

Bonding, Mentalising and Rationality

Auguste M.P. von Bayern^{1,2} and Nathan J. Emery^{1,3}

¹ Sub-Department of Animal Behaviour, University of Cambridge, UK

² ~~now at the~~ Department of Zoology, Oxford University, UK

³ ~~now at the~~ School of Biological and Chemical Sciences, Queen Mary University, UK
~~London, UK~~

In theory, reasoning about one's group-members' mental states and adjusting one's behaviour accordingly could be an example of process rationality. Whether animals evolved mentalising abilities as an adaptation to the competition arising within groups remains debated. Often simpler mechanisms, such as behaviour reading or embodied practices may be sufficient for appropriate behavioural responses. Selection for cooperative bond formation within the group may have similarly shaped the socio-cognitive abilities of social animals and may afford predicting and explaining the behaviours of one's partner in terms of mental states more than competition.

1 Introduction

Aristotle's teachings of rationality as being specific to mankind and so distinguishing us from nonhuman animals, still represents the opinion of many people today. Since interacting with our social environment determines most of our everyday lives, human rationality is to a large extent concerned with reflecting social scenarios, theorising about other's possible thoughts and intentions and devising appropriate strategies and counter-strategies. An important tool in making rational social decisions is our 'theory of mind' (ToM); we can de-centre from our selves and take the perspective of another person to predict what is rational for them to do. Based on this knowledge we can decide rationally ourselves what to do (Hurley and Nudds, 2006).

Over the last decade, evidence has accumulated to suggest that several animal species engage in complex social reasoning and are capable of predicting the behaviour of others and counteract accordingly and in a flexible manner (e.g. Hare et al., 2001; Emery and Clayton, 2001; Bugnyar and Heinrich, 2005; Dally et al., 2006; Clayton et al., 2007). This has ignited the debate over whether animals contemplate others' mental states and act upon their resulting beliefs in a human-like rational manner.

Certainly, the question of whether animals can be rational depends on how one defines

rationality. Animals can behave rationally without the underlying processes that generate their behaviour necessarily being rational (Hurley and Nudds, 2006). For example, the well concerted actions within an ant colony or a bee hive, or the foraging decisions of starlings, are clearly not the outcome of reasoning and rational thought processes. Evolution fine-tunes animals to behave in a way that maximises their genetic fitness (Kacelnik, 2006). In this sense, rational behaviour is indistinguishable from evolutionary adaptiveness, which is agnostic of the processes that lead to it.

In contrast, cognitive psychologists are interested in 'process rationality' (Hurley and Nudds, 2006), because they are investigating *how* animals think, i.e. the proximate cognitive mechanisms underlying the animals' behaviour. To be considered as rational, according to Hurley and Nudds' (2006) definition, the process by which an animal arrives at a decision has to be rational. In other words, an animal needs to be capable of selecting the appropriate means to achieve a given goal. Important questions in this context are whether animals can represent causality and whether their behaviour is generated by reasoning, e.g. reasoning in terms of mental states, or abstract causal relations. However, appropriate means can also be chosen through simpler, more practical mechanisms, such as behaviour reading and associatively learnt heuristics, and it remains debated whether such practical processes should be regarded as rationality (Hurley and Nudds, 2006).

This chapter is split into three parts. First, we provide a brief background on the most widely accepted and a more recent, hypothesised selection pressure for the evolution of social intelligence and ToM, namely competition and cooperative bond formation. Second, we present some preliminary data on the socio-cognitive abilities of a bond-forming corvid, the jackdaw. Third, we discuss the theoretical adaptiveness of mentalising comparing the two selective pressures.

2 How did the ability to reason about other minds evolve?

2.1 Two selection pressures for social intelligence

Group living entails both benefits and costs. The competition for resources inevitably arising within social groups represents a platform for cognitive abilities that reduce these costs to evolve. There are two efficient ways of coping with one's competitive social environment and hence two kinds of selection pressure that could be present in social living animals; the Machiavellian approach, i.e. manipulating, outwitting or tactically deceiving others and the Vysgotskian approach, i.e. forming bonds with collaborators and having allies to provide mutual support in competitive situations with other group-members.

The former has constituted the heart of the 'Machiavellian Intelligence Hypothesis' (Byrne and Whiten, 1988), which suggests that primates evolved superior cognitive abilities in an arms race with ever smarter and more deceptive conspecifics. Suggestive evidence for this is the finding that group size correlates with relative brain size in primates (Dunbar, 1998). The larger the group, the more complicated are the resulting networks of relationships, and hence the necessary social knowledge and social manoeuvring required.

