



Gaze following in common ravens, *Corvus corax*: ontogeny and habituation

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Co-orientation with others by using their gaze direction is considered to be adaptive for detecting food or predators or monitoring social interactions. Like the great apes, common ravens are capable of following human experimenters' gaze direction not only into distant space but also behind visual barriers. We investigated the ontogenetic development of these abilities by confronting birds with a human foster parent looking up (experiment 1) and behind visual barriers (experiment 3) and their modification by habituation (experiments 2 and 4). We tested a group of 12 hand-reared ravens during their first 10 months of life. Ravens responded to others' look-ups soon after fledging but could track their gaze behind a visual barrier only 4 months later, at the age they usually become independent from their parents. Furthermore, ravens quickly ceased responding to repeated look-ups by the model, but did not habituate to repeated gaze cues directed behind a barrier. Our findings support the idea that the two modes of gaze following reflect different cognitive levels in ravens and, possibly, have different functions.

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Gaze following (Emery et al. 1997) or visual co-orientation (Anderson & Mitchell 1999) is the ability to track the gaze direction (i.e. head and eye orientation) of another individual to a location in space. The adaptive advantage of this skill has been widely acknowledged as alerting individuals to the presence of relevant targets in the environment such as food, predators or conspecifics (Tomasello et al. 2001). Interest in gaze-following abilities of nonhuman animals has recently gained momentum (reviewed in Gomez 2005) since paying attention to another individual's eyes may improve social learning (Tomasello et al. 2005) and potentially signals the understanding of others as intentional beings (e.g. Baron-Cohen 1995; Gallese et al. 2002). Nevertheless, gaze following has been reported from only a few taxonomic groups (reviewed in Gomez 2005).

Gaze following has been assessed via different paradigms: (1) following another's gaze into distant space, e.g. to a point somewhere above the model individual

('look-up' task; e.g. Itakura 1996; Tomasello et al. 1998); (2) following another's gaze geometrically behind an obstacle ('barrier' task; Povinelli & Eddy 1996; Tomasello et al. 1999); and (3) using another's gaze as a cue to find hidden food ('object choice' task; Anderson et al. 1995; Miklósi et al. 1998). Comparing results across species is difficult because: (1) paradigms may reflect different goals on the side of the cue-giver and different functions for the responding subject (reviewed in Gomez 2005); (2) look-up experiments have been conducted with humans, with conspecifics as models (e.g. Tomasello et al. 1998; Bräuer et al. 2005), or even with images of models (e.g. Scerif et al. 2004), and with or without the presence of a target object (e.g. Tomasello et al. 1998; Okamoto et al. 2002); and (3) subjects differ in their rearing history (wild-caught versus captive-reared or hand-reared animals; e.g. Call et al. 2000; Bugnyar et al. 2004), living conditions (wild versus captive animals; e.g. Anderson et al. 1995; Flombaum & Santos 2005) or experiences before the experiments (naïve versus enculturated animals; e.g. Scheumann & Call 2004; Kaminski et al. 2005). Despite such methodological issues, it appears that several nonhuman primates (e.g. Emery et al. 1997; Tomasello et al. 1998),

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domestic goats, *Capra hircus* (Kaminski et al. 2005) and ravens, *Corvus corax* (Bugnyar et al. 2004) are capable of following another's gaze into distant space. Great apes (Tomasello et al. 1999; Bräuer et al. 2005) and ravens (Bugnyar et al. 2004) follow the other's gaze geometrically around visual barriers while dogs, *Canis familiaris*, seem to understand the function of visual barriers (Bräuer et al. 2004). Furthermore, dogs (Miklósi et al. 1998; Hare et al. 2002), bottlenose dolphins, *Tursiops truncatus* (Tschudin et al. 2001) and fur seals, *Arctocephalus pusillus* (Scheumann & Call 2004) may spontaneously use a model's gaze in object choice situations. Thus, different modes of gaze following can be found in phylogenetically distinct taxa, suggesting that these abilities have evolved several times (Miklósi et al. 1998; Emery 2000; Hare et al. 2002).

The underlying cognitive mechanism of gaze following remains unclear. Gaze following has been interpreted as a socially facilitated orientation response (i.e. a predisposition to look where others are looking) that can be modified by experience (Povinelli & Eddy 1996). Individuals may even learn the function of visual barriers and so adjust their orientation responses to take these into account (Call et al. 1998; Tomasello et al. 1999). Individuals may therefore make a representation of the internal mental states of others (Povinelli & Eddy 1996; Tomasello et al. 1999). Alternatively, they could respond to external cues that indicate the direction of another individual's attention (Gomez 2005).

It is likely to be adaptive for most socially living vertebrates to be able to use their social partner's gaze as a cue (e.g. Burger et al. 1992; Hampton 1994) and to be capable of following another's gaze into distant space (i.e. looking in the direction others are looking). This basic skill would probably require no more than an intrinsic tendency to co-orient with others, combined with associative learning (Tomasello et al. 1999; Triesch et al. 2006). However, species with high levels of cooperative and competitive interactions may develop the ability to track another's gaze around obstacles, for example to find hidden items. Building on such a basic co-orientation response, animals may learn to respond appropriately to the presence of visual barriers. Instead of a further development of this basic response, these two gaze-following abilities may even emerge independently. In either case, different developmental patterns should be found during ontogeny.

