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Gaze Direction – A Cue for Hidden Food in Rooks (*Corvus frugilegus*)?

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Verfasserin: Judith Schmidt
Studienrichtung /Studienzweig Biologie/Zoologie
(lt. Studienblatt):
Betreuer: Ao. Univ.-Prof. Dr. Kurt Kotrschal

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1. Abstract

Other individual's head- and eye-direction can be used as social cues indicating the presence of resources, predators or social interactions. A number of group-living species respond to these cues and among birds, ravens and rooks have been shown to co-orient with conspecifics and human models by following their gaze direction into distant space and behind visual barriers. Both species use barriers as a screen to cache food in private and it had been suggested that they may also rely on gaze cues to detect hidden food. However, in an object-choice task, ravens failed to do so. Potentially, the ravens' competitive lifestyle may have prevented them from relying on the gaze cues. Here we replicated our study with closely related but cooperative rooks. Food was hidden in one of two cups and the experimenter indicated the location of the hidden food by gazing at it. In a second experiment, we aimed to increase the birds' motivation to choose correctly by increasing the effort needed to obtain the reward. Therefore, birds had to pull on a string to obtain the cup. In both experiments, individual birds quickly learned to use the experimenter's cue. This suggests that rooks may not rely on gaze cues to find hidden food spontaneously, but they may quickly learn to do so.

2. Introduction

The expression “Two pairs of eyes are better than one” implies that humans may make use of what other individuals can see. Another individual’s gaze direction (i.e., head- and eye orientation) can be used as a directory to the looker’s visual target by following her gaze direction. Gaze following in its basic form, i.e. visual co-orientation with another subject’s looking direction, can be found in several group-living species like primates (e.g. Tomasello et al. 1998, Bräuer et al. 2005), goats *Capra hircus* (Kaminski et al. 2005), ravens *Corvus corax* (Bugnyar et al. 2004), rooks *Corvus frugilegus* (Schloegl et al. 2008a) and bald ibises *Geronticus eremita* (Loretto et al. 2010).

Following another individual’s gaze direction behind visual barriers is considered a cognitively more complex task, as it requires the tracking of a line of sight under consideration of a barrier’s potential influence of one’s own and other’s perspective (e.g. Povinelli and Eddy 1996, Bugnyar et al. 2004). This ability has so far been found only in apes (e.g. Bräuer et al. 2005) and corvids (ravens: Schloegl et al. 2007, rooks: Schloegl et al., 2008a), who both regularly use barriers for concealment of social interactions (apes) or of food caching (corvids). Additionally, both corvid species pilfer food caches and it had been suggested that they may use gaze cues to find food caches (Schloegl et al. 2008b).

However, when specifically tested for their reliance on gaze cues to detect hidden food in the common object-choice task, ravens did not base their choices on an experimenter’s or another raven’s gaze cue (Schloegl et al. 2008c). In this paradigm (Anderson et al. 1995), one of two cups is baited with food and an experimenter indicates the baited cup by looking at it (see reviews by Emery 2000, Itakura 2004). Beside ravens, also several other species failed to use the gaze cues in this task, e.g. grey seals *Halichoerus grypus* (Shapiro et al. 2003), goats (Kaminski et al. 2005), capuchin monkeys *Cebus apella* (Anderson et al. 1995) and rhesus macaques *Macaca mulatta* (Anderson et al.

1996). In contrast, only dogs (*Canis familiaris*) were highly successful across various studies and several modifications of the original paradigm (Miklosi et al. 1998, Hare and Tomasello 1999). The performance of chimpanzees (*Pan troglodytes*) is diverse, as enculturated subjects (i.e., individuals that were raised in a human-only environment) usually showed better performances than non-enculturated subjects (e.g. Itakura et al. 1999). However, the potential to learn to use gaze cues to find hidden food was found in chimpanzees (Itakura and Tanaka 1998) gorillas (*Gorilla gorilla*, Peignot and Anderson, 1999) and orang utans (*Pongo pygmaeus*, Byrnie 2004). Further, capuchin monkeys could learn to rely on gaze cues after intense training (Itakura and Anderson 1996, Vick and Anderson 2000).

Still, there is some evidence that unsuccessful subjects may still follow the model's gaze in object-choice tasks, i.e. they may look at the indicated cup (rhesus monkeys, *Macaca mulatta*, Emery et al. 1997), but do not choose it reliably (lemurs, *Eulemur fulvus* and *Eulemur macaco*, Ruiz et al. 2009). This suggests that rather than being unable to detect the target of the model's gaze, the animals are not motivated to choose the gazed-at target. Consequently, some subjects became more successful if the testing procedure was modified. Call et al. (1998) adapted the experimental setup to make it more similar to chimpanzees' natural foraging dispositions: when tubes were used instead of cups and thereby the food remained visible for the model, 4 of 6 chimpanzees were able to choose correctly. Further, chimpanzees were able to use gaze cues if the model approached and stood behind the baited cup (Itakura et al. 1999, Call et al. 2000). Schloegl et al. (2008b) tested similar methods in ravens: (1) they turned the cups by 90° to make the food visible for the model and (2) the model approached both cups but gazed only at the baited cup. Even though the ravens' performance increased, still only one out of seven ravens performed above chance in each condition.

