.019$) while they performed at chance level in the middle training pairs (one-sample t-test: B/C: $t = 1.893$, $df = 2$, $P = 0.199$; C/D: $t = 3.047$, $df = 2$, $P = 0.093$, Fig.2). The deterioration in pair B/C is due to the fact that Bruce and Udo did not perform significantly above chance level (Binomial test: both: $P \geq 0.185$, Pronto: $P < 0.001$). Failure to reach significance in pair C/D is a consequence of the individual performance of Udo, which was again not significantly above chance (Binomial test: $P = 0.185$, all others: $P \leq 0.036$). However, Bruce and Udo were still correct in more than 50% of the trials within each pair. Also, the mean performance of the birds did not increase or decrease over the course of testing (Pearson: $N = 8$, $r = -0.338$, $P = 0.413$). Finally, we calculated the reward/non-reward ratio ($R_x = N_r/N_n$) for stimulus B and D. For all three birds, R_B was larger than R_D (R_B:R_D: Bruce: 3.24:0.54; Udo: 3.43:1.21; Pronto: 5.00:0.45).

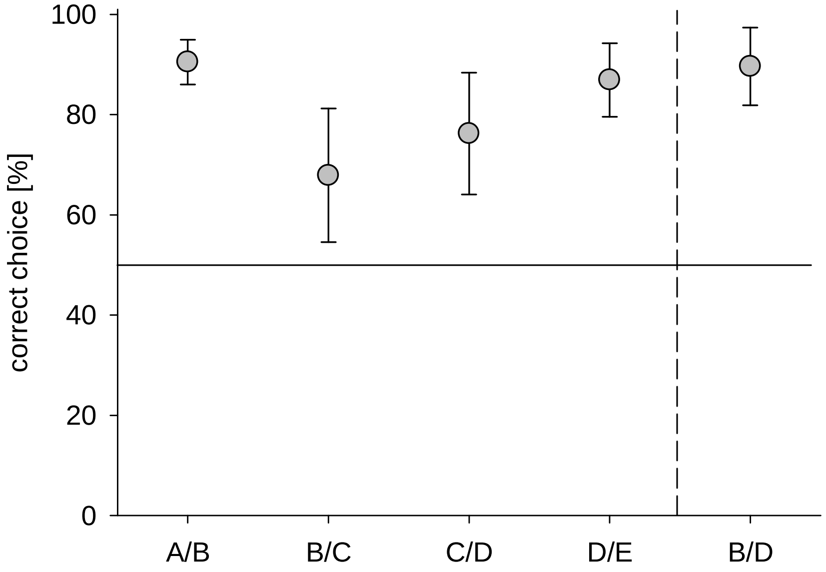

Figure 2: Choice accuracy of all three birds across the eight test blocks within the four familiar training pairs (left side of the dashed line) and the TI pair (right side of the dashed line). The horizontal line indicates chance level. Plots show mean ± SD.

Discussion

Our study shows that the three tested jackdaws were able to infer the relationship of two non-adjacent stimuli, which had never been presented together before. As other socially living animals, it seems that jackdaws possess the capability to transitively infer unknown relationships. The subjects of several other studies had been trained on the same five item series, but comparisons are difficult because of different training criteria and small differences in the daily training regime (Gillan 1981; Weiß, Kehmeier, and Schloegl 2010; Lazareva et al. 2004; Lazareva and Wasserman 2006). In the most comparable study, rhesus monkeys (Treichler and van Tilburg 1996) learned the sequence only slightly faster than the jackdaws.

Due to the non-reinforcement of the TI trials during the test, it is unlikely that the task was solved via a rapid learning mechanism. Additionally, Pronto was correct in 100% of the test trials and Udo was error-free until block seven, while Bruce made an error each in the first two blocks. Thus, the birds solved the task instantaneously. Generally, our data support the assumption that TI is a ubiquitous ability in social animals and seems to be wide-spread in the animal kingdom. Furthermore, performance seems to be linked to the degree of social complexity, as the studies by Bond et al. (2003; 2010) and Maclean et al. (2008) found that the accuracy and robustness of TI correlated with the degree of sociality. Additionally, Weiß et al. (2010) found that the early social environment of goslings seemed to have influenced their performance in a TI task; in this study, goslings that grew up in smaller families required less training to learn the artificial hierarchy presented in the test than goslings in larger families. The authors argued that small families are more involved in interactions with flock members and therefore, goslings of smaller families may have more opportunities to learn about dyadic relationships than goslings with more siblings. Accordingly, it seems as if the link between social complexity and TI is existent but whether it is dependent on group size, structure or the number of interactions within a social system is still unclear. However, the claim that TI is linked to social complexity depends so far on correlative data only, as non-social animals have not been tested. It is noteworthy that recent studies on a solitary living tortoise species indicate that despite their solitary lifestyle they possess socio-cognitive skills such as gaze following (Wilkinson, Mandl, et al. 2010) and social learning (Wilkinson, Kuenstner, et al. 2010) and an exploration of TI in these or other solitary living species seems worthwhile.