To our knowledge, only the ability to follow a gaze into distant space has been addressed developmentally in primates, with all species responding to human-given gaze cues by (late) infancy (Ferrari et al. 2000; Tomasello et al. 2001; Okamoto et al. 2002). Young chimpanzees, *Pan troglodytes*, appear to solve the task earlier when the experimenter is gazing at an object within their visual field (i.e. aside; Okamoto et al. 2002) than towards something outside their visual field (i.e. above; Tomasello et al. 2001), which is in line with findings in human children (Butterworth & Jarrett 1991).

In our assessment of the cognitive mechanisms underlying gaze following, the modification of a gaze-following response by learning may be of interest.

Tomasello et al. (2001) exposed subjects to repeatedly given gaze cues that did not target any object. The cessation of a response in this case may indicate a flexible deployment of gaze following. To date, habituation to repeated look cues has been investigated for following gaze into distant space in chimpanzees, rhesus macaques, *Macaca mulatta* (Tomasello et al. 2001) and common marmosets, *Callithrix jacchus* (Burkart & Heschl 2006). In chimpanzees and rhesus monkeys, only adult individuals ceased to respond in a series of 30 repeatedly given look-up cues, whereas marmosets did not habituate to series of 18 cues either to the left or to the ceiling.

Beside apes, ravens are the only species known to follow another's gaze in two different experimental settings. We examined the ontogeny of gaze following in young ravens that were hand reared by humans and kept in a social group with siblings of the same age and adult conspecifics. We systematically recorded the first occurrence of following the gaze of other ravens during daily ad libitum observations and then periodically tested the birds' responses to human-given gaze cues with two experimental paradigms, following gaze into distant space and following gaze behind barriers. In both treatments, we also investigated habituation patterns, that is, whether ravens would stop responding to a repeated presentation of gaze cues that do not lead to anything of interest.

GENERAL METHODS

Subjects and Housing

We used 13 hand-reared ravens (six males, seven females) all of which hatched in spring 2004. Two sibling groups were obtained from zoos at the age of 25 days (three birds) and 40 days (four birds), respectively; one sibling group (three birds) and three single birds were taken from the wild at approximately 27, 12, 14 and 17 days of age. Since ravens fledge at 42–48 days of age, the oldest birds were taken a few days before fledging. Nestlings were reared in artificial nests associated according to their origin (three sib-group nests and one nonsib nest) at the Konrad Lorenz Forschungsstelle, Austria. One wild-caught female received medical treatment during the nestling period and was excluded from the experiments because of delayed physical, motor and behavioural development. All birds were marked with coloured rings for individual identification.

Shortly before fledging, nestlings were transferred to an aviary complex (230 m² and 3–7 m high) in the local Cumberland game park, where they were subsequently housed together with two adults (8 and 4 years of age). This arrangement simulated a nonbreeder situation as in the wild young ravens regularly associate with older ones in mixed-sex groups (Heinrich et al. 1994; Parker et al. 1994). Throughout the study period, the birds were free to interact with each other and were not restricted in their behavioural repertoire, for example they had ample opportunity to cache food and pilfer caches. The aviary was composed of three outdoor sections and five small test compartments (Fig. 1) that were visually isolated

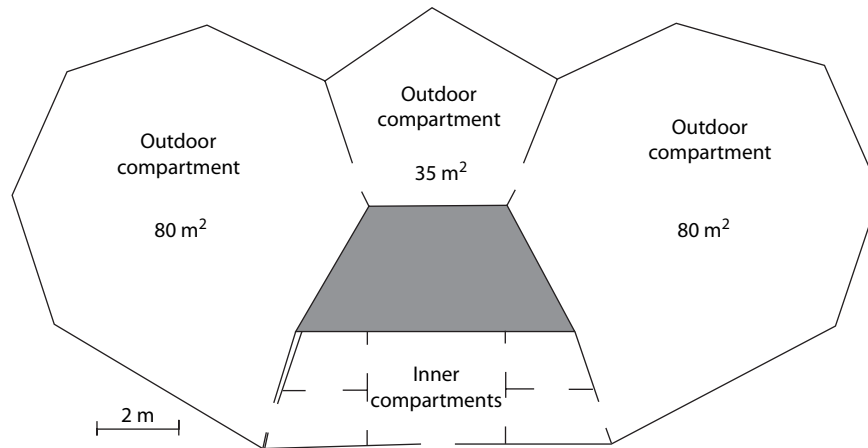


Figure 1. Sketch of the aviary complex. Inner compartments are covered with a semitransparent roof and outdoor compartments with a plastic net. Rooms marked with grey are not accessible for the birds. All compartments are connected through doors.

from the other parts of the aviary by wooden walls. When not being tested, birds were allowed to use the entire complex. The outdoor parts of the aviary were equipped with natural vegetation, bushes and 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. The birds received a diet of meat, fruits, milk products and kitchen leftovers (Kabicher & Fritz 1996) throughout the study period. Before fledging, they were fed five to six times per day at 3-h intervals. After fledging, they were fed three to five times a day, which was reduced to two feedings during summer.

