ORIGINAL PAPER

Do common ravens (*Corvus corax*) rely on human or conspecific gaze cues to detect hidden food?

Christian Schloegl · Kurt Kotrschal · Thomas Bugnyar

Abstract The ability of non-human animals to use experimenter-given cues in object-choice tasks has recently gained interest. In such experiments, the location of hidden food is indicated by an experimenter, e.g. by gazing, pointing or touching. Whereas dogs apparently outperform all other species so far tested, apes and monkeys have problems in using such cues. Since only mammalian species have been tested, information is lacking about the evolutionary origin of these abilities. We here present the first data on object-choice tasks conducted with an avian species, the common raven. Ravens are highly competitive scavengers, possessing sophisticated cognitive skills in protecting their food caches and pilfering others' caches. We conducted three experiments, exploring (i) which kind of cues ravens use for choosing a certain object, (ii) whether ravens use humans' gaze for detecting hidden food and (iii) whether ravens would find hidden food in the presence of an informed conspecific who potentially provides gaze cues. Our results indicate that ravens reliably respond to humans' touching of an object, but they hardly use point and gaze cues for their choices. Likewise, they do not perform above chance level in the presence of an informed conspecific. These findings mirror those obtained for primates and suggest that, although ravens may be aware of the gaze direction of humans and conspecifics, they apparently do not rely on this information to detect hidden food.

Keywords Object-choice · Gaze · Conspecific · Common Raven · *Corvus corax*

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Introduction

The interest in the ability to use others' gaze has recently gained momentum in cognitive science (see reviews by Emery 2000; Itakura 2004; Gomez 2005), particularly because such abilities may form a building block for a human-like "Theory of Mind" (Baron-Cohen 1995; Itakura et al. 1999). In gaze *following* tasks, an animal is tested for its ability to co-orientate with other individuals by responding to their eye or head and eye direction, either into distant space (e.g. Tomasello et al. 1998) or behind a visual barrier (e.g. Povinelli and Eddy 1996; Tomasello et al. 1999), with the latter so far only known for apes (e.g. Tomasello et al. 1999; Bräuer et al. 2005) and ravens (Bugnyar et al. 2004). In *object-choice* tasks, the gaze cue is directed at a specific object, often with food being hidden below (e.g. Anderson et al. 1995; Call et al. 1998) and the animal is required to choose an object on the basis of this cue.

Object-choice tasks are also used for testing responsiveness to a wide array of different types of social cues, such as touching and various forms of pointing (reviewed by Miklósi and Soproni 2006). Whereas nearly all species

tested seem to be capable of using touching an object by a demonstrator as a discriminative cue (e.g. McKinley and Sambrook 2000; Miklósi et al. 2003), the responses to gazing and pointing are less clear: dogs *Canis familiaris* instantly perform above chance with either cue (Miklósi et al. 1998; Hare and Tomasello 1999) and wolves *Canis lupus* (Miklósi et al. 2003), goats *Capra hircus* (Kaminski et al. 2005) and grey seals *Halichoerus grypus* (Shapiro et al. 2003) apparently respond to pointing. However, neither goats nor grey seals seem capable of choosing an object solely on the basis of the other's gaze. Similarly, one of the most prolific performers in gaze following tasks, chimpanzees *Pan troglodytes*, have produced only mixed results in object choice situations: whereas some authors report positive responses to point and gaze cues (i.e. Call et al. 2000; Barth et al. 2005), others found only weak or no responsiveness to pointing (Povinelli et al. 1997) and gazing (i.e. Call et al. 1998).

Hare (2001) suggested that chimpanzees perform poorly in object-choice tasks because they do not understand the cooperative nature of the task, i.e. that the experimenter helps them to find the food. Although it remains unclear whether animals indeed interpret the object-choice task in this way, some indication exists that chimpanzees perform better in a competitive version of the object-choice task, i.e. they used pointing cues of a human competitor more efficiently than cues of a cooperative experimenter (Hare and Tomasello 2004).

So far, the only non-mammalian species tested for their gaze following abilities is the common raven, which had been shown to track humans' gaze direction both into distant space and around visual barriers (Bugnyar et al. 2004). It had been suggested that these abilities are related to the birds' biology: following gaze into distant space may be primarily an anti-predator behaviour, whereas following gaze around barriers might be used during foraging (Bugnyar et al. 2004; Schloegl et al. 2007). Ravens cache food and pilfer food caches of others (Heinrich 1989), whereby the efficiency of finding others' caches relies on the ability to observe them being made. Presumably as a counter-tactic, caching ravens make use of visual barriers and thereby, obstruct the others' view (Heinrich and Pepper 1998; Bugnyar and Kotrschal 2002). Still, after finishing the caches, they do provide visual cues (looking at the cache from a distance, returning and inspecting the cache from close distance), which may be used by conspecifics to locate these caches (Bugnyar et al. 2007). Yet it is not known whether ravens can pick up on such gaze cues to find hidden food.