The exact cue type was also shown to be of importance: Rhesus monkeys used a communicative gesture to find hidden food, composed of head and eye movements that are engaged in the recruitment of an ally in a

fight, but not gazing alone (Hauser et al. 2007). Similarly, jackdaws (*Corvus monedula*, von Bayern and Emery 2009) used repeated glance alternations (looking back and forth between the subject and the cup without head movement), again a cue type suggested to be highly communicative. Therefore, an increased salience of the cue may help at least cooperative animals like jackdaws to be successful in an object-choice task.

Another crucial aspect in cue giving is the distance between the model and the cup. Some species, e.g. gorillas (Peignot and Anderson, 1999) and orang utans (Byrnit, 2004) learned more readily to use gaze cues when the distance between the target and the experimenter's head was 10 cm compared to a distance of 60 cm and 100cm, respectively. This effect is also known from pointing gestures as indicators for hidden food (Miklosi and Soproni 2006).

Whereas a large number of modifications have been applied to the general object-choice procedure, one aspect has been vastly neglected so far, namely the effort the animals have to invest to solve this task. In the typical object-choice task, the animals neither need to invest much energy nor time to be successful, as they simply have to grasp one of two small cups. Together with a relatively high chance-level of 50%, this may lead to a rather low motivation of the subjects. Of these two aspects (producing effort and chance probability), only chance probability has been manipulated systematically yet; e.g. when Burkart and Heschl (2006) introduced nine cups instead of two, the performance of common marmosets (*Callithrix jacchus*) increased.

Here, our aims were twofold. First, we wanted to test rooks, a more cooperative corvid than ravens. Rooks are highly socially corvids with a social system similar to jackdaws; however, similar to ravens, they cache food and possess geometrical gaze following skills. Secondly, we aimed to test the effect of producing effort on the rooks' performance. Therefore, we manipulated the effort needed to obtain the reward. To achieve this, the cups were placed on

wooden boards which the birds had to pull on a string through a lattice. Finally, to investigate the effect of the distance between the model and the cup on the performance of the birds, we used proximal (30 cm between experimenter and cup) and distal gaze cues (100 cm distance) in both experiments.

3. Methods

3.1. Subjects & Housing

We tested six one-year old, hand-reared rooks in July and August 2007. The birds were housed in a group of 14 birds (8 males, 6 females) and all birds could be identified with coloured rings. They were kept in an aviary complex in DEPE, CNRS Strasbourg, France. The complex consisted of an outdoor aviary (4.2 * 6 * 2m), divided in two sections and an indoor compartment (4.2 * 2 * 3m), divided in three sections (Fig 1). The test compartments had a few perches and tables on which the experimental apparatus was fixed (Fig. 2). Outside testing, the group had free access to all compartments. Birds were fed 3 times a day with cereals, cheese, eggs, meat and vegetables. Fresh water was available ad libitum. Previous to our study, the birds have participated in one study on the development of gaze following abilities (Schloegl et al, 2008b).