Procedure

In general, we tested subjects for their ability to follow human look-ups once per week (experiment 1) and to follow looks behind a barrier once per month (experiment 3). In both treatments, a habituation study followed acquisition (experiments 2, 4). Tests were conducted individually in the indoor compartments, except in the first few weeks after fledging, when birds were not fully accustomed to temporary visual isolation from their groupmates, and in the last few weeks of the study when deep snow cover on the transparent roof caused low light conditions, preventing some of the birds from entering these rooms. In these cases, individuals were tested outdoors with the walls of the observation hut functioning as a visual barrier to the other ravens in the adjacent compartments. The birds always received a treat for entering the test compartment. However, in none of the experiments were they rewarded for any response to human look cues.

If not stated otherwise, studies were conducted by the principal experimenter (C.S.) with a second experimenter assisting for videotaping during experiments 1 and 2. In experiments 3 and 4, an opened wooden door (90° angle to wooden wall) or standard aviary equipment such as big rocks or tree trunks functioned as a visual barrier for the test subject. Because the visual behaviour of birds consists mainly of head and eye movements (Dawkins 2002), all

look cues involved a change of the experimenter's head angle plus (binocular) eye direction.

Analysis

All trials were scored blind from videotapes by C.S. Owing to technical problems, one session in experiment 1 and two sessions in experiment 3 had to be scored live. Paying explicit attention to the visual behaviour of birds (Zeigler & Bischof 1993), we used head orientation (beak lateral or horizontal) and head movement (e.g. switching from right to left eye up) as criteria for looking up (Dawkins 2002). In the barrier task, distinct orientation behaviour (walking around or flying on top of the barrier) emphasized the birds' responses (Bugnyar et al. 2004). Twenty per cent of the trials were scored independently and blind by T.B. to assess inter-observer reliability (look up: 91.6% concordance, Cohen's $K = 0.78$; look around: 93.3% concordance, Cohen's $K = 0.85$).

In experiments 1 and 3 we used change-point tests (Siegel & Castellan 1988) to examine developmental patterns over time. In these tests N is the number of trials of testing and m indicates the trial after which a change in performance occurred. To investigate the performance of the birds further, we used McNemar tests to compare single test and control trials if a point of change in performance was indicated by the results of the change-point test. Because of the 1–0 sampling method, we used Cochran's Q test for comparisons of more than two habituation trials (Siegel & Castellan 1988). Results are given for two-tailed tests and alpha was set at 0.05. Bugnyar et al. (2004) reported a development of ravens' ability to follow gaze behind barriers. Therefore a clear prediction in one direction was possible, allowing the use of one-tailed statistics for experiment 3. For reasons of comparability between the different experiments, we tested conservatively and report for this experiment one-tailed and two-tailed results separately. We calculated statistics by hand using the statistical tables presented by Siegel & Castellan (1988) and report exact P values, as recommended for small sample sizes (Mundry & Fischer 1998).

Ethical Note

Wild ravens were collected with permission of the Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg, Germany. The zoos in Munich and Wuppertal, Germany provided raven chicks from captive breeding pairs. During the course of the study two birds were killed by martens. The remaining birds are currently housed at the Konrad Lorenz Forschungsstelle in Grünau, Austria, and will remain in captivity for further testing.

FOLLOWING OTHERS' LOOK-UPS

Bugnyar et al. (2004) showed that juvenile hand-reared ravens follow the gaze of humans into distant space. In the current study we investigated when this skill emerged. We tracked the visual behaviour (i.e. monocular look-ups) of ravens before and after fledging and noted the first occurrence of visual co-orientation with conspecifics. In parallel, we tested once a week the individuals' ability to follow look-ups of a familiar human under controlled conditions (experiment 1). We assumed that this mode of gaze following would function mainly for enhanced predator detection and thus should develop at an early age, presumably around fledging. Once young ravens had developed the ability to follow look-ups, we explored whether they would habituate to repeatedly given look cues (experiment 2). We predicted that birds would cease responding since antipredator behaviour is prone to habituation.

Methods

Observations: response to gaze cues of conspecifics

In the course of daily feedings, C.S. recorded ad libitum for each individual the first occurrence of looking up, defined as movement of the head so that the beak is positioned laterally and the bird is looking up with one eye, and visual co-orientation, defined as looking up within 5 s of a bird in its vicinity (i.e. within the compartment) looking up. Feeding lasted approximately 1 h and was conducted six times per day before fledging and five times per day after fledging. Minimum observation time was 6 and 5 h per day, respectively. One or two persons assisted C.S. during feedings. For analysis, the time of first occurrence was corrected for age at fledging.

Experiment 1: response to look cues of a human experimenter

We conducted tests once a week from the ravens' fifth week to the 17th week of life (i.e. 3 weeks pre-fledging to 10 weeks post-fledging). Eight nestlings were tested in their artificial nests, visually separated from their siblings by an opaque plastic sheet. All birds were habituated to this temporary isolation before the experiment. Four individuals arrived only shortly before fledging; these birds were tested right after fledging, that is, when they would perch on the experimenter's arm and could be carried into adjacent compartments. In the first few weeks post-fledging,

the young birds were easily disturbed and hesitated to enter the test compartments; hence, not all birds participated in every session.