Recently, more attention has also been focused on the latter evolutionary pressure that may select for higher socio-cognitive abilities, namely forming and maintaining (a) relationship(s) with (a) collaborator(s). Although strategic alliances and coalition formation also form part of the Machiavellian or Social Intelligence Hypothesis (Harcourt, 1992), little research has been carried out on the cognitive mechanisms that may underlie the formation and cultivation of such relationships. Recently, it has been suggested that it is not the quantity, but the quality of valuable relationships (van Schaik and Aureli, 2000) or hereafter bonds, that may pose cognitive demands (Emery et al., 2007). Across several mammalian and vertebrate taxa (including ungulates, carnivores, bats and birds), long-term pair-bonded species exhibit larger relative brains than species with other mating systems (Dunbar, 2007; Emery et al., 2007; Shultz and Dunbar, 2007; Dunbar and Shultz, 2007) indicating that pair bonding may also pose cognitive demands. This phenomenon is independent of bi-parental care, the most accepted evolutionary explanation for long-term monogamy, even in birds (Shultz and Dunbar, 2007). Although no such relationship between mating system and brain size was found in primates (Shultz and Dunbar, 2007; Dunbar and Shultz, 2007), primates, irrespective of their mating system, characteristically live in *bonded* social groups, i.e. large social groups with a stable structure of matrilineal or patrilineal kin relations, in addition to coalitions and long-term valuable relationships between unrelated individuals of either sex. Hence, according to Dunbar and Shultz (2007) "[...] the relationships of anthropoid primates involve a form of "*bondedness* only found elsewhere in reproductive pair bonds" (p. 1346).

Although the ultimate and proximate causes of animal bonding are only beginning to be understood, it has become very clear that social bonds have consequences for virtually all aspects of behaviour (Carter et al., 2006). They may be one of the most fundamental solutions to both social and ecological as well as emotional challenges (Carter, Ahnert et al. 2006). Yet, relationships are still seen as mere epiphenomena, spawned by the issues of real biological interest, i.e. mate choice and parental investment (Dunbar 2007). This fails to recognize the fact that attachment and bonding are evolved processes and that the mechanisms permitting the development of social bonds are most likely to be very ancient (Carter, Ahnert et al. 2006) ~~(Carter, 2005: #2450)~~.

2.2 Cognitive challenges of bonding

What exactly may make bonding cognitively complex has yet to be investigated, however one can speculate that the ability to coordinate and fine-tune with one's partner in order to improve the quality of one's collaboration may be an essential component. This may involve cognitive abilities such as co-orienting and sensitivity to the partner's attentional state and focus. Another component may be the cognitive skills necessary for cooperative action. Given the presumed adaptiveness of cooperative bonds for group-living, Tomasello et al.'s (2005) proposition that cooperation has only been an important driving force in the evolution of human cognition seems premature. They arrived at this conclusion because it explained the superior performance of young human infants compared to great apes, in cognitive tests involving cooperative problem solving and communication (Tomasello et al.,

2005). From an early age, human infants exhibit powerful skills and motivations for cooperative action and joint communication, and other forms of shared intentionality (Moll and Tomasello, 2007). Therefore, they are judged to be biologically adapted for cooperation whereas great apes are not (however see Melis et al., 2006a; Melis et al., 2006b). This idea has been termed the Vygotskian Intelligence Hypothesis (VIH) to emphasize the impact of cooperation on the development and evolution of the human intellect (Moll and Tomasello, 2007). Tomasello et al.'s (2005) conception of the VIH, as well as the cognitive study of cooperation in general (Seed, Clayton et al. 2008) has largely been anthropocentric and primatocentric. Avian species have not been considered until very recently, even though the pair bond in birds is an excellent example of cooperative behaviour in action (Black, 1996) and cooperation in avian species has been a major issue in behavioural ecology for years (Ligon, 1983).

According to Moll and Tomasello (2007), the special skills for cooperative action that distinguish human infants from apes include joint attention, creating joint goals with others, joint intentionality, cooperative communication and special motivations for helping and sharing with others. In the following, we present preliminary data and argue that such abilities may also be found in long-term pair bonded corvids.

3 Pair-bonded jackdaws are sensitive to their partner's direction of attention

Jackdaws are semi-colonial corvids that form long-term pair bonds like most other corvids. The pair bonds of jackdaws form the basic unit of jackdaw society (Roëll, 1978). Jackdaw partners are virtually inseparable and exhibit a wide range of mutual affiliative and bond-reinforcing behaviours, which they perform at high frequencies (Wechsler, 1989; von Bayern, 2008). For example they are strongly motivated to share food with their partner and actively offer and give them food (von Bayern et al., 2007). Jackdaws benefit from their bond in various ways, for example, mutually supporting each other in agonistic situations and selectively intervening in fights on their partner's behalf (Roëll, 1978). Jackdaws also cooperate in the acquisition of resources, most importantly a nest cavity, their most crucial fitness determinant. Nest hole acquisition and defence requires long-term cooperation and tight coordination throughout the entire year, because competition for suitable cavities is so high that breeding holes may only be successfully defended by experienced pairs (Roëll, 1978). Moreover, like the most other corvids, jackdaws exhibit extended biparental care and rely on close cooperation during the breeding season and thereafter to raise their offspring.