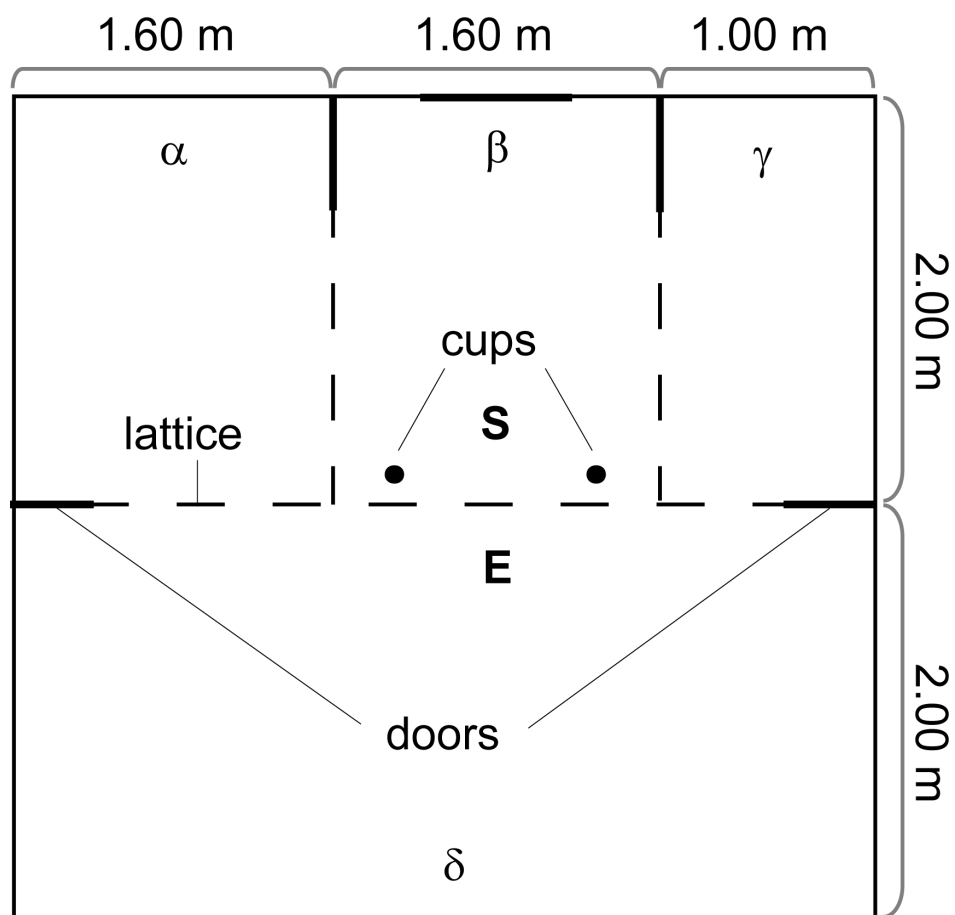


Fig.1. Setup for Experiment 1

$\alpha, \beta, \gamma, \delta$ = Compartments, E = Experimenter, S = Subject

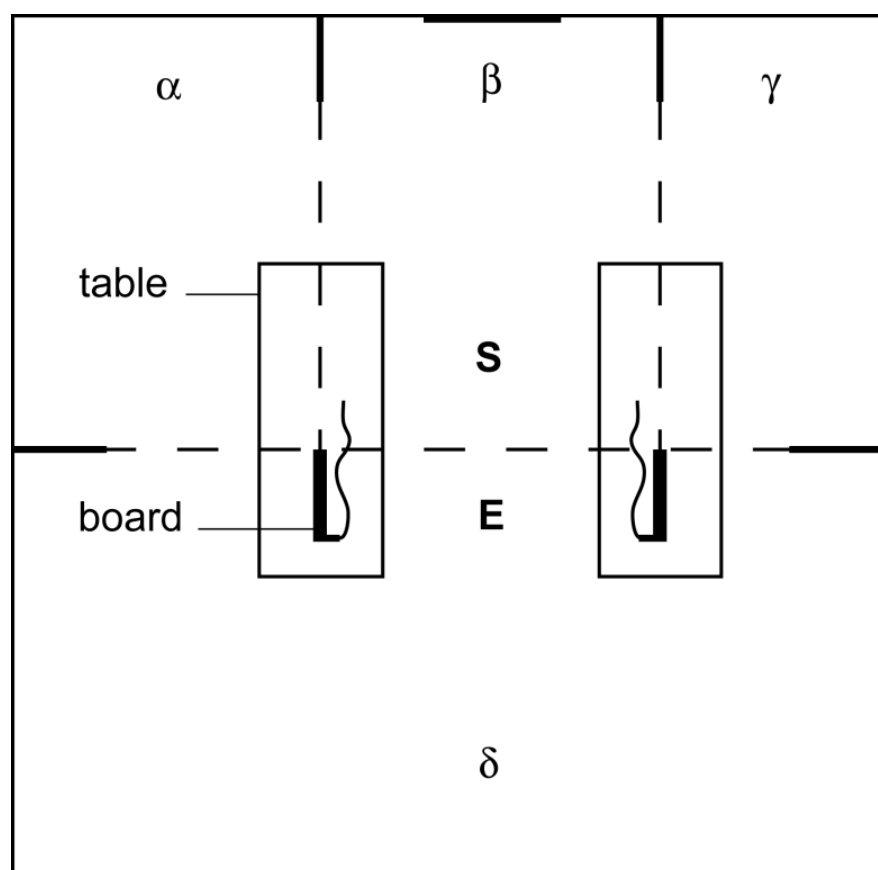


Fig.2. Setup for Experiment 2

$\alpha, \beta, \gamma, \delta$ =Compartments, E=Experimenter, S=Subject.

3.2. Ethical notes

Animals were taken from the wild under permission from the Direction Départementale de l'Agriculture et de la Forêt, permit n. 67/9. Experimental research on these birds was approved by the Direction Départementale des Services Vétérinaires, permit n. 67-288. After this study, birds remained in captivity for further ethological studies.

3.3. General experimental procedure

All tests were conducted by JS in the experimental compartments and were video-taped with a camera fixed on a tripod. Prior to this study, the birds had already been habituated to being tested individually in visual isolation from conspecifics; participation was voluntarily and the birds were free to leave the test-compartment between the trials. In both experiments, the experimenter (E) was positioned behind the wire mesh partition in compartment δ , facing the subject (S) in compartment β through the lattice (see Fig.1 & 2).

We used opaque, round, 30 ml plastic cups (approx. height of 1 cm) for hiding the food; these cups were covered with square black plastic cards (8*8 cm). The bottom of each cup was covered with a piece of cloth to avoid any noise caused by movements of the food. To avoid olfactory cues, we kept food inside the cups before we used them in the experiments. As reward, we used corn-sized pieces (0.5*0.5cm) of commercial dog food pellets or sausage, both highly favoured food types unavailable outside testing.

3.4. Experiment 1 - The standard object-choice task

3.4.1. Training

Prior to the experiment, the birds received training sessions to habituate them to the setup and to ensure that the birds had learned to make a choice. Therefore, the cups were positioned in 1m distance to each other in compartment δ , separated from the birds by the lattice but visible for them in a distance of approximately 10 cm from the lattice (Fig. 1, page 7). E was kneeling equidistantly between the cups, showed the food to the bird and put it into the left or the right cup in semi-randomized order, with the food placed on the same side for not more than two consecutive trials. Then, both cups were covered with identical plastic cards and simultaneously slipped under the lattice to give the bird access to the cups. The subjects made a choice, opened one cup and - if choosing the baited cup - retrieved the food. If the bird intended to approach the second cup, E removed the cup.