A weekly session consisted of one look-up trial and one control trial. At the start of a trial, the experimenter (E) looked directly at the bird to get its attention and called the bird's name. As soon as the bird looked towards E, E gave a gaze cue. In look-up trials, E looked to a point above the bird. Since the artificial nests were protected by a roof (see above), E looked at the ceiling when testing pre-fledging and towards the sky when testing post-fledging. Control trials were conducted in almost the same way as test trials, but E looked to a point behind the bird instead of looking up. We decided not to look permanently at the bird in control trials, since this might have given the cue a different quality compared to test trials. The order of control and test trials was randomized. A look cue was given for 5 s and the bird's response (i.e. whether or not it looked up) was considered for 15 s after the onset of presentation (5 s presentation + 10 s after presentation). Trials were at least 30 s apart, the exact time depending on the bird's attention towards E. The birds tested by Bugnyar et al. (2004) showed a gaze-following response when 8 weeks old. Since the birds tested here did not show a response through their 10th week of life, habituation was likely. We therefore cancelled tests in weeks 11 and 12 post-hatching and a different, but equally familiar person (the second hand-rearer, also male and of comparable age to C.S.) served as E in the 15th week post-hatching.

Experiment 2: habituation

Each bird was tested once in its 18th week of life (11th post-fledging), i.e. 1 week after finishing experiment 1. The test procedure was similar to that in experiment 1 with the exception that five look-up (i.e. test) cues were given in a row instead of one test and one control trial. The time interval between cues was set at 30 s. Another well-known person (T.B.) functioned as cue-giver to avoid habituation to the model. A second experimenter (C.S.) assisted with videotaping.

Results

Observations: response to look cues of conspecifics

Ravens started to look up (lateral beak, one eye up) in the last 12 days before fledging (Fig. 2). First instances of visual co-orientation with a conspecific looking up were recorded a few days after fledging and within 3 weeks all birds were observed to follow another's gaze at least once (Fig. 2).

Experiment 1: response to look cues of a human experimenter

During the course of this experiment, birds changed their response behaviour during look-up trials, but not during control trials (change-point test; look-up trials: $W = 36.5$, $N = 11$, $m = 8$, $P = 0.01$; control trials: $W = 23$, $N = 11$, $m = 5$, $P > 0.99$; Fig. 3). This indicates that with the beginning of their 15th week of life (8th week

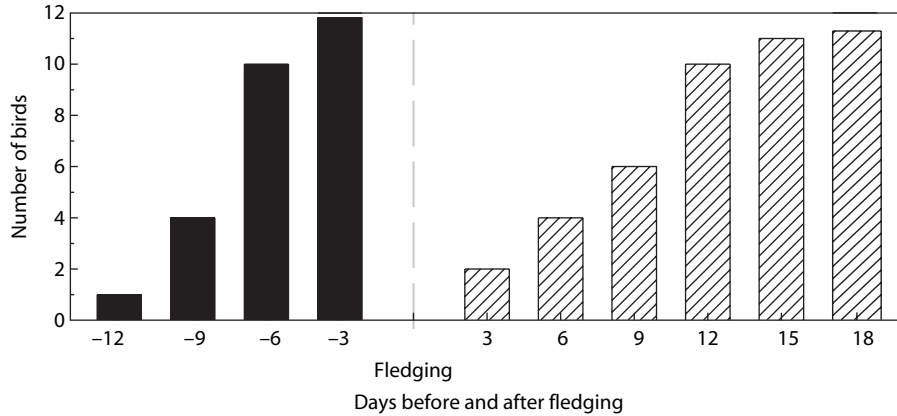


Figure 2. Cumulative number of birds showing one-eyed looking up (■) and gaze following (▨) during daily observations. Bars represent 3-day blocks; vertical dashed line represents day of fledging.

postfledging) birds started to respond to E's gaze cues. At the indicated point of change in response, ravens responded significantly more often in look-up than in control trials (McNemar test: $N = 12, P = 0.008$; Fig. 3); in this week, we replaced the principal experimenter with another familiar human and, instantly, eight of 12 ravens (67%) showed gaze following in the test but not in the control situation. In the 16th week, eight of 12 birds responded when the principal experimenter gave the gaze cue again; however, because three birds responded in the control trial, the difference was not significant (McNemar test: $N = 12, P = 0.125$); this was also true in the 17th week ($N = 12, P = 0.25$).

Experiment 2: habituation

Overall, a steady and significant decline in response was found (Cochran's Q: $Q_4 = 12.22, N = 12, P = 0.016$; Fig. 4). Of the 12 birds that participated in this test, eight followed the gaze of the experimenter, but none did so

more than twice. The maximum response occurred to the first cue (5 of 12 birds; 42%) while no bird responded to cues 4 and 5 (Fig. 4).