We here present the first data on ravens' performance in an object-choice task, testing a group of hand-raised sub-adult birds: first, we evaluated the importance of gaze direction relative to other social cues by trying to attract a bird's attention towards one of five objects either by touching,

pointing, or gazing. Secondly, we tested the same birds for their ability to use gaze in the standard object-choice paradigm with food hidden under one of two opaque bowls and a human experimenter indicating the correct location via gaze. In a modification of this condition, we explored possible effects of motivational state on the birds' propensity to use other's gaze cues: since ravens compete heavily over food (e.g. Heinrich and Pepper 1998; Bugnyar and Kotrschal 2002), we introduced a second bird in the next experiment, which received the food reward in case the focal individual chose wrong. Finally, we tested the ravens' performance in an object-choice task with conspecific models. Specifically, we were interested whether ravens could extract information about the location of hidden food by observing another bird that could actually see the food. In a previous study on the ontogeny of gaze following, we had established that these birds are highly responsive to humans' visual orientation (Schloegl et al. 2007); therefore we expected them to be responsive to human-given gaze cues in object choice situations. Based on their advanced pilfer behaviour, we expected ravens to readily use conspecific' social cues for detecting hidden food. However, due to their competitive life-style, we had no clear prediction whether raven models would provide adequate cues in the presence of another raven.

General methods

Subjects and housing

We used 11 hand-raised ravens (six males, five females) all of which hatched in spring 2004, consisting of two groups of three siblings each, one group of four siblings, and one single individual. Four birds descended from two wild breeding pairs (collected with permission of the Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg, Germany) and the remaining birds hatched in the zoos in Munich and Wuppertal, Germany. All birds were transferred to the Konrad Lorenz Research station when approximately 12–40 days old and were hand-raised by CS. Birds were housed together with two adults (8 and 4 years of age) in a 230 m^2-aviary complex in the local Cumberland game park. The aviary was composed of three outdoor sections and five small testing compartments (Fig. 1) that were visually isolated from the other parts of the aviary by wooden walls. When not being experimentally tested, birds were allowed to use the entire complex. The outdoor parts of the aviary contained natural vegetation, bushes, conifer trees providing shade as well as rocks and logs. Indoor compartments had a floor of fine-grained sand and a few perches. Water for bathing and drinking was permanently available. Subjects were given a
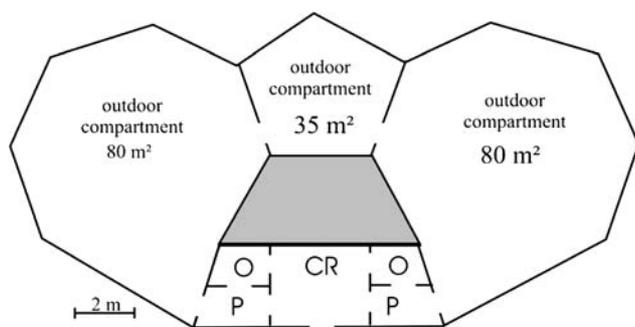
Fig. 1 Sketch of the aviary complex. The test compartments are indicated by O, P and CR and are covered with semi-transparent roof, outdoor compartments with plastic net. Rooms marked with *grey* are not accessible for the birds. Test compartments are separated from outdoor compartments by solid wooden walls. O, P and CR are connected by wire-mesh doors, allowing individuals visual access to adjacent rooms

diet of meat, fruits, milk products and kitchen leftovers (Kabicher and Fritz 1996) throughout the study period. These birds were also tested for the ontogenetic development of their ability to follow human's gaze into distant space and behind visual barriers (Schloegl et al. 2007). All birds were marked with coloured rings for individual identification.

General procedure

Experiment 1 was conducted in July 2004, when the birds were 4 months old. Parallel to this experiment, birds were also tested for their ability to geometrically track humans' gaze direction behind visual barriers (Schloegl et al. 2007). Experiment 2 was conducted between March and August 2005, experiment 3 between September and November 2005, with birds being between 12 and 20 months of age. Birds were tested individually in the indoor-compartments and always received a treat for entering the test compartment before the actual start of testing. During testing, no food reward was given in experiment 1, whereas in experiments 2 and 3, food was involved (see below). All experiments were conducted by CS and were filmed through a window with the camera fixed on a tripod, which was hidden by a solid wall.

Experiment 1: The importance of social cues in choice tasks

In this experiment, we aimed to explore how young ravens respond to touching, pointing to and gazing at an object. Since Burkart and Heschl (2006) had suggested that the reliance on gaze cues in such a choice-task may represent geometrical gaze following, we were interested whether ravens would rely on gaze cues before being capable of

geometrical gaze following in the standard barrier-task (Tomasello et al. 1999).