In addition to the question of which animals are capable of TI, the underlying mechanisms are not yet fully understood. To answer this question longer hierarchical sequences which contain more than one TI pair are advantageous, because then pairs with different number of stimuli in between are available ("symbolic distance effect" Moyer and Bayer 1976) and more possibilities to clarify the underlying mechanisms of TI are given (Bond, Wei, and Kamil 2010). Unfortunately, we were only able to test a five item series due to logistical reasons and the already very long testing procedure of two years. In consequence, we are restricted in our possibilities to assess the cognitive mechanism the jackdaws relied on.

Nevertheless, we were able to calculate the reward/non-reward ratio R_x for the different stimuli of a TI pair. Similar to other studies (Lazareva et al. 2004; Lazareva and Wasserman 2006; Zorina, Kalinina, and Markina 1996), for all three jackdaws was this ratio biased towards B, thus suggesting the possibility that the birds solved the task associatively. Lazareva and colleagues (2006) tested pigeons and designed the experiment in the way that for some pigeons, $R_B > R_D$ and in others it was vice versa with $R_B < R_D$. However, independent of the relative associative strength of B, all pigeons preferred B over D in the TI test. Thus, it is only suggestive and not conclusive that our jackdaws solved the TI test according to an associative model and not to a relational one. In conclusion our study shows that jackdaws are capable of TI, but the underlying mechanisms they used to solve the task are still unclear.

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Chapter 6: Conclusion

The present dissertation supports the notion that parrots are capable of reasoning. One African grey parrot *Psittacus erithacus* has demonstrated the ability of inference by exclusion, which has so far only been shown in Great apes (Call 2006). Therefore, the results support the convergent evolution hypothesis (Emery and Clayton 2004) which suggests that similar levels and expressions of intelligence have developed in parallel in birds and mammals.

As shown in Chapter 4, one Grey parrot succeeded in an inference by exclusion task. The possibility that this success was based on associative learning mechanisms was controlled and tested for and was rejected as a valid explanation for the bird's behaviour. It is, therefore, concluded that the bird had formed a mental representation of the contents of the cup. The result contradicts Penn and Povinelli's (2007a, b) conclusion that insight and reasoning is not expressed in non-human animals and supports the notion that non-human animals are capable of this complex form of reasoning (Bird and Emery 2009; Call 2004, 2006; Emery and Clayton 2004; Pepperberg 1999; Taylor et al. 2009). The fact that only one animal succeeded in the inference by exclusion task might leave the data open to criticism. However, the successful performance of this one animal shows that the cognitive skill tested for lies within the general capabilities of the species. In fact, there is evidence suggesting that individual differences in performance levels, such as some animals succeeding while others do not, might give a deeper insight into the nature of the cognitive processes underlying a specific task (Plomin 2001). Such differences can, for example, be explained by differences in general intelligence, pre-experience, or personality.

Species with high general intelligence are prone to large individual differences on complex tasks, while easy tasks produce relatively unanimous results (Plomin 2001). Thus, within a species some individuals can sport more strongly expressed cognitive abilities than others. Colloquially said, some individuals within a species might just be smarter or differently motivated than others. Intra-species variability within the more complex tasks as compared to the simple tasks is exactly what has been shown in the present dissertation. No individual differences were found in a simple object manipulation task performed by carrion crows *Corvus corone corone*, jackdaws *Corvus monedula*, and African grey parrots in Chapter 2 and 3 where the birds were tested for the effects of a simple low-level mechanism, local enhancement. In contrast, large differences were found in the more difficult exclusion task in the crows in Chapter 2, where the birds were required to choose one target based on the knowledge about another target. Similarly, Grey parrots showed great intra-specific variability in a highly complex inference by exclusion task described in Chapter 4, in which the parrots were prevented from using any low-level mechanisms in their choice of the correct target. Interestingly, there also seem to be differences between individuals within the same species of how enhancement affects their ability to solve higher order problems. While some birds are unable to solve a problem due to overshadowing from low-level mechanisms, others appear unaffected.

While the individual differences may be explained within the general intelligence framework, it is also possible that the birds' previous experiences and histories, which are sometimes not fully known, are responsible for the differences in performance. Supporting this assumption a study by Pepperberg (2007) found that Grey parrots varied in the methods with which they tried to master a means-end understanding task. Even though her study offered the inequality of the language training the birds had received as a possible explanation for the individual differences, the author states that different personalities cannot be excluded as an explanation.