The corvid family has attracted much attention in animal cognition research during the last decade, because they appear to parallel apes in their cognitive abilities as well as exhibiting a comparable relative brain size (Emery and Clayton, 2004). Along with Hare's studies on chimpanzees (2001; 2000), studies conducted on food-caching corvids have provided some of the best available evidence for visual perspective taking and knowledge attribution in non-human animals to date (Emery and Clayton, 2001; Clayton and Emery, 2007).

However, the studies on corvids to date have focussed on the competitive dimension of

social life taking advantage of the food-caching and pilfering paradigm. We tested jackdaws in a cooperative paradigm, the object-choice task, a benchmark test for examining whether animals can use others' focus of attention or social communicatory cues to locate food hidden under one of two containers (Anderson et al., 1996). Determining others' direction of attention and identifying the object in their focus are socio-cognitive skills regarded as prerequisites for a mentalistic understanding of others' visual perception (perceptual ToM; Premack and Woodruff, 1978), the most fundamental form of mental state attribution. The object choice task not only requires the subject to attend to the same object another individual is looking at (joint attention), but also requires some understanding of the communicative intent of the cue-giver, hence 'shared attention' (i.e. two individuals attend to the same object and are aware that they are both attending to it; Emery, 2000). The cooperative context of the object choice task has turned out to be problematic for some species, which compete for food under natural circumstances. Several species require training before they can use the provided cues. Another problem has been that in most experiments the cue-givers were humans rather than conspecifics which could have masked the investigated abilities in some species.

In this experiment, we tested the jackdaws with conspecifics in order to determine whether subtle behavioural cues (other than local enhancement) could be used to locate hidden food, and whether the jackdaws' performance in this cooperative task depended on the identity of the cue-provider, i.e. their partner or another group-member.

3.1 Methods

Subjects. The subjects were 12 hand-raised jackdaws kept in a 10m x 12m outdoor aviary with natural vegetation and adjacent experimental compartments. They were fed on an ad-libitum diet consisting of minced beef heart, curd, rice, dried insects, a cereal and seed mixture and several kinds of fruit and berries. Prior to the experiment they received an extensive training and habituation phase to a test box in which the experiment was conducted (see **Figures 1 and 2**). They had been trained to fly into the test box, and were accustomed to being confined in the different compartments for up to 6 min, alone or with others and were used to the operating noises and movements of the guillotine doors. During experiment 1, the subjects were 2 yr old, apart from one 1 yr old bird and one 3 yr old bird, which had been hand-raised and kept under similar conditions. To increase the sample size for each group (non-affiliate and partner), all the birds served as both subjects and informants.

Set-up. The experiment was conducted in a test box (150cm x 45cm x 50cm), consisting of 3 adjacent compartments (45cm x 50cm x 50cm). During the test, the subject and another bird, the informant, sat opposite one another in the 2 extreme compartments (Figure 2), which were both separated from the middle section (Figure 1a) by transparent wire-net guillotine doors (Figure 1b and c). The two birds could therefore see each other whilst having full view of two cups in the middle section (Figure 1c, Figure 2).

The middle section itself was split into two parallel corridors by a semi-transparent Plexiglass partition (Figure 1c, e, f). The cups were placed in the centre of the middle section at either side of the partition over two circular hollows, which could be baited from underneath