One session consisted of six trials only, to ensure that the birds kept their motivation throughout testing. If a bird left the testing compartment and did not return within five minutes, a session was abandoned. If this happened before the bird had taken at least four trials, this session was abandoned and re-started on the following day. Otherwise, the missing trials were conducted on the next day. In this case, a session could last up to eight trials. The birds had to choose the baited cup on 5 out of 6 trials (83%) in two consecutive sessions (Binomial test, $p=0.039$) to advance to the tests. See Table 1 for the number of training-trials of each bird.

3.4.2. Test

For the experiment, we followed the same protocol as in the training sessions with the following exceptions: Not visible for the bird, E baited the cups in an adjacent room, entered the compartment δ and took a kneeling position. The baited or the unbaited cup was put down first not more than twice in a row with a distance of one meter between the cups. Then, E called the bird's name to attract its attention, and as soon as the bird attended to E, one of two types of cues was presented; the same cue type was not presented more than twice in a row.

For proximal cues, E looked at the baited cup, and the distance between E's face and the cup was set to approx. 30 cm. For distal cues, the distance between E's head and the cup was approx. 1m. Inevitable, proximal cues included a stronger trunk-movement than distal cues. In both cases, E looked at the baited cup for 5 sec. with her hands resting on her legs. After the cue, E slipped the cups under the lattice to the birds, thereby looking straight ahead at the door until the bird had made its choice.

The birds received a total of 30 trials across five sessions. Again, a session lasted for six trials, and the inter-trial interval was set to at least 30 sec, depending on the bird's attention to the setup. If a bird left the testing compartment and did not return within five minutes, a session was abandoned. The missing trials were conducted on the next day. In this case, a session could last up to eight trials.

If an individual chose the baited cup above chance in any of the conditions, 20 control trials were conducted in 4 sessions á 5 trials after the test. This en-bloc testing was introduced to avoid potential confusion effects due to the mixing of test- and control-trials (Schloegl et al. 2008b). In control trials, the procedure was the same as in test trials, but E's gaze was directed straight ahead instead towards a cup.

3.5. Experiment 2 - The string-choice task

The experimental procedure was similar to experiment 1 with the following exceptions. In compartment δ , two boards (8cm * 30 cm) were positioned with a distance of 1.6 m between them (Fig. 2, page 8). A one-meter long string was attached to each board and reached through the lattice into compartment β . The cups were placed on the boards, i.e. to obtain access to a cup the birds had to use the string to pull the board through a hole in the lattice in compartment β . One of the six birds (E) participating in Experiment 1 refused to pull the board and was therefore excluded from Experiment 2.

3.5.1. Training

Training sessions were conducted as in Experiment 1 with the exception that they had to pull the board to obtain the cup. See Table 2 for the number of training-trials of each subject.

3.5.2. Test

The test procedure was identical to experiment 1, with the exception that the birds had to pull the board to gain access to the cup. To ensure that the birds did not make a choice before the cue had been presented, they had been trained before testing to sit on the floor until E had returned into a neutral position after cue-presentation. Then, the subject had to jump on the respective table and make its choice. During cue presentation, E stood between the tables in compartment δ (2-3m distance to S) and turned her head towards the baited cup, with her hands behind her back. Again, proximal and distal cues were given for 5 seconds.

3.6. Analysis

Trials were scored live (2 damaged videos: H: Exp. 1, Session 2; K: Exp.1, Session 3) and from videotapes by JS. Two parameters were measured. First, we took choice of the baited / unbaited cup as a measurement of efficiency. Secondly, we took the latency between the time the experimenter had slipped the cups under the lattice (Exp. 1) or the end of the cue (Exp. 2), respectively, and the time the birds touched the cup. This measurement was used to quantify the required producing effort in the experiments. Producing time was measured from tape in tenth of seconds. For statistical analyses we used SPSS software package 12. Normal distribution was tested using Shapiro-Wilk-Test. We used binomial-test to assess individual deviations from chance-level in each experiment and for both types of gaze cues. We used a paired t-test to compare the mean producing times in both experiment. Results are given two-tailed with an alpha-level of 0.05.

4. Results and Discussion

4.1. Experiment 1

Across both gaze-cues, one out of six birds (B) chose the indicated cup significantly above chance (Binomial-Test: $P = 0.016$), whereas the other rooks performed at chance level (all $P \geq 0.585$, Tab. 1). The performance of the successful bird increased nearly continuously over the course of the experiment (Tab. 3, page 18), indicating a learning progress; additionally, it chose the baited cup significantly above chance with distal gaze cues only (proximal gaze: 10 out of 15 correct; $P = 0.302$; distal gaze: 12 out of 15 correct; $P = 0.035$); still, even though non-significant with proximal cues, in both conditions it chose correctly above 50% of the trials. In control trials, B chose at random ($P = 0.503$). This result demonstrates the ability of a single rook to learn to use gaze cues within 30 trials of the standard object choice task, which could not be found in comparable tasks in ravens (Schloegl et al. 2008c) or jackdaws (Von Bayern et al. 2009): Whereas the ravens did not use gaze cues reliably within 160 trials, the jackdaws did not respond to gaze cues within 24 trials, although they used alternating glance cues.