Procedure

Each bird received three sessions in which four cues each were presented in randomized order. The three sessions were presented within a 3-week period. Since young ravens often engage in playful manipulation of objects (Fritz and Kotrschal 1999), we used known objects (small stones, pieces of bark) instead of food rewards, aiming to reduce reinforcement effects. Throughout the experiment, the bird and the experimenter (E) were in the testing compartment CR (Fig. 1) in visual isolation from the rest of the group. Kneeling on the ground, E positioned five objects in a half-circle around himself on the ground. The distance between the objects was approximately 30 cm, the distance from E to the objects was set at approximately 50 cm. Then, the raven was allowed to freely explore the objects. When the raven had lost interest and had not manipulated any of the objects for at least 30 s, E rearranged the position of the objects (with a randomized order of the objects). Since the bird's view at E was not obstructed from any position in the room, E did not pay explicit attention that the bird was located at a specific location at the onset of a cue presentation. However, before presenting the cue, E called the bird's name. As soon as the bird orientated towards E, he presented one of four different cue types:

> *Gaze:* E bent forward and looked at one of the objects by turning his head and eyes in the direction of the object.
> *Point:* E pointed at one of the objects by extending his arm, while looking straight ahead; the distance from the extended index finger to the object was approximately 20 cm.
> *Touching:* E extended his arm to one of the objects, took it and turned it in his hand; during the manipulation, E was looking straight ahead.
> *Control:* no cue was given. E looked straight ahead with hands resting in his lap.

After the cue, E remained in position and looked straight ahead. All cues were given for 5 s. While the birds were free to respond during the cue presentation, most birds responded after E finished the cue. The inter-cue interval was set to at least 30 s with the exact time depending on when the bird again attended to E. To be recorded, birds had to respond within 15 s (5 s of cue duration plus additional 10 s). Since the different cues might be of different quality to the birds (i.e. touching might be a more prominent cue than gazing), we distinguished between three respond-types:

Correct choice: the bird approached the indicated object and touched it with its beak.

Approach: the bird approached the object to a distance of at least 15 cm, but did not touch the object; we used both approach distance and body orientation, i.e. whether the body-beak axis was orientated towards the object as indication for an approach.

No response: the bird did neither approach nor touch the object within the 15 s time-period.

We recorded the number and type of responses the birds showed for each cue, thereby recording the first object the bird approached or touched only. In the control condition, a choice was considered if the bird chose one of the five objects, whereas during the cue-trials a correct choice was considered if the bird chose one particular object. To control for this effect, we divided the number of responses during the control trials by five.

We aimed to analyse which object the birds chose, if they did not choose the indicated object; however, birds chose one of the other four objects in only six trials, not allowing a detailed analysis.

Analysis

All trials were scored from videotapes by CS. We recorded the number of trials, in which the birds responded by choosing the indicated object and whether they approached the indicated object. A second rater, who was familiar with the birds, scored 50% of all trials and inter-observer reliability was excellent (Cohen's Kappa = 0.979). Data was tested for normal distribution using Shapiro–Wilk tests. For comparison of response ratios, we used repeated measures ANOVA or Friedman-tests. As post-hoc procedures, we applied Sidak–Holm tests and Student-Newman–Keuls test, respectively. Throughout the paper, we report test results two-tailed, with Alpha set at 0.05. Statistical analysis was conducted using the SPSS for Windows 12.0 and SigmaStat 3.5 software packages.

Results

Across the three trials and conditions, birds touched the indicated object in 25.7% of all trials, whereas they touched a non-indicated object in only 5.7% of trials. Quite often, birds did not touch any item at all (32.3%) or they manipulated the experimenter and/or some part of the regular aviary equipment (36.2%). The frequency with which birds chose the indicated object depended on the type of cue given by the experimenter (Friedman: $N = 11$, Chi^2 = 21.0, $df = 3$, $P < 0.001$; Fig. 2a). When E touched an object, birds touched the object significantly more often than during control trials (Student-Newman–Keuls: $N = 11$, $q = 6.183$; $P < 0.05$), whereas birds' response to E's gaze cues (Student-Newman–Keuls: $N = 11$, $q = 1.706$, $P > 0.05$) and pointing cues (Student-Newman–Keuls: $N = 11$, $q = 2.563$, $P > 0.05$) was not different to control trials.

Considering also the mere approach of the object, birds still showed different responses to the three cue types (rm ANOVA: $F_{10,3} = 30.847$, $P < 0.001$; Fig. 2b). When E touched the object, ravens approached and/or touched the object in 78.8% of the cases, which differed significantly from the control condition (Holm-Sidak: $N = 11$, $t = 8.853$, $P < 0.001$). In contrast to the prior analysis, birds respond significantly to pointing on the 0.05-level (Holm-Sidak: $N = 11$, $t = 2.116$, $P = 0.043$; critical post-hoc value: $P = 0.017$), but not to gazing (Holm-Sidak: $N = 11$, $t = 1.751$, $P = 0.09$).