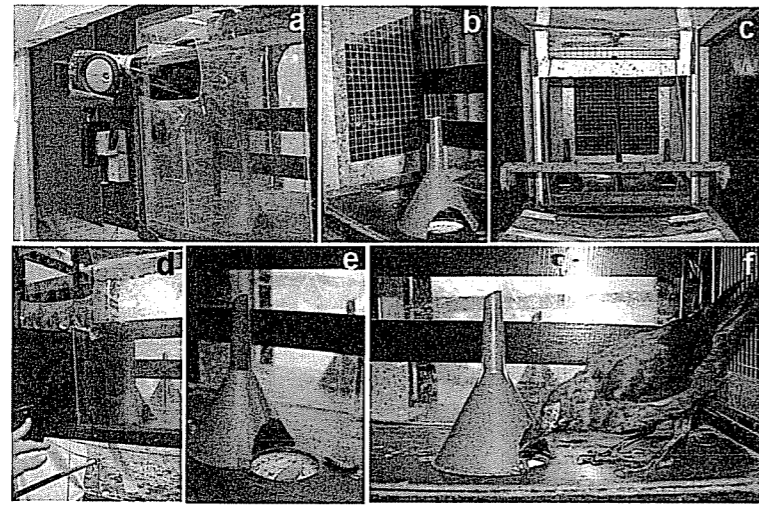


Figure 1. Experimental setup inside the test box (a) middle section with camera and middle partition; (b) cup with opening and visible hollow; (c) view from the informant's compartment into the 2 corridors of the middle section the 2 cups; (d) opaque screen that can be inserted into the middle section to cover the cups from the subject's view during baiting; (e) baiting through the opening in the hollow under the cup; (f) jackdaw retrieving food.

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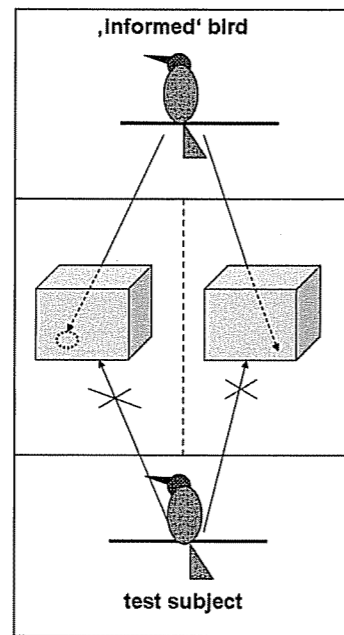


Figure 2. Experimental setup. The arrows represent the line of sight of the informant (the dotted arrows indicates that it can look into both cups. The crossed out arrows symbolise that the subject has no visual access into the two cups. The dotted circle denotes the hidden food reward.

Table 1. Individual and group performance for the 3 test conditions tested.

Subject	Subject's Sex	Sex N.A.	Dominance	Partner	Non-Aff.	Control
Leo	♂	opposite	>	8	6	4
Mucke	♀	same	>	7	7	3
Anders	♀	same	<	7	5	3
Chocolate	♀	same	<	9	6	5
Tschok	♂	opposite	=	9	7	7
Csoka	♀	opposite	<	6	7	7
Magret	♀	same	<	7	6	6
Spinni	♂	opposite	>	8	4	6
Franzi	♀	opposite	<	7	4	7
Traute	♀	opposite	>	8	7	8
Zorro	♂	opposite	>	5	7	5
Average				7.36*	6.00	5.55

*above chance performance, binomial probability for 12 trials (or t for groups), $p < 0.5$

7 point

through a re-sealable opening (Figure 1e). Towards the side of the informant, the cups had a large opening so that the informant could look inside and see which cup contained food (Figure 1b and f). An opaque screen could be inserted sideways in the middle section blocking the cups in the two corridors from the subject's view during the baiting process (Figure 1d).

One problem was controlling the position of the informant in order to ensure that the subject did not receive local enhancement cues; i.e. the informant did not just sit close to the baited cup, and so the subject use this information rather than specific social cues. The informant was therefore restricted to sit only on the middle of the perch. This was achieved by fitting the perch with reversed blunt pins sparing a 10cm section in the middle so that the bird could just perch in the centre. Additionally, the floor of the compartment was layered with double-sided sticky tape, which the birds avoided walking or standing on. The tape was omitted in the centre of the floor beneath and in front of the perch since some individuals refused to sit on the perch, even if the ground was sticky.

12

Pre-test training. Test trials was preceded by a training phase during which the birds had to learn (a) how to retrieve food from a cup by pushing it off the hollow, (b) that just one of the two cups was baited at a particular time and finally (c) that they only had one choice after which the other door was blocked and the subject was confined again to its compartment. During the initial training phase, the opening in the cup was turned towards the subject so that they could witness the baiting process and see which cup contained food. After some initial training, the cups were turned around each time the baiting had been completed before the subject bird could choose. Following the training phase and prior to the experiment, each

bird had been given a further 30 side randomised practice trials. The pre-training thus ensured that the subjects had a comparable level of prior experience to the test situation.