Discussion

Our observations indicate that young ravens acquire the ability to look up with one eye in the week before fledging, whereas visual co-orientation with conspecifics' looking up emerges shortly after fledging, at about 8 weeks of age. Although we expected a gaze-following response within this time frame, we are cautious of interpreting the observed behaviours as 'true' gaze following since birds could have perceived something of interest such as a passing bird or a moving twig independently. Nevertheless, this seems unlikely because instances of simultaneous orientation towards one and the same target should have been evident to some extent in the days before and around fledging when all ravens possessed the ability to

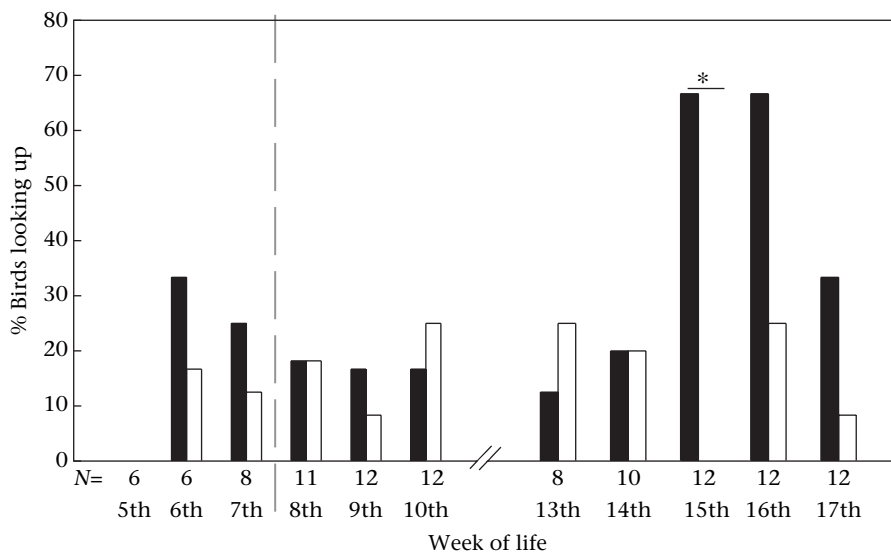


Figure 3. Percentage of ravens looking up in experiment 1. ■: Test condition; □: control condition. Vertical dashed line represents day of fledging. * $P < 0.01$, McNemar test.

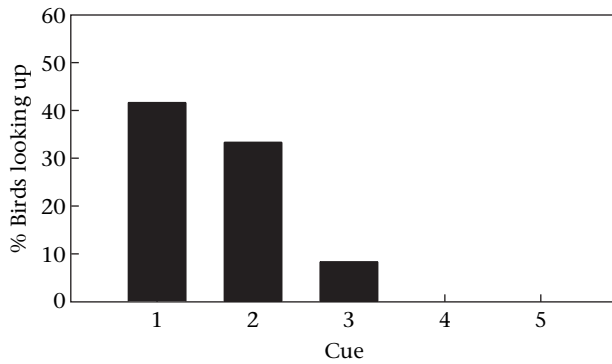


Figure 4. Percentage of birds responding to each of the five human gaze cues in experiment 2.

(independently) look up. Significant gaze follow responses to human-given cues in a controlled experimental setting could not be found before the age of 15 weeks, which is approximately 7 weeks after the first co-orientation with conspecifics.

There are two, not mutually exclusive, explanations for this difference: (1) gaze following into distant space was originally applied to conspecifics only and generalization to familiar humans needed time, thereby coinciding with the replacement of the experimenter or (2) rapid habituation to the experimental design delayed gaze follow responses until the set-up had been modified by replacing the first experimenter. Even though we cannot distinguish between these two explanations, the latter possibility seems likely. From Bugnyar et al.'s (2004) study it is known that similarly treated, hand-reared ravens instantly followed human gaze cues at the age of 2 months but showed habituation within a series of five tests that were conducted in a 15-day period. It is also known from other studies on predator perception of galliformes that captive animals rapidly habituate to a variety of cues, including predator-related cues (e.g. Schleidt 1961; Schleidt et al. 1983). Testing in the same spatial arrangement (Schleidt et al. 1983) and artificial stimuli (Magurran & Girling 1986) can enhance the occurrence of habituation. Owing to the constraints of captivity, our birds had to be tested in a certain spatial arrangement. Furthermore, a human model may not be capable of providing the same stimulus quality as another raven, since aspects other than gaze direction (e.g. body posture) may be of importance for eliciting gaze-following behaviour.

Strong support for the habituation hypothesis comes from the fact that ravens instantly responded when another experimenter gave the cues but did not show a clear significant response when the original experimenter returned (Fig. 2). In an explicit test for habituation with five consecutively given look cues, ravens stopped responding within three cues, and the bird looking up on the third cue had not responded before. Furthermore, if birds did not respond to the first two or three cues, they did not respond at all. Even though the new model person had not given any gaze cues to these ravens before, birds were less responsive at the first cue than with the newly introduced person in experiment 1 (42% versus 67%). This suggests that young ravens may habituate rapidly

not only to a meaningless gaze cue but also to the exchange of models, that is, they generalize from one experimenter to the other.