Table 1. Number of correct choices of rooks in experiment 1. Significant performances (according to a Binomial-Test) are printed bold.

Bird	Required no. of Training-Trials	Choices (no. correct / all trials)			
		All Cues	Proximal	Distal	Control
B (Brain)	42	22/30	10/15	12/15	8/20
E (Elie)	69	13/30	6/15	7/15	
H (Hugo)	55	14/30	7/15	7/15	
K (Kafka)	49	15/30	9/15	7/15	
M (Merlin)	67	14/30	7/15	7/15	
T (Tom)	24	16/30	9/15	5/15	

4.2. Experiment 2

A comparison between the producing time in Exp. 1 and 2 revealed that in Exp. 1 the birds needed $2.48 \text{ s} \pm 1.25\text{s}$ ($X+SD$) to obtain a cup, whereas in Exp. 2 it took them $10.72 \text{ s} \pm 1.58\text{s}$ ($X+SD$; paired t-test: $T=-7.926$, $df=4$, $p=0.0014$). In consequence, the initial assumption that our modification increased the effort to solve the task is fulfilled.

None of the five birds chose the indicated cup significantly above chance across 30 trials (Tab. 2). However, one bird (H) chose correctly on 11 out of 15 trials (73.3%) when proximal cues were given (Binomial-Test: $P=0.118$; the other rooks $P \geq 0.607$), in contrast to 7 out of 15 trials (46.6%) when distal cues were given ($P > 0.999$). Therefore, this bird received 3 more sessions á 6 trials following the same protocol using both cues. Over all 24 trials using proximal cues, H chose correct in 76% of the trials (Binomial-Test: $P=0.023$). Table 3 shows an increase of performance over time, suggesting a case of quick learning similar to B's performance in Exp.1. When distal cues were given, H chose correctly in only 52% of the trials (Binomial-Test: $P > 0.999$). In control trials, H performed on chance level again (50%, Binomial-Test: $P > 0.999$). The discrepancy between the response to proximal and distal cues suggests that the better performance of H with proximal trials was due to the enhanced salience of the cue through E's stronger body orientation.

Table 2. Number of correct choices of rooks in experiment 2. Significant performances (according to a binomial-test) are printed bold.

Bird	Required no. of Training-Trials	Choices (no. correct / all trials)			
		All Cues	Proximal	Distal	Control
B (Brain)	38	16/30	9/15	7/15	
H (Hugo)	33	18/30	11/15	7/15	
		30/48	18/24	12/24	10/20
K (Kafka)	36	15/30	7/14	8/16 ¹	
M (Merlin)	49	16/30	6/15	10/15	
T (Tom)	18	18/30	8/15	10/15	

Table 3. Choices of B and H responding to proximal (p) and distal (d) cues. Grey box=correct choice; White box=incorrect choice.

Ind.	Cue	No. of trial	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
B	p		Grey	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White
	d		White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White
H	p		White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White
	d		White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White

5. General discussion

We proposed that the rooks' ecological, cognitive and social characteristics may be prerequisites for the use of gaze cues to find hidden food, but none of the tested rooks did so spontaneously in our experiments. However, single rooks were able to learn quickly to find the hidden food, which is the first evidence for a corvid species to respond to experimenter given head-and eye cues. Since these birds responded correctly only in a particular setup, they did most likely not refer to the communicative intention of the gaze cue but rather learned a specific discrimination rule. Further, we did not find an effect of producing effort on the performance of the rooks. Either our methodology did not increase the effort sufficiently to be perceived as such by the birds or the effort had no influence on the birds' motivation or attentiveness.

Although this is the first study in which a bird correctly relied on head-and eye cues in the standard object choice task (Exp. 1), we interpret this as an individual disposition to associatively learn to respond to gaze directions in different setups. Interestingly, the subject B did not transfer his learned discrimination from experiment 1 to experiment 2. This is consistent with the findings of Schloegl et al. (2008b), demonstrating that two ravens failed to transfer a learned rule from one modification of the object-choice task to another modification. Also chimpanzees use gaze cues in object choice tasks in certain procedures only (Call et al. 1998, Itakura et al. 1999).

One rook learned a discriminatory rule on the basis of proximal, but not distal gaze cues. However, in the proximal and in the distal condition, the experimenter's head was closer to the correct cup than to the incorrect cup. Hence, rather than learning to choose the cup nearest to the experimenter's head, this bird may have learned a rule concerning the specific spatial arrangement in one condition (Anderson et al. 1995, 1996, Povinelli et al. 1997). This would explain the inability of the bird to transfer its discriminatory

rule to the other condition. Similarly, Schloegl et al. (unpublished data) varied the position of the experimenter in relation to the correct cup, i.e. the experimenter was sometimes closer to the correct or the incorrect cup. Here, some birds avoided or preferred the cup closer to the experimenter, which is again indicative of a sensitivity for the cue-configuration.