12 > **Experimental conditions.** The subjects were tested in 3 experimental conditions: (a) with their Partner as the informant; (b) with a Non-affiliate informant (the same individual across all trials) and (c) without an informant (Control condition). Since the dominance relationship between the Non-affiliate and the subject may have affected the subject's choice, dominance was balanced across individuals. 5 subjects were tested with a higher-ranking and 5 subjects with a lower-ranking individual. The remaining subject was tested with an individual of the same rank position (see **Table 1**). The sex of the Non-affiliate was opposite to the subject's sex in most cases, but since the group was female biased and contained two female-female pairs, females from such pairs were also tested with a female Non-affiliate. Each experimental condition consisted of 3 tests, which in turn comprised 4 trials, thus 12 trials per condition. The tests were arranged into 3 blocks of one test per condition whereby the order of conditions was randomised across individuals. In order to counterbalance sides, each cup (L = left and R = right) was baited twice in every test, resulting in six possible test sequences (i.e. LLRR, RRLL, LRRL, RLRL, RLLR and LRLR). The order of these test sequences was randomised across the different tests (and conditions). During the experiment, one test was conducted per bird with a 60 sec interval between trials.

12 > **Procedure and Scoring.** Once both the subject and the informant were in their respective compartments, they were given a brief habituation phase until they had settled down and had seen each other for ca. 1 min. before the first trial started. The opaque screen was inserted, occluding the two cups from the subject's view while at the same time alerting the subject that baiting was in progress. One of the two cups was then baited from underneath through an opening in the hollow. To ensure that the subject did not receive any acoustic cues from the baited side, both of the hollow's lids were opened and closed simultaneously¹. On the baited side, the experimenter pushed a giant mealworm (*Zoophoba morio*) into the hollow so that informant could clearly see it through the cup opening. Approximately 15 sec after baiting, the screen was pulled out so that the subject could see both the two cups and the informant. After the subject had observed the informant for 30 sec, the guillotine door was lifted allowing the subject to enter one of the corridors of the middle section and choose a cup. Only if the subject pushed a cup was this regarded as a choice. Once the subject had made a choice and entered one of the two corridors, it was prevented from entering the other corridor. After it had collected the food — if the choice had been correct — it was confined to its compartment again. All trials were scored live by the experimenter, who could see into the middle section from their position 2m away from the test box (because the middle section had transparent windows) and observe which cup the bird had chosen and then operate the door to the other corridor.²

¹ Although olfactory cues were unlikely to be important, they were ruled out by putting some *Zoophoba* liquid in both hollows.

² The experimenter had always taken this position during training, so the birds were from used to it. Moreover, the experimenter stood in a place where the subject could not see them before it had made its choice. Behavioural cueing was therefore not an issue.

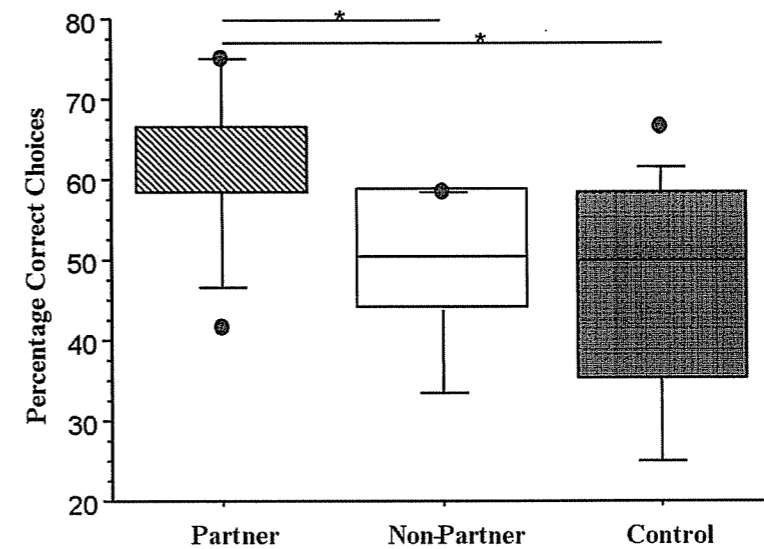


Figure 3. Box plots displaying the median percentage correct performance in choosing the box containing the hidden food across the 3 conditions. Asterisks denote significant differences. Black dots indicate outliers.

12 > **Statistical Analysis.** The tests were conducted using SPSS Version 15.0 or according to Zar's Biostatistical Analysis (1999). Alpha was set at 0.05 and the results are given one-tailed. A Friedman's test was conducted to examine whether there was an effect of experimental condition on choice of the baited cup. Planned comparisons between the conditions were performed using Wilcoxon Signed Rank tests for both the first test (i.e. first 4 trials) and across all tests (i.e. 12 trials). One-sample t-tests (assuming 50% chance of choosing either cup) examined whether the group performed above chance for each condition. Individual performance in each condition was assessed using Binomial probabilities (in order to score above chance an individual had to choose correctly in at least 10 of the 12 trials, assuming 50% chance). A one-way ANOVA for unrelated samples was applied to investigate whether the relative dominance status of the Non-affiliate had an effect on the performance of the subjects in the Non-affiliate condition.