In summary, ravens develop the ability to follow another individual's look-ups within their first few weeks postfledging, and are prone to habituation at a young age. Because of, methodological issues, it is likely that the 15th week of life does not mark the exact onset of the ability of ravens to follow another's look-ups. Nevertheless, it shows that ravens develop this ability early in life.

GAZE FOLLOWING BEHIND A BARRIER

Bugnyar et al.'s (2004) study indicates that the ravens' ability to track the direction of a human's gaze behind obstacles may emerge later than the ability to follow a human's gaze into distant space. We therefore investigated on a monthly basis when young ravens were capable of dealing adequately with visual barriers (experiment 3). In contrast to the look-up task, there is no previous record of the habituation of ravens to gaze cues during the barrier task. Therefore, we further aimed at explicitly testing for habituation during a series of repeated looks behind a barrier by adopting the same procedure used in the look-up task (experiment 4).

Methods

Experiment 3: ontogeny

The experiment started in June when the birds were 15 weeks old (fourth month posthatching) and lasted until the end of November. At that age, all birds had reached full mobility and had successfully passed the look-up test. To avoid possible habituation effects, we conducted only one session per month. As in experiment 1, sessions consisted of one test and one control trial per bird, carried out in random order. The birds were tested individually and had the opportunity to inspect the whole test compartment before the experiment. E was positioned in line with the barrier (see also Bugnyar et al. 2004) and a trial started as soon as the test subject had moved to one side of the barrier, so that its view to the other side of the test compartment was blocked. E gazed at the bird's side of the barrier, without looking directly at the bird, in control trials and at the other side of the barrier in test trials. Gaze following was recorded if the bird moved over and searched on the indicated side of the barrier within 15 s (5 s presentation + 10 s after presentation); the birds could change sides either by walking around or, as a short-cut, by flying on top of the barrier to look down. One bird received medical treatment during the time of the experiment and was tested only in the first session (at 4 months of age) and in the two last sessions (at 8 and 9 months of age).

Experiment 4: habituation

We conducted this experiment 6 weeks after finishing experiment 3, in mid-January when the birds were 10 months old. The test procedure was similar to that in

experiment 3, but E gave a total of five gaze cues, each 5 s long, to the opposite side of the barrier. The time interval between cues was set at a minimum of 30 s, with the exact time depending on when the bird was again in the correct position. Again, a well-known person that had not been involved in any of the gaze-following experiments functioned as the cue-giver. A second experimenter (C.S.) was present assisting with videotaping. Three birds had to be excluded from the test: two were killed by a marten entering the housing compartments (see [General methods](#)) and one had to be temporarily removed from the group for medical reasons.

Results

Experiment 3: ontogeny

During the course of the 6 months of this experiment ravens increased their response during test trials, but not during control trials (change-point test; test trials: $W = 6$, $N = 6$, $m = 3$, one-tailed $P = 0.05$, two-tailed $P = 0.1$; control trials: $W = 1$, $N = 6$, $m = 1$, one-tailed $P > 0.4$, two-tailed $P > 0.8$; [Fig. 5](#)). The result for the test trials is the lowest P value achievable for $N = 6$ (see [Table J](#), page 339, [Siegel & Castellan 1988](#)). This indicates that a change in performance occurred after the sixth month of life. When we analysed the performance of the birds for each month after the indicated change point separately, we found no difference in the seventh month (McNemar test: $N = 11$, two-tailed $P > 0.999$). In the eighth month, seven of 12 birds (58%) responded during test trials and only one bird (8%) during control trials ($N = 12$, two-tailed $P = 0.07$). Probably because of the low statistical power of the McNemar test, no significant response could be found. In the ninth month of life, 33.3% of the birds responded to E gazing behind the barrier ($N = 12$, two-tailed $P = 0.25$).

Experiment 4: habituation

In contrast to experiment 2, no significant decrease in response could be found (Cochran's Q : $Q_4 = 4.76$, $N = 9$,

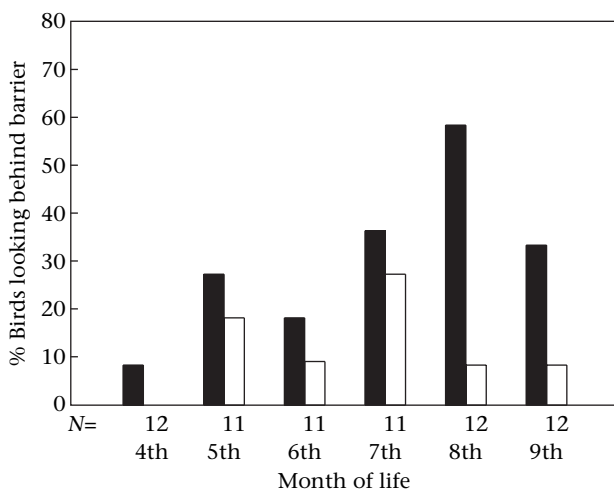


Figure 5. Percentage of ravens moving around the barrier in experiment 3. ■: Test condition; □: control condition.