Recently, von Bayern et al. (2009) found jackdaws to rely on alternating glance cues in an object choice task, but not on glance or gaze cues presented with only one movement. Although glance cues appear less salient than gaze cues due the lack of head orientation, the repeated movement of the eyes is apparently a stronger indicator than a single head movement. Still, it is not clear if the jackdaws responded primarily to the enhanced movement of the cue or if they perceived the communicative intention of the cue. Rooks and ravens, on the other hand, have been confronted with momentary cues only (Miklosi and Soproni 2006), i.e. cues in which the experimenter looked at the subject, turned the head towards the object and returned in a neutral position before the birds made their choice. Therefore, a comparison of the performance of all three species is not applicable by now, but gaze and glance alternations are promising cues for future comparative studies. This is particularly true as responsiveness to glance may be a special adaptation of jackdaws due to the stark contrast of their light iris and dark pupil.

Still, the question remains why rooks and ravens follow gaze behind a barrier, but do not rely on the same gaze cue when the target is a potentially food containing cup within view. Apparently, others' gaze direction may act as a directory to potential important events, but not as an indicator for a potential food source. The food-indicating character of a gaze cue can be learned in certain experimental configurations, but food caching animals do not seem to be more likely to use gaze to find hidden food than non-caching animals.

Long-tailed macaques (*Macaca fascicularis*) as well as juvenile barbary macaques (*Macaca sylvanis*) are more likely to follow gaze cues when they are accompanied by specific facial expressions. Long tailed macaques respond preferentially to a signal of submission (Goossens et al. 2008) and in juvenile barbary macaques, a facial expression that is given in response to social interactions between third parties was particularly efficient in eliciting gaze following responses (Teufel et al. 2010). Also in Hauser et al.'s (2007) 'communicative gesture', a facial expression was involved in contrast to the 'basic' gaze cue, which was not used as an indicator by the rhesus monkeys. Even though this 'communicative gesture' is not used in the foraging context but to recruit an ally in a fight, the rhesus monkeys were able to use these cues to find food. Accompanying social signals seem to be crucial when it comes to the reliance of a gaze cue in the object choice task. However, in this paradigm rooks are able to learn using gaze cues only, even though without becoming to understand the intentional value of the cue but by following very specific rules.

6. References

Anderson, J. R., Sallaberry, P., Barbier, H., 1995. Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*. 49, 201-208.

Anderson, J. R., Montant, M., Schmitt, D., 1996. Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes*. 37, 47–55.

Bräuer, J., Call, J., Tomasello, M., 2005. All Great Ape Species Follow Gaze to Distant Locations and Around Barriers. *Journal of Comparative Psychology*. 119, 145-154.

Bugnyar, T., Stöwe, M., Heinrich, B., 2004. Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society London, B*. 271, 1331-1336.

Burkart, J. M., Heschl, A. 2006. Geometrical gaze following in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*. 120, 120-130.

Byrnit, J. T., 2004. Nonenculturated Orangutans' (*Pongo pygmaeus*) Use of Experimenter-Given Manual and Facial Cues in an Object-Choice Task. *Journal of Comparative Psychology*. 118, 309-315.

Call, J., Hare, B., Tomasello, M., 1998. Chimpanzee gaze following in an object-choice task. *Animal Cognition*. 1, 89-99.

Call, J., Agnetta, B., Tomasello, M., 2000. Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*. 3, 23-34.

Emery, N.J., Lorincz, E.N., Perret, D.I., Oram, M.W., Baker, C.I., 1997. Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*. 111, 286-293.

Emery, N. J., 2000. The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience & Biobehavioral Reviews*. 24, 581-604.

Goossens, B.M.A., Dekleva, M., Reader, S.M., Sterck, E.H.M., Bolhuis, J.J., 2008. Gaze following in monkeys is modulated by observed facial expressions. *Animal Behaviour*. 75, 1673-1681.

Hare, B., Tomasello, M., 1999. Domestic Dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*. 113, 173-177.

Hauser, M.D., Glynn, D., Wood, J., 2007. Rhesus monkeys correctly read the goal-relevant gestures of a human agent. *Proc. R. Soc. B*. 274, 1913-1918.

Itakura, S., Anderson, J.R., 1996. Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. *Current Psychology of Cognition*. 15, 103-112.

Itakura, S., Tanaka, M., 1998. Use of Experimenter-Given cues during object choice tasks by Chimpanzees (*Pan troglodytes*), an Orangutan (*Pongo pygmaeus*), and Human infants (*Homo sapiens*). *Journal of Comparative Psychology*. 112, 119-126.

Itakura, S., Agnetta, B., Hare, B., Tomasello, M., 1999. Chimpanzees use human and conspecific social cues to locate hidden food. *Developmental Science*. 2, 448-456.

Itakura, S., 2004. Gaze-following and joint visual attention in nonhuman animals. *Japanese Psychological Research*. 46, 216-226.

Kaminski, J., Riedel, J., Call, J., Tomasello, M., 2005. Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*. 69, 11-18.

Loretto, M.-C., Schloegl, C., Bugnyar, T., 2010. Northern bald ibises follow others' gaze into distant space but not behind barriers. *Biology letters*. 6, 14-17. doi:10.1098/rsbl.2009.0510

Miklósi, Á., Polgárdi, R., Topál, J., Csányi, V., 1998. Use of experimenter-given cues in dogs. *Animal Cognition*. 1, 113-121.