The possibility that differences between individuals are biologically meaningful variations has in the past often been neglected (Wilson 1998), but now it is generally accepted that animals have different personality types which appear to be closely linked to those of humans (Carere and Eens 2005; Carere and Locurto 2011). The effects of personality on fitness (Dingemanse and Réale 2005), learning (Titulaer et al. 2012), and the ability to form sets of routine (Groothuis and Carere 2005) have already been established, while there is little empirical evidence linking personality traits with other cognitive abilities. For a personality trait to be established as such, it is paramount to provide, besides trait linkage, evidence of behavioural consistency over time and across circumstances in a large number of animals. However, the present thesis was not designed to test for personality differences in birds. In reverse though, differences in personality could explain the large individual differences found in Chapter 2 and 4. Furthermore, it appears that similar to the notion of general intelligence, personality differences are only reflected in difficult tasks (Titulaer et al. 2012), again reflecting the data presented above.

A promising avenue for future studies would be to test for personality differences in a large number of birds and to link these to a whole battery of cognitive tasks, including tests of various different cognitive domains. A comprehensive cognitive test battery has already been established for human children and Great apes by Herrmann (2007) and adapted by Schmitt and colleagues (2012) for the use with monkeys. It is now time for an equivalent test battery for the use with birds. Testing the effect of personality differences on cognitive performance would be particularly interesting in a long-term study providing a closely controlled environment for all subjects from fledgling on, thus avoiding any differences in prior experience. Additionally, it would be worthwhile to attend to differences in motivation and distractibility within and between species as those factors could also lead to individual differences in cognitive tasks.

Besides the interesting intra-specific differences the present thesis has also revealed meaningful inter-specific differences. Various studies of the project ‘reasoning in birds’ of our study group have found that ravens *Corvus corax* (Schloegl et al. 2009), African grey parrots (Schmidt et al. unpubl.), and carrion crows (Chapter 2) were able to show successful exclusion performance in a cup-lifting experiment, while jackdaws (Schloegl 2011) and keas *Nestor notabilis* (Schloegl et al. 2009) were unsuccessfully in the same setup. It has been suggested that, at least in corvids, caching abilities might be a key to solving this task (Schloegl et al. 2009; Schloegl 2011; Chapter 2), as both ravens and carrion crows are caching species and jackdaws are not. However, this does not explain the differential performance of the parrots. Although the keas failure might well be due to an overshadowing effect of their extreme neophilia (O'Hara et al. 2012), no obvious explanation appears to fit in the successful performance of the Grey parrots.

However, it is possible that the dissimilarities can be explained with differences in general intelligence levels of the different species. Grey parrots, for example, might possess a high level of general intelligence and might, thus, be able to solve tasks which are not immediately ecologically relevant for them. Similarly, it is possible that the jackdaws have a lower level of general intelligence than the other corvid species that have been tested on the same task, thus, failing the exclusion task which appears to be of little ecological relevance for them.

The adaptive specialization hypothesis (de Kort and Clayton 2006; Kamil 1987), however, would be in favour of the aforementioned adaptive qualities of the task. As jackdaws do not cache food they might have less strongly expressed physical cognition abilities. Nonetheless, jackdaws are very social birds that have been shown to be sensitive to social cues and social learning (Scheid et al. 2007; Schwab et al. 2008). Chapter 5 describes a task which is believed to experimentally reflect a social network – transitive inference. The results show that jackdaws were able to solve this task successfully. However, at present it is not possible to determine with reasonable certainty which mechanism the birds used to solve the task, mental representations or associative learning. To find out which of the two possible mechanisms was used, future studies should introduce dissociation between the two targets by artificially increasing the value of one stimulus against the direction expected by the mental representation of the target list, as was done by Lazareva (2006) with pigeons *Columba livia*. However, the results point to the notion that the jackdaws’ ecology might influence their abilities and, thus, lend support to the adaptive specialization hypothesis. To further investigate this issue, future studies should test the performance of the only other non-caching corvid species, the white-throated magpie-jay *Calositta formosa*.

In contrast to the adaptive specialization hypothesis, the general process view states that closely related species with different ecologies should not show large differences in their cognitive abilities (Bolhuis and Macphail 2001). As such high cognitive performances amongst birds would be expected in the parrot and corvid families. Overall, high cognitive performance has been found in all the tested species (Gould-Beierle 2000; Pepperberg 1999; Wascher et al. 2012; Chapter 2-5). However, significant differences within the families have also been noted (Schloegl et al. 2009; Schloegl 2011; Chapter 2-5). At present, it is impossible to know whether these differences are based on a true inability of some species to succeed in the given tasks or whether they are simply due to the experimental design and execution of the tasks.