$P = 0.313$; [Fig. 6](#)). Six of nine birds responded to the second cue whereas only three and two birds responded to the first and fourth cue, respectively. The mean response ratio in this experiment was 44.4% (range 0–80%) which is comparable to the birds' response ratio in the test trials of the autumn period (42.42%; range: 0–100%) but marginally higher than the response ratio in control trials of experiment 3 (15.15%; range 0–66.67%; Wilcoxon test: $Z = -1.724$, $N = 9$, $P = 0.085$).

Discussion

Our results parallel previous findings ([Bugnyar et al. 2004](#)) that showed that after their first summer, hand-reared ravens can track the gaze direction of humans geometrically behind visual obstacles. This skill did not develop earlier than during the birds' first autumn in our present study. Although some birds moved around the barrier in the months before, they were likely to do so in both test and control trials. This suggests that juvenile ravens are inclined to search behind obstacles regardless of the gaze cues provided by the experimenter or, at best, are likely to search on both sides of the barrier as a response to the human's head and eye orientation. From October, a number of birds responded to the human's gaze in the test trials but not in the control trials, indicating that by that time, they could take into account the physical functions of barriers, that is, that barriers can block their view. This 'understanding' does not necessarily require an attribution of mental states to the model and may develop through individuals' daily life experiences with conspecifics that move in front of or behind obstacles ([Tomasello et al. 1999](#)). Nevertheless, it is puzzling that not all birds expressed this 'understanding' before a certain age. The time when young ravens passed the barrier task is comparable with the time when they use obstacles to hide themselves during caching ([Bugnyar et al. 2007](#)) which raises the possibility that maturation processes may affect the ravens' sensitivity to their own and/or the others' visual perspective.

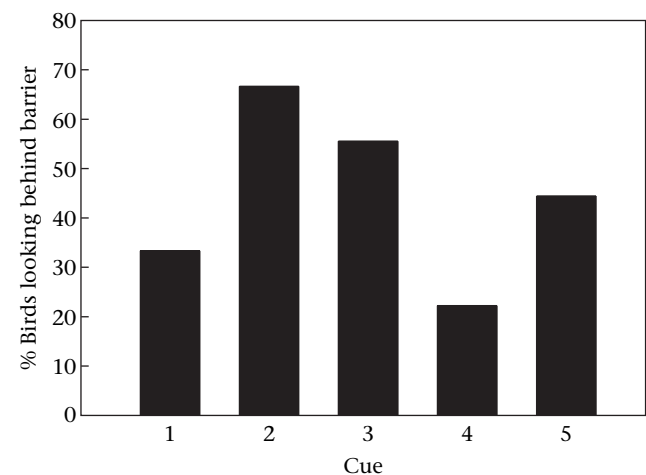


Figure 6. Percentage of birds responding to each of the five human gaze cues in experiment 4.

When tested for habituation, ravens did not stop responding to consecutively given looks behind barriers, which is in contrast to our findings for repeated look-ups (experiment 2). Although birds could explore the opposite side of the barrier before and during the experiment (e.g. when they were following the experimenter's gaze), they were likely to keep on moving to that side after experiencing the experimenter gazing in that direction again. Possibly, high rates of moving to the other side simply reflect the birds' propensity to wander around in the aviary rather than repeated responses to human look cues, but if this were the case, we should have found similar transposition rates during controls of experiment 3, which we did not.

Given that the birds' moves were indeed responses to the experimenter's gaze cues, the lack of rapid habituation appears puzzling, even though the longer intersession intervals and fewer sessions in experiment 3 might have influenced these results. Tomasello et al. (2001) have argued that one way of demonstrating a sophisticated cognitive basis of gaze following is to show that an animal has the ability to stop following the other's looks when nothing of interest can be detected. However, considering the biology of ravens as short-term food cachers (Heinrich & Pepper 1998), not finding something of interest behind an obstacle after following a social cue could simply be an indication that it is hidden; and checking back or searching again after perceiving another social cue in that direction could be advantageous. Nevertheless, it would be interesting to investigate whether ravens habituate to longer series of repeated looks and whether there are any effects of age and experience in pilfering caches.

GENERAL DISCUSSION

Our experiments corroborate previous findings that ravens are capable of tracking the gaze of human models (i.e. head and eye direction) into distant space and geometrically behind obstacles (Bugnyar et al. 2004). We have also shown that the two modes of gaze following occur at different times during ontogeny, with different habituation patterns.

Young ravens started to follow the gaze of conspecifics and humans into distant space shortly after fledging, between 8 and 15 weeks of age. At this developmental period, ravens would normally stay with their family group and still be (partially) fed by their parents. Macaques and chimpanzees have been shown to start following humans' look-ups at the end of infancy (Ferrari et al. 2000; Tomasello et al. 2001) and human children between 6 and 18 months of age (e.g. Butterworth & Jarrett 1991; Deák et al. 2000). Thus, from a developmental perspective, the onset of gaze following in ravens may be roughly comparable with those in nonhuman and human primates. However, in contrast to primates that do not habituate to repeatedly given look cues until adulthood (Tomasello et al. 2001), ravens are capable of ceasing their response to other individuals' look-ups that lead to nothing of interest at this early developmental stage.