Discussion

To our knowledge, this is the first study that distinguishes not only between different experimenter-given cues but also
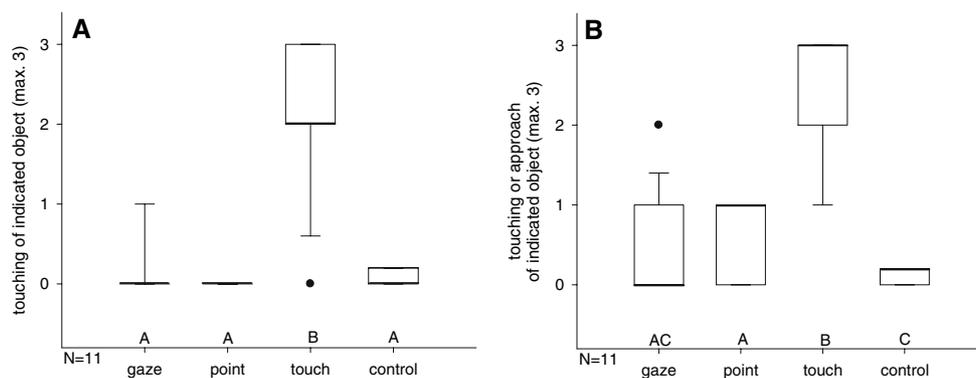

Fig. 2 Number of choices (with a maximum of 3) of the indicated object by the ravens in Experiment 1. Panel **a** shows how often the birds actually touched the indicated object, **b** shows how often birds approached (without touching) or touched the indicated object. *Boxplots* represent median and upper and lower quartile. *Whiskers* indicate 10%- and 90% range, *dots* indicate outliers. *Bars* marked with different letters differ significantly (post-hoc-Test; $P < 0.05$)

between different responses to those cues. Interestingly, touching by E could lead ravens to manipulate the object, whereas pointing at best led them to approach and visually inspect the object. The clear-cut response to touching may be explained by local enhancement, which had been shown to be a powerful mechanism in social species, including ravens (Fritz and Kotrschal 1999). In object-choice tasks, touching of an object lead to a likely choice of that object also in goats (Kaminski et al. 2005), wolves (Miklósi et al. 2003) and horses (McKinley and Sambrook 2000). In a similar experiment, only a minority of chimpanzees tested were found to use a combination of touching and gazing at the object (Call et al. 2000). For responding solely to point and gaze cues, individuals would have to track the other's point/gaze direction to a specific location, extrapolating a line from the body to the object. Possibly the ravens' stronger response to pointing may simply be a result of the shorter distance between fingertip and object compared to the distance between face and object in the gazing condition. Preliminary data of two naïve ravens indeed indicate that their use of pointing cues decreased with increasing distance from the extended hand to the food (Jaksch, Kotrschal, Bugnyar and Schloegl, unpublished data).

Beside the mechanisms triggering a response to different cues, the "value" and/or information content might be different between cues. In other words, gazing at an object might attribute less importance to that object than touching it and the animal simply behaves in the same way towards the object as the model did. Still another point may be that the objects were of rather limited interest for the ravens, and therefore they only responded to rather strong cues, namely the handling of the object and—to a lesser extent—pointing at the object. Therefore, in the next step we aimed to increase the value of the target by confronting birds with a two-choice task, in which they had to find a piece of highly preferred food hidden in opaque cups.

Since touching had such a strong effect in experiment 1, and pointing (as a primate gesture) may be a rather odd cue for birds, we now focus on gaze cues only.

Experiment 2: The use of gaze cues to find hidden food

Methods

Seven of the birds that had participated in experiment 1 were tested. As covers we used 500 ml-yogurt cups, which all birds were familiar with. Although ravens do not seem to be capable of using olfactory cues for detecting food (Heinrich and Pepper 1998), all cups were filled with food prior to the experiment to allow cups to acquire an identical smell. Throughout the experiment, pieces of commercial dog food and cereals were used, both highly preferred food

items which where not available outside the experimental context. During experiments, the bottom of each cup contained 0.5 cm of fine-grained sand to avoid any noise due to movements of the food inside the cup.

All training and testing took place in the testing compartments and birds were tested individually. At the onset of each trial, the bird was positioned in the pathway P, whereas E was positioned in the central room CR (Fig. 1). Birds had full visual access to CR via a closed wire-mesh door.

Training sessions

Birds were trained to choose one of two identical cups with only one cup containing food. Therefore, E called the bird's name to obtain its attention and placed two cups with an approximate distance of 1 m to each other on the ground of the experimental compartment. Then, E hid food in one of the two cups while the bird was watching. After placing the food, the cups were covered with a piece of grey cardboard. The bird was allowed to enter CR and choose on of the cups and—if choosing the correct cup—to retrieve and eat the food. If the bird chose the unbaited cup, the lid of the other cup was raised and the food was shown to the bird. After each choice, birds returned to CR to expect the onset of the next trial. To advance to the test session, birds had to choose the correct cup in eight out of ten trials in two sessions.

Two birds (Lo and Ilias) reached this criterion within the minimum of two sessions and three birds needed three (Xara) or four (Nemo, Pluto) sessions respectively. Only one bird (Columbo) did not reach the criterion in two consecutive sessions, but was correct on 23 of her last 30 training trials (binomial-test: $P = 0.005$), so that she was advanced to testing. The final bird (Gwaihir) reached 90% in the second session and scored 70% in the sixth and seventh session, but then his performance declined from the eighth to the twelveth session, probably because of lack of motivation. We then advanced the bird to testing and since his performance was not different from the other birds, we include him in the analysis.