3.2 Results

The data differed significantly from a random distribution (Friedman's ANOVA; $\chi^2 = 6.054$; $n = 11$; $p = 0.048$; two-tailed). Overall, the subjects made significantly more correct choices when paired with their Partner than with a Non-affiliate (Wilcoxon Signed Rank Test; $n = 11$; $T = 7.5$; $p = 0.025$) or alone (in the Control condition; Wilcoxon Signed Rank Test; $n = 11$; $T = 1.5$; $p = 0.005$). The Non-affiliate condition did not differ significantly from the

Control condition (Wilcoxon Signed Rank Test; $n = 11$; $T = 13$; $p = 0.25$; see [Figure 3](#)).

In the first test (i.e. first 4 trials), the group performed better in the Partner condition than in the Non-affiliate condition (Wilcoxon Signed Rank Test; $n = 9$; $T_{-} = 1$; $p = 0.005$). In the Partner condition, the performance was significantly better than the Control condition (Wilcoxon Signed Rank Test; $n = 7$; $T_{-} = 3$; $p = 0.05$), whereas the Non-affiliate condition was significantly worse than the Control condition (Wilcoxon Signed Rank Test; $n = 9$; $T_{+} = 3$; $p = 0.01$).

Across all trials, the group performed significantly above chance in the Partner (one-sample t-test; $t(10) = 3.750$; $n = 11$; $p < 0.002$) and just above chance in the Non-affiliate condition ($t(10) = 0.000$, $p < 0.05$). In the control t was < 1 ($t(10) = -0.889$; $p > 0.198$). However, even though the group average was significant, none of the birds scored above chance in the Partner condition in terms of individual performance (binomial test; see Table 1).

As depicted in Table 1, the relative dominance status of subjects and non-affiliates was counterbalanced across individuals. Additionally, a one-way independent measures ANOVA tested whether dominance status affected the performance of the subjects in the Non-affiliate condition and found no effect ($F(1,8) = 0.6$; $n = 5$; $p > 0.461$).

3.3 Discussion

These results suggest that the search behaviour of jackdaws can be influenced by conspecifics' social cues and that they can identify the attentional focus of conspecifics under certain circumstances, hence that they exhibit joint attention (Butterworth, 1991). In an object-choice task, in which another jackdaw could look into two cups and see which one was baited, the subjects were capable, unlike ravens *Corvus corax* (Schlöggl et al., 2008), of using cues by the another individual to locate hidden food. However, this was only the case if the other jackdaw was the subject's partner. Potential cues from a non-affiliated group member did not appear to be used.

We can conclude from this experiment that behaviour reading may indeed play an important role in jackdaw social cognition, but the results are not sufficient to say whether jackdaws understand other's visual behaviour as a representation of their mental states. In theory, the jackdaws' sensitivity to social cues could be explained by automatic processing of behavioural stimuli, however this seems unlikely given that the mechanism worked exclusively for the partner.

There are two ways of interpreting the differential performance depending on the identity of the informant. Either the performance reflects genuine cognitive ability and the subjects are better at reading attentional cues from their partner, or jackdaws are generally capable of responding to cues of conspecifics, but it does not emerge in the object-choice paradigm. The former interpretation is reasonable given that bonded jackdaws spend the majority of their time in close proximity to one another, synchronise their activities and fine-tune their cooperative and affiliative behaviours (von Bayern, 2008; Wechsler, 1989; von Bayern et al., 2007).

However, if jackdaws have evolved sensitivity to the social cues of their partner, it would make sense that they should also have been able to generalise to non-bonded conspe-

cifics, and possibly heterospecifics. It is possible that the experimental paradigm masks this skill. Indeed, several reasons could account for the inferior performance of subjects when facing a Non-affiliate.

First, the subjects may have been actively averting their gaze away from the non-affiliated jackdaw. Direct gaze can be a threat signal for jackdaws (von Bayern, 2008) like in European jays (Bossema and Burgler, 1980) and thus may provoke aggressive behaviour. Many animals, including several bird species avoid gazing at each other directly (Eibl-Eibesfeldt, 1999). Jackdaws also typically turn their head away when near other individuals to also avoid conflict (Katzir, 1981). Second, — possible but unlikely — the non-affiliate informants may have 'intentionally deceived' the subject by cueing towards the wrong cup or not providing a reliable cue. There is suggestive evidence for tactical deception in other corvids. Ravens show some indication of tactical deception in a object choice study with conspecifics (Schlöggl et al., 2008), and in a competitive foraging context (Bugnyar and Kotrschal, 2004) and have been reported to make 'false caches' (Heinrich, 1999). Western scrub-jays move caches around multiple times in front of a potential pilferer, possibly as a form of a confusion strategy, as they did not necessarily leave the cache in the last place in which they probed the ground (Dally et al, 2006). Third, there may have been a lack of motivation or attention in the cooperative nature of the task; the jackdaws might simply have not been interested in individuals other than their partner and therefore paid no attention to them. Other jackdaws represent competitors rather than collaborators, as food is only shared within pairs (von Bayern, 2008; von Bayern et al., 2007). The experimental set-up is cooperative in nature, even though the other jackdaw was not trained to actively indicate the hidden food.

