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Report

Jackdaws Respond to Human Attentional States and Communicative Cues in Different Contexts

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Summary

Humans communicate their intentions and disposition using their eyes [1, 2], whereas the communicative function of eyes in animals is less clear [3]. Many species show aversive reactions to eyes [4–6], and several species gain information from conspecifics' gaze direction by automatically co-orienting with them [7]. However, most species show little sensitivity to more subtle indicators of attention than head orientation [3, 8] and have difficulties using such cues in a cooperative context [9, 10]. Recently, some species have been found responsive to gaze direction in competitive situations [11–13]. We investigated the sensitivity of jackdaws, pair-bonded social corvids that exhibit an analogous eye morphology to humans, to subtle attentional and communicative cues in two contexts and paradigms. In a conflict paradigm, we measured the birds' latency to retrieve food in front of an unfamiliar or familiar human, depending on the state and orientation of their eyes toward food. In a cooperative paradigm, we tested whether the jackdaws used familiar human's attentional or communicative cues to locate hidden food. Jackdaws were sensitive to human attentional states in the conflict situation but only responded to communicative cues in the cooperative situation. These findings may be the result of a natural tendency to attend to conspecifics' eyes or the effect of intense human contact during socialization.

Results and Discussion

Placed into a conflict situation in which preferred food was presented in front of a human, ten hand-raised jackdaws took longer to retrieve the reward when the person was directing their eyes toward the food than if they were looking away from it, but only when the person was unfamiliar, thus potentially threatening. The jackdaws responded to subtle differences in the state and orientation of the human's eyes and their spontaneous approach latency in the five different conditions, "back turned" (B), "eyes closed" (C), "gaze averted," (G), "profile" (P), or "facing" (F), that appeared to reflect the attentiveness of the unfamiliar person (Figure 1). A general linear model (GLM) revealed a significant effect of condition ($F_{4,\ 32} = 14.99$, $p = 0.00$) and subject ($F_{9,\ 32} = 5.54$, $p = 0.00$), but no effect of the order in which the conditions were tested ($F_{4,\ 32} = 1.85$, $p = 0.14$). Tukey post-hoc tests were significant for all comparisons with the baseline condition F (B-F, $T = 7.02$, $p = 0.00$; C-F, $T = 6.05$, $p = 0.00$; F-P, $T = 5.33$, $p = 0.0001$; F-G, $T = 4.14$, $p = 0.002$). Additionally, the extreme baseline condition B differed significantly from G (B-G, $T = 3.26$, $p = 0.02$). The results mirror recent findings on starlings that approached food more quickly when a predator's eye gaze is averted rather than direct [11] as opposed to sparrows that are not sensitive to eye-gaze direction [4]. There was no effect of condition ($F_{4,\ 40} = 0.48$, $p = 0.75$) or order ($F_{4,\ 40} = 1.02$, $p = 0.41$) when the person was familiar to the subjects, suggesting a flexible response rather than a rigid gaze-aversion mechanism.

In order to test the jackdaws' response to more subtle attentional cues and to control for any potentially unwanted behavioral cues by the human, we tested the jackdaws with digital photographs of several attentional states displayed by another unfamiliar person's face, which were presented on a TFT screen. Again, we found a significant effect of condition (GLM: $F_{5,\ 50} = 3.09$, $p = 0.02$) and subject ($F_{11,\ 50} = 2.39$, $p = 0.02$) but not order ($F_{5,\ 50} = 0.83$, $p = 0.53$). The jackdaws appeared to perceive the baseline condition F as equally threatening as the new conditions "profile glancing" (PG; the human faced away, but glanced toward the food with one eye) and "one eye open" (O; the human faced the food keeping one eye closed) (Figure 2). Tukey tests revealed significant differences between F and C and between F and P (C-F, $T = 3.42$, $p = 0.01$; F-P, $T = 3.2$, $p = 0.03$) but not between F and G, PG, or O (all $p > 0.05$). An additional analysis comparing attentional (F, O, and PG) with inattentional states (G, C, and P), found a significant effect of state (one-way ANOVA: $F_{1,70} = 5.53$, $p = 0.02$) with higher approach latencies when the experimenter presented attentional rather than inattentional states. Unlike the other species tested so far [6, 11], except for rhesus monkeys [13], the jackdaws' aversive response did not depend on a "two eyes present" rule (i.e., a low-level gaze-aversion mechanism).

Therefore, independent of the facial orientation, the number of visible eyes, or the perceptual similarity or dissimilarity of the attentional states, the jackdaws' approach latency depended on whether the human's eye(s) were oriented toward the food. Although this may indicate an intuitive understanding of the eyes' role in perception in jackdaws, the results may also be explained by a low-level cognitive mechanism, i.e., sensitivity to eye orientation. This sensitivity could be an adaptation to the assessment of predation risk. However, given that jackdaws' main predators are birds of prey [14] that turn their head rather than their eyes, sensitivity to eye orientation would seem irrelevant. Instead, it may have evolved in response to within species selection pressures (involving both cooperation with a bonding partner and conflict with competitors). Analogous to human eyes (white sclera and dark iris) [2], the morphology of jackdaw eyes (light iris and dark pupil) makes their eye orientation discernible (which may also predispose them to detect human eye gaze). Also behaviorally, there are several indications that jackdaws employ eye signals to communicate with conspecifics, most importantly their long-term bonding partner [15].