Test sessions

The birds received a total of 20 sessions each, with only one session per day; after finishing the first ten sessions, we split the seven ravens in two groups. Whereas four birds continued to be tested with the original set-up, three randomly chosen birds (one male, two females) were tested in the presence of another raven (the observer). The observer was not informed about the position of the food and could not physically interfere with the focus individual for the entire test-period; however, it received the reward in case

the focus bird made a mistake. We first used one selected male (Gwaihir) as observer to minimize the impact of experience as observer on individual performance. This bird was lower-ranking than the three other males in the test, but was higher-ranking than the three females. Gwaihir was later tested as focus bird as well; since he did not perform differently from the other birds, we include him in the analysis. The first individuals that had passed the entire sequence of twenty sessions were also used as observer-birds.

Each session consisted of ten trials and the inter-trial interval was set to at least 20 s with the exact time depending on when the bird again attended to E. In contrast to training, E hid the food invisibly for the birds in an adjacent room. When returning to the experimental compartment, E placed both cups on the ground and paid explicit attention to alternate between placing the cup with food and the cup without food first. Food was placed randomly on the left or right side with the exception that food was not placed on the same side more than twice in a row. Then, E kneeled approx. half a meter behind the cups on the ground, called the bird's name to gain its attention and then gazed (head and eye-orientation) at the location of the food for 5 s. Hereby, four different conditions were used:

Central gazing (four times per session): E kneeled equidistantly between the two cups and gazed at the cup containing the food.
Proximal gazing (twice per session): E kneeled behind the cup containing the food while gazing at it.
Distal gazing (twice per session): E kneeled behind the cup not containing the food while gazing at the cup that contained the food.
Control (twice per session): E kneeled equidistantly between the two cups and gazed straight ahead at the wall behind the raven.

During all trials, E held his hands in his lap. After the cue, E stood up and stepped approximately 2 m back while looking straight ahead. In contrast to experiment 1, no rigid time limit for responding was given; however, if birds did not respond within 60 s, the cue was repeated once and the session cancelled if the bird again did not respond. If birds did stop participating within the first three trials of a session, the complete session was repeated on the following day. If birds stopped responding after at least six trials had already presented, the missing trials were conducted on the following days (occurred twice within 140 sessions). Finally, if birds refused to respond on the last two trials, the session was terminated and treated as a complete session (occurred six times within 140 sessions). If birds chose the correct cup, they were allowed to retrieve the food; if they chose the incorrect cup, E stepped forward, removed the cover of the correct cup and retrieved the food without giving it to the bird. If tested with an observer, E gave the food

to the observer. For the analysis, we recorded whether the bird chose the correct cup.

Analysis

We calculated for each session the percentage of trials in which the birds chose the correct cup, i.e. the cup containing the reward; since choice of cup was unambiguous in every case, we did not control for inter-observer reliability. We used Wilcoxon signed-rank tests for comparison between test and control trials. Binomial-tests were used to assess overall individual performance.

Results

Sessions 1–10

Whether E kneeled behind the correct/incorrect cup or in equal distance between the two cups did not influence birds' success in choosing the correct cup (Friedman: $N = 7$, $Chi^2 = 0.286$, $df = 2$, $P = 0.867$). Therefore, we combined these conditions for further analysis. Compared to control trials, ravens did not use gaze cues for detecting the food over the course of the first ten sessions (Wilcoxon: $N = 7$, $Z = -1.521$, $P = 0.128$). Also, performance did not improve during the course of the experiment, i.e. the mean number of correct choices was not different between sessions 1–5 and sessions 6–10 (Wilcoxon: $N = 7$, $Z = -0.254$, $P = 0.799$). Finally, individual performance did not deviate from 50%—chance level, neither in control nor test trials (Binomial-Test; Table 1).

Sessions 11–20

Again, the position of E in relation to the cup did not influence the birds' choice of cups (Friedman: $N = 7$, $Chi^2 = 2.741$, $df = 2$, $P = 0.254$). Therefore, we combined these conditions for further analysis. After introducing the observer for some birds, performance changed only marginally, with no bird choosing the baited cup significantly above chance level, neither in the test conditions, nor in the control condition (Table 1).

Discussion

Apparently, ravens did not use human-given gaze cues to detect hidden food. Since the results of experiment 1 suggested that local enhancement improves the birds' performance, we expected that the kneeling of the experimenter next to the rewarded cup may enhance the birds' performance. However, ravens apparently did not rely on the experimenter's position, which differs from the results obtained with chimpanzees (Call et al. 2000) and dogs

Table 1 Number of correct choices by the seven ravens in the different cue-conditions in experiment 2

Individuals	Sessions 1–10				Sessions 11–20			
	Test trials	P	Control trials	P	Test trials	P	Control trials	P
Xara[a]	39	0.911	10	>0.999	48	0.094	11	0.824
Ilias	38	0.737	10	>0.999	42	0.571	11	0.824
Lo[a]	34	0.219	11	0.824	35	0.368	11	0.824
Pluto	41	0.82	9	0.824	36	0.5	7	0.263
Nemo	38	0.91	10	>0.999	41	0.911	10	>0.999
Gwaihir	35	0.314	10	>0.999	35	0.314	9	0.824
Columbo[a]	43	0.576	13	0.263	41	0.822	11	0.824
Chance level	40[b]		10		40[c]		10	