Miklósi, A., Soproni, K. 2006. A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*. 9, 81-93.

Peignot, P., Anderson, J.R., 1999. Use of experimenter given manual and facial cues by gorillas (*Gorilla gorilla*) in an object choice task. *Journal of Comparative Psychology*. 113, 253-260.

Povinelli, D. J., Eddy, T.J., 1996. Chimpanzees joint visual attention. *Psychological Science*. 7, 129-135.

Povinelli, D.J., Reaux, J.E., Bierschwale, D. T., Allain, A.D., Simon, B.B., 1997. Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cognitive Development*. 12, 423-461.

Ruiz, A., Gómez, J.C., Roeder, J.J., Byrne, R.W., 2009. Gaze following and gaze priming in lemurs. *Animal Cognition*. 12, 427-434.

Schloegl, C., Kotrschal, K., Bugnyar, T., 2007. Gaze following in common ravens, *Corvus corax*: ontogeny and habituation. *Animal Behaviour*. 74, 769-778.

Schloegl, C., Schmidt, J., Scheid, C., Kotrschal, K., Bugnyar, T., 2008a. Gaze following in non-human animals: The corvid example, in: Weber, E.A., Krause L.H. (Eds), *Animal Behaviour: New Research*. New York: Nova Science Publishers, pp. 73-92.

Schloegl, C., Kotrschal, K., Bugnyar, T., 2008b. Modifying the object-choice task: Is the way you look important for ravens? *Behavioural Processes*. 77, 61-65.

Schloegl, C., Kotrschal, K., Bugnyar, T., 2008c. Do common ravens (*Corvus corax*) rely on human or conspecific gaze cues to detect hidden food? *Animal Cognition*. 11, 231-241.

Shapiro, A. D., Janik, V. M., Slater, P. J. B., 2003. A Gray Seal's (*Halichoerus grypus*) Responses to Experimenter-Given Pointing and Directional Cues. *Journal of Comparative Psychology*. 117, 355-362.

Teufel, C., Gutmann, A., Pirow, R., Fischer, J., 2010. Facial expressions modulate the ontogenetic trajectory of gaze-following among monkeys. *Developmental Science*. In press.

Tomasello, M., Call, J., Hare, B., 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*. 55, 1063-1069.

Vick, S.-J., Anderson, J. R., 2000. Learning and Limits of Use of Eye Gaze by Capuchin Monkeys (*Cebus apella*) in an Object-Choice Task. *Journal of Comparative Psychology*. 114, 200-207.

Von Bayern, A. M. P., Emery, N.J., 2009. Jackdaws respond to Human Attentional States and Communicative Cues in Different Contexts. *Current Biology*. 19, 602-606.

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8. Abstract

Other individual's head- and eye-direction can be used as social cues indicating the presence of resources, predators or social interactions. A number of group-living species respond to these cues and among birds, ravens and rooks have been shown to co-orient with conspecifics and human models by following their gaze direction into distant space and behind visual barriers. Both species use barriers as a screen to cache food in private and it had been suggested that they may also rely on gaze cues to detect hidden food. However, in an object-choice task, ravens failed to do so. Potentially, the ravens' competitive lifestyle may have prevented them from relying on the gaze cues. Here we replicated our study with closely related but cooperative rooks. Food was hidden in one of two cups and the experimenter indicated the location of the hidden food by gazing at it. In a second experiment, we aimed to increase the birds' motivation to choose correctly by increasing the effort needed to obtain the reward. Therefore, birds had to pull on a string to obtain the cup. In both experiments, individual birds quickly learned to use the experimenter's cue. This suggests that rooks may not rely on gaze cues to find hidden food spontaneously, but they may quickly learn to do so.

9. Zusammenfassung (German summary)

Die Blickrichtung anderer Individuen wird durch Kopf- und Augenorientierung angezeigt und kann als Hinweis auf das Vorhandensein von Ressourcen, Räubern oder sozialen Interaktionen genutzt werden. Eine Reihe von in Gruppen lebenden Arten orientieren sich an der Blickrichtung von Artgenossen und Menschen und passen ihren Fokus an die Blickrichtung Anderer an. Bei Vögeln wurde dies bei Raben und Saatkrähen gezeigt, die dabei auch Blicken hinter visuelle Barrieren folgen. Beide Arten verwenden Barrieren als Sichtschutz um Futter zu verstecken und es wurde vermutet, ob sie den Blick auf verstecktes Futter als Hinweis auf dessen Existenz verwenden können. Allerdings scheiterten Raben an der Aufgabe einen derartigen Hinweis zu nutzen um ein Objekt zu wählen, in welchem Futter versteckt war. Potenziell könnte die konkurrenzbetonte Lebensweise der Raben die Verlässlichkeit solcher Hinweise beeinträchtigt haben. Hier haben wir unsere Untersuchung mit eng verwandten, aber kooperativen Saatkrähen wiederholt. Das Futter war in einem von zwei Bechern versteckt und die Experimentatorin gab den Ort des Futters durch ihre Blickrichtung an. In einem zweiten Experiment wollten wir die Motivation der Vögel erhöhen, in dem wir den benötigten Aufwand, um die Belohnung zu erhalten, steigerten. Daher mussten die Vögel an einer Schnur ziehen, um den gewählten Becher zu erhalten. In beiden Versuchen haben einzelne Vögel schnell gelernt, die Blickrichtung als Hinweis richtig zu verwenden. Dies deutet darauf hin, dass Saatkrähen nicht die Blickrichtung Anderer spontan verwenden um verstecktes Futter finden, jedoch können sie schnell lernen, dies zu tun.