The finding that the jackdaws were particularly sensitive to the direction of attention of their partner indicates that this cognitive ability may have evolved as an adaptation to bonding, i.e. to coordinate one's actions with a bonded partner. Other experiments we conducted on jackdaws, provide additional experimental evidence that they exhibit joint attention and that they may have a more subtle understanding of attention and the direction and focus of attention than primates (von Bayern and Emery, submitted). Unlike chimpanzees, the jackdaws responded well to communicatory signals in another object-choice experiment with their human care-taker providing the cues. As discussed earlier, the object choice task is in essence a shared attention task and also involves cooperative communication, because it only makes sense to choose the container attended by the cue provider if one understands their communicative intentions. These findings suggests that jackdaws possess the cognitive pre-requisites for forming joint attentional frames, which are a precondition for sharing goals and shared intentionality, abilities Tomasello and colleagues (2005; 2007) consider to be uniquely human. Although so far not investigated, such abilities may be adaptive cognitive skills for long-term pair-bonded species because they may improve the communication, coordination and cooperation between the members of a pair.

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4 Bonding and mentalising

Considering the underestimated importance of cooperative bonding for the evolution of intelligence, one may question whether it has also played a role in evolving a ToM. Given the importance of a well-functioning collaboration and bond for the success of both individuals, understanding one's partner's perspective and reading its mental and emotional states may be more crucial than reasoning about the minds of other non-affiliated conspecifics. We have discussed some examples of complex cognitive skills that might be important for pair living animals with regard to the quality of their collaboration and have discussed that some of these skills are found in jackdaws and other long-term pair-bonded species. It therefore seems justified to examine this question more closely. In the following, we will propose that cooperative bonding could have constituted an evolutionary platform that has made the evolution of ToM in humans and perhaps in several other animals possible.

4.1 Embodied social cognition

Recently, the embodied approach to cognition (Varela et al., 1991; Clark, 1997; Damasio, 1999; Anderson, 2003) has gained increasing acceptance and is considered crucially important for understanding cognition. Its central tenet is that there is a close interaction between brain, body and the world, or, in other words, that the body shapes the mind. Socio-cognitive processes are rooted in body experiences and interwoven with action and interaction with other individuals (Clark, 1997; Damasio, 1999; Anderson, 2003; Barrett and Henzi, 2005). This is because the motor system is in various ways closely tied to perception (i.e. the observation of others' movements) and other forms of cognition and emotion (Gallese, 2007; Frith, 2007).

The important issue here is that by embodied *interaction* with the environment, animals as well as humans acquire an *understanding* of the world around them. This is particularly vital when considering the social world by interacting with conspecifics and through social practice animals and humans gradually gain an understanding of 'others' (Anderson, 2003), which may at least in the case of humans culminate in a fully developed ToM. Such experience-dependent understanding comprises implicit (pre-theoretical and non-conceptual) embodied knowledge of how others behave in particular contexts. Without a ToM (or prior to its development), others are understood in terms of their expressions, goal directed movements and emotions, and in terms of their attentional orientation and their actions toward others and oneself in the pragmatically contextualised activities of everyday life (Gallagher, 2005). Mammals and birds come biologically well-equipped for developing this kind of understanding of others. There are at least two specifically social brain systems that interconnect social brains through interaction: the mirror neuron system (Frith, 2007), and the brain regions controlling social emotions (Rolls, 2006).

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4.2 Embodiment and bonding

Crucially for our argument, most intense and frequent bodily interactions occur between bonded individuals, no matter whether they are parent-offspring, familial, pair or other valuable social bonds. In humans, from birth onwards, the brain develops in the context of our relationships. Initially, the mother-child bond and later in development also other social bonds are crucial for the ontogenetic expression and development of cognitive abilities. The dramatic effect of social deprivation on cognitive development has been drastically documented by Harlow's isolation studies on rhesus monkeys (Suomi et al., 1975). This is because our brain is a highly plastic social organ built through experience (Cozolino, 2006). When we interact, we are impacting on each other's internal biological state and also influence the long-term construction of our brains (Cozolino, 2006), for example during imprinting. Research on human interpersonal neurobiology is only beginning to show how our brains exit in relationship with the brains of other agents. But it is clear that we have evolved as social creatures and that our bonding partners play a part in regulating our emotional and social behaviour (Cozolino, 2006).