Given is the P value of a binomial test

[a] Tested in the presence of another raven in sessions 11–20

[b] Pluto and Nemo did not participate in one and two trials, respectively. Therefore, the corrected chance levels are: Pluto: 39.5; Nemo: 39.0

[c] Lo, Pluto and Columbo did not participate in one trial each and Ilias in two trials. Therefore, the corrected chance levels are: Pluto, Columbo and Lo: 39.5; Ilias: 39.0

(Hare and Tomasello 1999). In contrast to these experiments, our ravens were confronted with four different positions presented in an interspersed order, with proximal gazing representing only 20% of the cues of a session. Such a cue presentation may have prevented birds from quickly learning across trials.

Although the ravens tested here had been shown to be attentive to humans' visual orientation (Schloegl et al. 2007), the birds may have been less motivated to extract information from interactions with humans. In a first step, we tried to counteract this effect by introducing a second bird as observer, who obtained the food if the focal bird chose wrong. However, with the potential exception of Xara (see Table 1), this had hardly any effect on the birds' performance. Potentially, ravens may not have understood that the observer obtained the food as a consequence of their choice of the wrong cup, since the observer did not take the food from the baited cup but the experimenter gave the food to the observer. Alternatively, ravens may not have understood the significance of the experimenter's gaze direction. In order to create a more realistic foraging context, we then introduced a conspecific model, which could

see the food from its position. Thus, we aimed at testing if the focal individual would be able to extract any information of the other's visual behaviour about the location of the hidden food.

Experiment 3: Object-choice task with a conspecific model

Methods

The seven birds used in the previous experiment and one additional bird (a female of same age, which had been tested in experiment 1) participated. Tests were conducted in the experimental compartments, with model and focal bird positioned in the opposite pathways P (Fig. 1). These were closed by wire mesh doors, but birds had full visual access to the central room CR (Fig. 3a). The cups used in experiment 2 were modified in two ways: on the side oriented to the model, we cut a 2 cm × 1.5 cm hole, to allow the model to see the food inside the cup (Fig. 3b). Additionally, we fixed a cardboard disk horizontally inside the cup, so
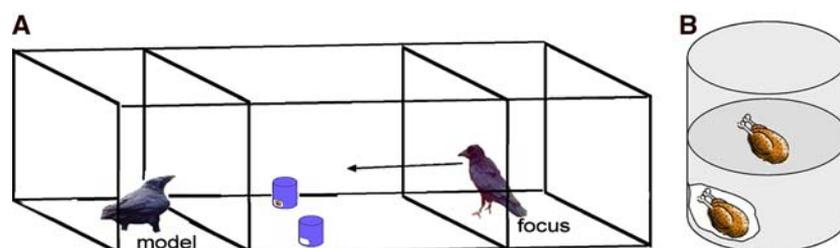

Fig. 3 **a** Experimental setup of Experiment 2: Model and focus bird are separated by wire-mesh doors. **b** Cups used in experiment 2. A cardboard divider was fixed in the middle of the cup. Food in the lower part of the cup was visible for the model, and food visible in the upper part of the cup could be obtained by the focal individual

that the food inside the cup could be placed independently from the food visible to the model bird (Fig. 3b). Otherwise, the cups were prepared identically to experiment 1. Prior to this experiment, we had established that these modifications enabled models to see food inside the cups.

In an attempt to test how accurate ravens are in judging where another bird is looking, we tested birds in two conditions with different distances between the cups: in the close condition, the cups were positioned approximately 50 cm apart, whereas in the far condition, cups were placed approximately 100 cm apart. Food was placed equally on the left and right side, with food neither placed more than twice in a row on the same side nor more than twice in a row in the far and close condition, respectively. Each bird was tested once a day, receiving ten trials. Among these ten trials, two control and eight test trials were randomly distributed, with four test trials each in the far and close condition, respectively. In the control trials, food was placed visible for the model bird in both cups, whereas food could be found by the focal individual only in one of the cups; hence, the focus bird had a 50% probability of finding the food.

At the start of each session, both birds were present and E baited the cup out of sight for both birds in an adjacent room. When returning to the experimental compartments, E placed the cups approximately 70 cm away from the model bird, paying explicit attention that the food was not visible for the focus individual. E than stood next to the door of the focus individual and opened the door after the model bird had been positioned visible at its door for at least 3 s. After release, the focus individual was allowed to open one cup and—if choosing correctly—to retrieve and consume the food. A second trial started as soon as the bird had returned to the pathway P. To keep the model bird motivated, it received the food reward visible for it in half of the trials, independent whether the focus bird had chosen correctly.

If a bird had been tested, it could not be used as model on the same day and birds were not used as models more than once per day. Beside these restrictions, the identity of the model bird was chosen semi-randomly: Each bird received first six sessions with a dominant model, since preliminary results from a parallel experiment indicated that birds might be more attentive to a dominant individual (Bugnyar, unpublished data). However, these results did not hold, and we conducted six more sessions with a randomly selected subordinate model. Birds were employed as models 9.75 ± 5.11 times ($x \pm$ SD; range 5–19). In total, birds received six or twelve sessions, depending on their rank position within the group. The most dominant male (Pluto) could not be tested with a dominant individual; accordingly, the most subordinate female (Dora) was not tested with a subordinate individual. Lo (the second-ranking male) refused to participate in tests with a dominant individual.