10. Curriculum Vitae

Personal Information

Name	Judith Domenica Schmidt
E-mail	Judith.schmidt@gmx.at
Nationality	Austrian
Date of Birth	20. April 1983

Education

1989-1993	Volksschule Schwechat
1993-2001	Bundesgymnasium Schwechat Graduation 2001(in German, English, Mathematics, Latin, Psychology, Biology)
October 2001- September 2003	University of Vienna, Biology Practical Courses: Zoology, Botany, Chemistry, Physics
October 2003- June 2009	University Vienna, Zoology Practical Courses: Scientific Documentation, Scientific English, Animal Identification, Animal Anatomy, Animal Physiology, Bird Song Identification, Communication and Presentation, Neurobiology, Ethology, Practical Ornithology, Excursions to Austria and Greek.

Work Experience (with Biological Background)

February 2004 - November 2007	Guiding at Zoo Vienna
September - October 2005	Ethological Practical Training at Konrad Lorenz Research Station , Grünau im Almtal, Austria
February 2006	Ethological Practical Training at Konrad Lorenz Research Station, Grünau im Almtal, Austria
May - September 2006	Practical Training in Strasbourg, France: <ul style="list-style-type: none"> • Handraising a group of rooks (<i>Corvus frugilugus</i>); • Observations, Experiments on the Ontogeny of Gaze Following
September 2006	Posterpresentation at the 3 rd European Conference of Behavioural Biology, Belfast, Northern Ireland
February 2007	Posterpresentation at the Ethological Society Conference Grünau im Almtal, Austria
July - September 2007	Data-Taking for Diplomathesis in Strasbourg, France
2008	Co-Author of Dr. Christian Schloegl of a bookchapter in 'Behaviour: New Research' New York: Nova Science Publishers.
	Co-Author of Dr. Christelle Scheid of a paper in 'Animal Behaviour'.

- February 2009 – April 2010 Experiments on “Choice by Exclusion – Causal Understanding in African Grey Parrots?” at Arbeitsgemeinschaft Papageienschutz, Vienna and University Vienna
- June 2009 – Now Animal Caretaking (Parrots) at Arbeitsgemeinschaft Papageienschutz, Vienna
- November 2009 Oral Presentation of Diplomathesis at ‘Graduiertentreffen der Ethologischen Gesellschaft’, Seewiesen, Germany
- February 2010 Posterpresentation of Diplomathesis at the ‘5. Thementagung der Ethologischen Gesellschaft’, Berlin, Germany
- April 2010 – Now Vice Leader of the home for parrots at Arbeitsgemeinschaft Papageienschutz, Vienna
- July 2010 Posterpresentation at the 5th European Conference on Behavioural Biology, Ferrara, Italy

Posterpresentations:

Schmidt, J., Schloegl, C., Bugnyar, T., Kotrschal, K. (2006). Lateralisation of eye- and foot-use in captive common ravens (*Corvus corax*). 3rd European Conference on Behavioural Biology, 4 – 6 September, Belfast, Nordirland.

Schmidt J., Schloegl C., Scheid C., Erbrech A., Hindelang T., Bugnyar T., Noe R. & Kotrschal, K. (2007). Further evidence for gaze use in corvids: Ontogeny of gaze-following in rooks (*Corvus frugilegus*). Ethological Society Conference, 22- 25 February, Grünau, Austria.

Schmidt J., Scheid C., Kotrschal, K., Bugnyar T., Schloegl C. (2010). Gaze direction – a cue for hidden food in rooks (*Corvus frugilegus*)? 5. Thementagung der Ethologischen Gesellschaft, 21-23 February, Berlin, Germany.

Schmidt J., Kotrschal K., Schloegl C. (2010). Grey parrots (*Psittacus erithacus*) use indirect information to find hidden food. 5th European Conference on Behavioural Biology, 16-18 July, Ferrara, Italy.

Oral Presentations:

Schmidt, J., C. Scheid, K. Kotrschal, T. Bugnyar and C. Schloegl (2009): Impact of rooks' (*Corvus frugilegus*) investment and informative value of gaze cues in the object choice task. Graduiertentreffen der DZG und der Ethologischen Gesellschaft. 11-13 November, Max Planck Institut f. Ornithologie Seewiesen, Germany.

Publications:

Scheid, C., Schmidt, J. & Noë, R. (2008): Distinct patterns of food offering and co-feeding in rooks. *Animal Behaviour*, 76, 1701-1707

Schloegl, C., Schmidt, J., Scheid, C., Kotrschal, K. & Bugnyar, T. (2008): Gaze following in non-human animals: The corvid example. in: *Animal Behaviour: New Research* (ed. E. A. Weber & L. H. Krause), New York: Nova Science Publishers