Ravens were capable of following the gaze of humans geometrically behind obstacles starting at 8 months of age, which is well after fledging and around the time they become independent from their (foster)-parents but long before adulthood at about 3 years of age. At this time (the birds' first autumn), wild ravens would temporarily associate with nonkin in vagrant nonbreeder flocks (Haffner & Kirchner 1993; Heinrich et al. 1994). Although our birds were fairly advanced in age when following gaze behind obstacles compared to when following gaze into distant space, they did not habituate as rapidly to gaze cues behind barriers as to gaze cues into distant space. As this is, to our knowledge, one of the first systematic studies on both ontogeny and habituation of geometrical gaze following in nonhuman animals, it is difficult to compare our findings with those of other species. In a study by Tomasello et al. (1999), infant chimpanzees followed a human's gaze behind barriers; however, since this study did not focus on the developmental aspect of gaze following, only their average age of 4 years was reported. In contrast to ravens, humans start to follow another's gaze into distant space and geometrically behind barriers within a short time frame between 9 and 12 months of age (Butterworth & Jarrett 1991; Flom et al. 2004; Moll & Tomasello 2004).

It is unclear whether the ravens' response to gaze cues given by humans is due to the hand-rearing procedure or reflects a general responsiveness of ravens to gaze cues of others. Since ravens regularly associate and compete with wolves over food (Heinrich 1989; Stahler 2000), and have long associated with people (Marzluff & Angell 2005), the general ability to respond to heterospecifics' gaze direction, including that of people, may be of adaptive value. With the exception of birds in Alaska and northern Canada (Heinrich 1999), wild ravens are strongly neophobic (Heinrich 1988; Kijne & Kotschal 2002); therefore, it appears not possible to test single wild ravens with a human experimenter.

From a cognitive point of view, our results fit the idea that different modes of gaze following (i.e. into distant space, behind barriers) may reflect different cognitive mechanisms (Povinelli & Eddy 1996; Tomasello et al. 1999). Following another's gaze into distant space may be a predisposition to respond to the visual behaviour of others which is then shaped by learning ('low-level model', Povinelli & Eddy 1996; 'orienting-response model', Emery 2000). Accordingly, it is not surprising that ravens stop responding to gaze cues that do not target anything of interest (e.g. an avian predator). Nevertheless, they come to adjust their visual behaviour flexibly to those of others much earlier than primates, including apes. Possibly, following the look-ups of other individuals has different functions for different taxa so that the 'openness' for learning is under different selection pressures. For example, for birds mainly foraging in relatively open fields a single response may suffice to detect an avian predator. In contrast, for species living under dense canopy, the visibility of approaching predators or conspecifics might be reduced and therefore repeated gaze-following responses might be a more secure strategy. Furthermore, for different species repeated gaze follow responses may have different costs, for example some species may be more vulnerable to conspecifics attempting to steal food.

The prolonged development in ontogeny and the apparent absence of (rapid) habituation with tracking another's gaze behind obstacles supports the idea that geometrical gaze following is qualitatively different from following another's look-ups. However, our findings do not allow us to draw conclusions on the exact mechanism involved. Taking the properties of visual barriers into account may require some understanding of function (i.e. that barriers can block one's view) and, possibly, about the other's perspective (i.e. what others can and cannot see; 'high-level model' by Povinelli & Eddy 1996; 'perspective-taking model' by Emery 2000; Bräuer et al. 2005). Nevertheless, this understanding may derive from learning about the other's behaviour (e.g. cues that are associated with seeing) in daily social interactions (Tomasello et al. 1999). For instance, studies on geometrical gaze following in human infants report that 12-month-old children may respond properly to the presence of a barrier (Moll & Tomasello 2004), but may not have an understanding for the other's perception (Butler et al. 2000). To pinpoint the effects of learning on geometrical gaze following, studies need to manipulate individuals' experience with visual barriers during ontogeny.

From a functional point of view, we propose that developmental differences between modes of gaze following may reflect different ecological demands. Hence, once species have evolved the ability to follow the gaze of others, they may face different selection pressures depending on what it is (mainly) used for, detecting predators, food resources or important social interactions. Adopting such an ecological perspective may explain why species perform well with some, but fail with other test paradigms (e.g. primates versus dogs; Miklósi et al. 1998; Hare et al. 2002; Gomez 2005), show different habituation patterns within a particular paradigm (e.g. primates versus ravens) and, possibly, rely on different mechanisms for functionally different problems. In ravens, following other individuals' look-ups may serve mainly for enhanced predator detection (monocular looking up is a typical antipredator behaviour of birds), whereas following their gaze behind obstacles may be important during foraging, in particular for finding their food caches (Bugnyar et al. 2004). Indeed, the ability to follow look-ups develops exactly at the time when young naïve birds leave the nest and become most vulnerable to aerial or arboreal predators. In contrast, tracking another's gaze around obstacles emerges when birds are fully independent and engage regularly in competition with nonkin conspecifics over food. Nevertheless, to understand further the differences between various modes of gaze following, more comparative data from other mammalian and avian species are needed.

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