Analysis

We calculated the percentage of trials in which the birds chose the baited cup; since choice of cup was unambiguous in each case, we did not control for inter-observer reliability. To assess the impact of the position of the model, we scored for each trial if, at the time the focus bird chose a cup, the model was positioned in the back part of the pathway (>1 m away from the wire mesh partition) and therefore outside view of the camera, equidistant between the two cups or close to the baited and the unbaited cup, respectively. A second rater, who was familiar with the birds, scored 10% of the trials and inter-observer reliability was excellent (87.3% agreement of both raters; Cohen's Kappa = 0.84).

Since ravens have lateral eyes, two foveae and all-black pupils and sclera, it is difficult to code from video-tapes at which specific point a raven is looking at close range: if the bird's beak points at the baited cup, the bird may focus at this cup (using the central fovea), but still may also focus at the other cup using the lateral fovea (note that when orientating in the far range, birds use only one eye and direction of orientation can easily be distinguished, i.e. when looking up; Dawkins 2002; Schloegl et al. 2007). Consequently, we did not rate whether birds orientated towards the correct cup, but restricted our analysis to positional cues only.

Results

Overall performance

On an individual level, none of the eight birds tested chose the baited cup above chance (Binomial-Test; Table 2); whether cups were positioned close or far from each other, did not influence the choice behaviour of the birds, regardless whether they were tested with a dominant model (Wilcoxon: $N = 6$; $Z = -0.948$; $P = 0.343$), or a subordinate model (Wilcoxon: $N = 7$; $Z = -0.105$; $P = 0.916$). Subse-

Table 2 Number of correct choices by eight ravens in experiment 2; given is the P value of a binomial test

Individuals	Model rank	No. correct overall	Chance level	P
Xara	Both	49	48	0.919
Ilias	Both	50	48	0.76
Lo	Subordinate only	25	24	0.886
Pluto	Subordinate only	23	24	0.886
Nemo	Both	43	48	0.358
Gwaihir	Both	45	48	0.61
Columbo	Both	50	48	0.759
Dora	Dominant only	22	24	0.665

quently, we combined data from close-trials and far-trials for subsequent analysis.

Impact of the models identity

Performance did not differ between sessions using dominant and subordinate models (Wilcoxon: $N = 5$; $Z = -0.813$; $P = 0.416$). Additionally, the identity of the model did not influence the mean number of correct choices per session (Kruskal–Wallis: $N = 8$; $H = 5.352$; $df = 7$; $P = 0.617$).

Did models provide positional cues?

Positional cues may probably be the most simple cue provided by models. However, dominant models positioned themselves equidistantly between both cups in $34.2 \pm 18.86\%$ of all trials and on the side of the baited cup in $22.37 \pm 7.7\%$ of trials. In $16.37 \pm 7.74\%$ of trials they sat on the side of the unbaited cup (Wilcoxon: $N = 6$; $Z = -1.095$; $P = 0.375$) and in $27.1 \pm 20.1\%$ ($x \pm$ SD) of all trials, dominants stayed in the back of the compartment, providing no positional cue at all. Similarly, subdominant models were scored as being equidistantly between both cups in $54.32 \pm 21.13\%$ of all trials, positioned close to the baited cup in $13.1 \pm 10.27\%$, close to the unbaited cup in $9.82 \pm 6.07\%$ (Wilcoxon: $N = 7$; $Z = -1.214$; $P = 0.313$) and in the back of he compartment in $22.77 \pm 16.45\%$ of all trials. Focus animals did not show a preference for choosing a particular cup when a model was positioned close by one of the cups, neither with dominant models (Wilcoxon-tests: $N = 6$; $Z = 0.314$; $P = 0.844$) nor with subordinate models (Wilcoxon: $N = 7$; $Z = -1.992$; $P = 0.063$).

Discussion

Again, ravens were not capable of finding the hidden food above chance level, although this time another raven served as model. In contrast to the previous experiments, we did not control for the kind of cue the raven models provided. Our data suggest that models did not provide consistent positional cues, since they did not prefer to sit close to or away from the baited cup. Additionally, observers did not reveal any clear preference for the location of the model. In sum, these findings suggest that ravens hardly rely on conspecific social cues in an object choice situation, possibly because the models provide subtle cues, if any, making it difficult for observers to pick on.

General discussion

In contrast to our predictions, ravens performed poorly in object choice situations involving gaze cues: (i) in all three experiments, birds failed to consistently choose the indicated objects, (ii) in experiments with a human demonstrator, most birds did not learn to associate the model's head and eye direction as an indicator for the location of food over more than 150 trials; (iii) in experiments with a conspecific, ravens did not reliably choose above chance level.