Interactions between members of a pair bond and pair formation certainly affect the brain. In many species, including jackdaws, the coordination between partners increases with social practice. Pair displays could be viewed as evolved social practices that interconnect partners through interaction. Many courtship displays involve synchronous movements or involve coordinated sequences of alternating behaviour, hence some kind of 'ritualised imitation', and may therefore activate the mirror neuron system and attune the partners. Birds also have very expressive and very subtle body signals and emotional expressions. These also include vocal emotional and mood signals. Pair duets, pair specific contact and convergence calls and vocal mimicry may be other examples of avian bodily and mental interaction. Recently, mirror neurons have been reported to play a role in learnt vocal communication in birds (Prather et al., 2008). These examples provide some initial clues as to how pair bonded birds may 'connect' to and shape their partner through joint action and interaction and emotional attunement. That joint practice also affects the fitness of a pair is indicated by studies showing that pairs increase their breeding success over time (Emslie et al., 1992).

4.3 Bonding and ToM

So far we have argued that embodied practices between bonded individuals, practices that are emotional, sensory, motor, perceptual, but not necessarily conceptual, most likely form the basis for understanding the bonding partner and other conspecifics.

In humans, such a basic pre-theoretical understanding of others is an important pre-requisite for developing ToM during ontogeny (Baron-Cohen, 1995). But, it has been suggested that, even when we have developed a full ToM, our primary understanding of the social world continues to be pragmatic interaction rather than mentalistic or conceptual contemplation (Gallagher, 2005). Our understanding of the other person may primarily neither be theoretical nor an internal simulation, but a form of embodied practice. We interpret the ac-

tions of others at a highly pragmatic level, i.e. in terms of their goal-directed actions set in contextualised situations, rather than abstractly in terms of their mental states (Gallagher, 2005).

Hence, why should bonding represent an evolutionary platform for mentalising abilities to evolve, considering that embodied practices may be efficient mechanisms regulating social behaviour without the necessity to theorise about abstract mental states, even for humans? Two considerations that may be helpful in this context both of which relate to bonding are argued below. First, considering that embodied practices are generally sufficient, we should ask under what circumstances seeking causal and theoretical explanations of the others' behaviour may really be needed. Second, we should follow Penn and Povinelli's (2007) advice and think about what extra causal work representations about mental states really perform over and above what can be achieved by mechanisms relying on observable features alone.

Only in situations in which the behaviour of others *varies* from their everyday behaviour and familiar behavioural patterns, i.e. when the usual embodied and pattern recognition mechanisms fail, may it pay to start searching for motives in order to explain the other's behaviour and only in these situations may social practices not suffice whilst contemplating about mental states does additional causal work (Andrews, 2005). Such unusual situations may occur most frequently in species with flexible behaviour living in an unpredictable social (and ecological) environment. Another implication from this could be that we (and animals) may be in the best situation to detect such differences in individuals we know very well, because we share the most embodied practices with them as compared to individuals with which we interact less. Consequently, mentalising may be most frequently needed between bonded individuals. Whether searching for motives and seeking explanations is an exclusively human trait, whether it is/was most frequent between bonded individuals and what is adaptive about it remains to be seen. However, keeping such considerations in mind may be productive for future research.

4.4 Future research

As has been postulated by several researchers (Barrett and Henzi 2005; Moll and Tomasello, 2007; Emery et al., 2007), more attention should be drawn to the socio-positive dimensions of social life, which remain poorly understood and according to the above may have more relative evolutionary impact than social competition. The cognitive complexity that may underlie social bonding opens up an entirely new field for future research. Future studies on the cognitive complexity and proximate mechanisms underpinning pair or social bond formation (incl. mate choice and the selection of bonding partners) and maintenance are urgently needed. Other examples that have yet to be studied are the mechanism by which bonded animals coordinate and fine-tune their interactions, cooperation and bi-parental care. Also, the neuronal and hormonal correlates of attachment and bonding as well as the social emotions involved, deserve more research effort. Whilst the neurochemistry of human social bonds has been studied intensely (for review see Cozolino, 2006), research on the ultimate and proximate causes of animals bonding is still in its infancy (Carter, Ahnert et al., 2006).

Furthermore, in order to understand more about the evolution of social intelligence, comparative studies need to study the behavioural differences and the associated differences in cognitive ability in different mating and social systems in greater detail.

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