To date only little information is available on any possible interactions between the different models integrating, for example, general intelligence with the adaptive specialization hypothesis (Reader et al. 2011). Based on the results presented in the present thesis it appears possible that the importance of adaptive specialization is dependent on the level of general intelligence. Thus, for those animals that possess only comparatively low general intelligence areas of adaptive value might be of great importance. They might show outstanding performances in one particular area which is especially relevant to their ecological situation while not being very advanced in performing tasks outside their ecological niche. Those animals that sport high general intelligence, however, might be able to succeed in a whole range of complex tasks, independent of whether these are of immediate adaptive value to them. General intelligence might originally have been an adaptive trait because it increased flexibility, but through its development it might have freed the species possessing this trait from the immediate adaptive pressures of their particular niche.

Thus, assuming that African grey parrots have high general intelligence, this combined model would explain their impressive performance on the inference by exclusion task which might not be of great adaptive value to a non-caching species. Similarly, assuming comparatively low general intelligence in jackdaws, the model would explain their good performance in the transitive inference task while failing in tasks of a similar level of complexity in a different cognitive domain, which might be less adaptive to their social but non-caching nature.

To clarify the respective importance of ecological relevance and general intelligence future studies should test ecologically irrelevant tasks as part of a large cognitive test battery which approaches each species' general intelligence across domains. For example, tests on tool-use related abilities in non-tool-using species are likely to provide a clearer idea of a species' general intelligence (Bird and Emery 2009; Tebbich et al. 2007), given that the species' physical abilities are taken into account. Furthermore, additional investigations of transitive inference in non-social species are needed to determine whether this mechanism, which is generally accepted as social throughout the literature (Bond et al. 2003; Bond et al. 2010; Maclean et al. 2008), is indeed only found in social animals. Here it would be particularly interesting to test species which are truly solitary from hatching onwards and have never received any parental care, such as red-footed tortoises *Geochelone carbonaria* or octopus *Octopus vulgaris*. Thus, a detailed comparison of the performance on ecologically relevant and irrelevant tasks in both closely related bird species and those of distantly related families is called for at this stage.

In conclusion, the results of the present dissertation support convergent evolution, as different bird species have been proven proficient in complex cognitive tasks. In particular, inference by exclusion has been shown in an African grey parrot, which is the first demonstration of this ability outside of great apes and humans (Call 2006). Furthermore, the results suggest that the cognitive abilities of birds might be best explained by a model combining the notion of general intelligence with the adaptive specialization hypothesis. As such, it is suggested that Grey parrots have a high general intelligence level allowing them to readily solve even adaptively irrelevant tasks. In contrast, jackdaws are suggested to possess low general intelligence in comparison with other corvids, therefore, excelling only in tasks that are ecologically relevant to them. Interestingly, low-level mechanisms such as local enhancement affected all tested species, suggesting that these are basic traits which are independent of the level of general intelligence and adaptive relevance. Finally, my present results show that reasoning does not only exist in humans, but also in non-human animals and might help bridge the gap between general intelligence and adaptive specialization.

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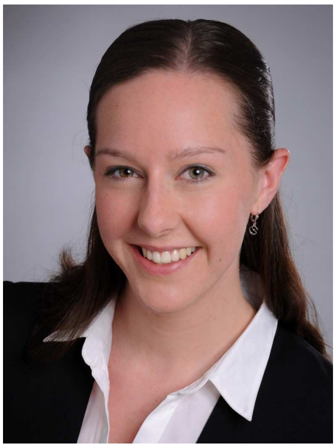

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Poster	Mikolasch, S., Kotrschal, K., Schloegl, C.: “Transitive inference in jackdaws (*Corvus monedula*)” ASAB summer conference in St. Andrews, Scotland; August 2011
Poster	Mikolasch, S., Kotrschal, K., Schloegl, C.: ”African grey parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food” Compcog Conference in Prague, Czech Republic; May 2011
Talk	Mikolasch, S., Kotrschal, K., Schloegl, C.: “Making the best of a bad job: African grey parrots use inference by exclusion to find hidden food” Ethological Society meeting in Zurich, Switzerland; February 2011
Talk	Mikolasch, S., Kotrschal, K., Schloegl, C.: “It is hard to see food go: do grey parrots and jackdaws rely on causal or social information to find hidden food?” ECBB – European Conference on Behavioural Biology 2010 in Ferrara, Italy; July 2010
Talk	Mikolasch, S., Kotrschal, K., Schloegl, C.: “Causal knowledge vs. local enhancement: How do crows find their food?” ASAB Easter meeting 2010 in Exeter, Great Britain; April 2010
Poster	Mikolasch, S., Kotrschal, K., Schloegl, C.:” Do crows use causal reasoning or social information to locate hidden food?” 5. Thementagung der Ethologischen Gesellschaft in Berlin, Germany; February 2010
Talk	Mikolasch, S., Kotrschal, K., Schloegl, C.:” Do crows use inference to locate hidden food?” Graduiertentreffen Verhaltensbiologie in Seewiesen”, Germany; November 2009

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