Ravens are attentive to conspecifics and humans manipulating objects (Scheid et al. 2007; Fritz and Kotrschal 1999) and they are highly aware of conspecifics' and humans' visual orientation (Bugnyar et al. 2004; Schloegl et al. 2007). Thus, their apparent failure in responding to (most) social cues in object choice tasks may indicate that ravens have problems in "understanding" the salience of gaze cues in this particular context. It might be expected that species with a sufficiently complex social organisation should be able to rely on other's gaze direction to find food (Tomasello et al. 1998). However, so far most studies testing for gaze use in object-choice tasks revealed negative results (e.g. Povinelli et al. 1997; Call et al. 1998). Apparently, the only species which has been found to reliably respond to human gazing in this context is the domestic dog (e.g. Miklósi et al. 1998; Hare et al. 2002; Soproni et al. 2002).

The poor performance of apes and ravens in object choice situations may appear even more puzzling, since these animals are capable of geometrical gaze following, i.e. they understand that barriers impair their own and others' perception (i.e. Povinelli and Eddy 1996; Tomasello et al. 1999; Bugnyar et al. 2004). Chimpanzees may even understand the importance of the eyes when assessing other's attentional state (Hostetter et al. 2007). Recently, Burkart and Heschl have argued that the use of gaze cues by common marmosets *Callithrix jacchus* in a modified version of the object-choice task might qualify as geometrical gaze-following since those animals have to understand that under the bowl something of interest is hidden. However, our results do not support this argumentation. At the time we conducted experiment 1, our birds had not passed the standard test for geometrical gaze following, tracking other's gaze behind a visual barrier, but they clearly possessed this skill at the time of experiment 2 (Schloegl et al. 2007). Still, their performance in the two object choice experiments was similar. Consequently, our results are in concordance with the hypothesis that the use of gaze cues in object-choice task is—on a cognitive and/or motivational level—distinct from following gaze by visual co-orientation.

When chimpanzees were confronted with a dominant conspecific in a different experimental context, chimpanzees preferred to choose food sources only visible for themselves, indicating that they can judge what others can and cannot see (Hare et al. 2000, 2001). This prompted the competitive cognition hypotheses (Hare 2001), suggesting that chimpanzees may reveal their cognitive abilities

mainly in competitive tasks. However, it remains unclear whether the performances of chimpanzees in the studies by Hare et al. (2000, 2001) were a result of the competitive design per se or whether some other feature of the task may have helped the chimpanzees to exploit the competitors' gaze direction. In fact, evidence for the effect of competition on the performance in object-choice tasks remains scarce. Vick and Anderson (2003) demonstrated that olive baboons can avoid the gaze direction of competitors, whereas the results by Hare and Tomasello (2004) suggest that chimpanzees may have used pointing cues of competitors but not of cooperators. In our third experiment, we provided a conspecific with information about the location of food, leading to a situation similar to the studies on food caching (i.e. a focus bird competes with a conspecific who is knowledgeable about the location of hidden food; Bugnyar and Heinrich 2006). Hence, we likely created a competitive scenario without changing the basic characteristics of the object-choice task, namely providing information about the location of food without physical interaction of the two animals. However, our results did not provide evidence that ravens may be capable of detecting hidden food solely by relying on others' gaze direction or body orientation, which may at least partially due to models providing insufficient cues.

These findings may have two important implications: First, recent studies revealed that ravens (Bugnyar and Heinrich 2005, 2006) and scrub-jays *Aphelocoma coerulescens* (Dally et al. 2006) are capable of differentiating between conspecifics that have been visually present or absent at the time of caching and even between conspecifics that were present at different caching events; one possible interpretation of these findings is that birds are skilful in picking up on subtle behavioural cues of conspecifics at the time of recovery, e.g. a knowledgeable competitor might orient more often towards or away from the correct cache site than an ignorant competitor. However, in the current study we explicitly tested for the use of such cues but found no evidence that ravens could distinguish between two (artificial) caches on the basis of others' location and orientation, rendering the behavioural-cueing alternative in the knower-guesser experiments unlikely. Second, the ravens' repeated failure in object choice experiments raises the question of the functional value of gaze following skills in this species. We have recently argued that geometrical gaze following may represent an adaptation for cache protection (Bugnyar et al. 2004; Schloegl et al. 2007). Our new results make it unlikely that ravens are capable of finding exact caching sites of others by orienting towards their gaze. In consequence, geometrical gaze following might have been evolved as a prerequisite for using natural occurring obstacles as barriers (stones, trunks, etc.) to cache out of sight of conspecifics rather than to locate others' caches.

Relying on gaze cues in object-choice tasks may require an understanding of other's cooperative intentions; for social and cooperatively hunting carnivors such as wolves (as the predecessor of dogs; Vila et al. 1997), this may be a prerequisite for successful hunting (Itakura et al. 1999), but may be absent in the mainly competitive chimpanzees and ravens (but see Boesch and Boesch 1989 for an example on cooperative hunting in chimpanzees). Still, chimpanzees are capable of relying on gaze in modifications of the object-choice task (i.e. Call et al. 2000; Barth et al. 2005). Whether the same is true for ravens needs further investigation.

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