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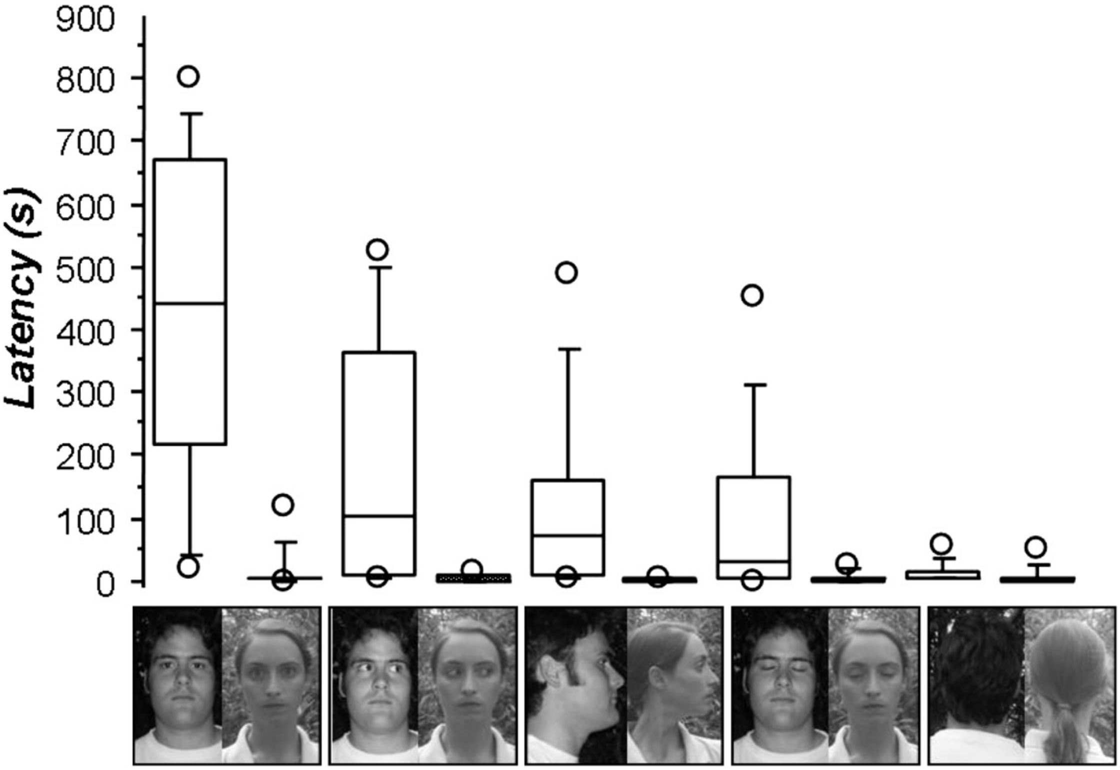

Figure 1. The Jackdaws' Response to Five Different Attentional States Displayed by an Unfamiliar and a Familiar Human

Box plots displaying median latency (s) to retrieve the food in the presence of an unfamiliar (white box plots) and a familiar (shaded box plots) human displaying different attentional states (B, C, G, P, or F). Whiskers designate the 90% and 10% confidence intervals. Open circles denote outliers.

To further investigate the interpretation that jackdaws may be sensitive to eyes because they need to communicate and cooperate with a partner, we assessed their sensitivity to attentional and communicatory social cues in a cooperative context, the object-choice task. This is a standard paradigm employed to investigate animals' understanding of others' focus of attention [16]. Typically, a human experimenter provides cues indicating the location of the food, which is hidden under one of two containers. As such, the task not only requires the subject to be able to follow a cue and understand that it refers to the location of hidden food but may also involve some understanding of communicative intent. Most species tested so far, including apes, required intense training to use head and gaze, eye gaze alone, or pointing as discriminative cues in the object-choice task or could not use them at all [10, 17–20]; however, there has been greater success for domestic dogs and enculturated chimpanzees [19, 21–23], as well as free-ranging rhesus monkeys if cues were naturally communicative [24]. Many species that have difficulties using gaze cues provided by conspecifics or humans to locate food in this cooperative task [16, 21, 25] successfully use such cues in competitive tasks [12, 13, 26, 27]. One suggestion for this difference is that species that do not communicate cooperatively [28] and that share intentions during their natural social interactions cannot use gaze cues in a cooperative context, such as in the object choice task [29]. Jackdaw partners however cooperate, e.g., they share food and jointly explore their environment, and communicate by directing each other's attention to food and interesting objects [15, 30, 31].

In our experiment, the jackdaws only utilized cues provided by their familiar caretaker (same person as in experiment 1b) if they were communicatory. These were cues humans use to actively indicate something to others, i.e., gaze alternation (GA) and a subtle cross-distal pointing cue (CDP). Static cues signifying direction of attention toward a container, i.e., eye-gaze (G) and/or head (H) orientation (Figure 3B), were not used successfully. There were significant effects of subject (GLM: $F_{8,94} = 2.22$, $p = 0.03$) and cue type (GLM: $F_{3,94} = 6.85$, $p = 0.00$), but not trial (GLM: $F_{2,94} = 1.09$, $p = 0.34$) on success in locating the hidden food. Tukey tests revealed significantly greater correct responses to CDP compared to G ($T = 3.84$, $p = 0.001$) and H ($T = 3.24$, $p = 0.01$), but not GA ($T = 0.84$, $p = 0.84$). There was also a significantly greater correct response to GA compared to G ($T = 3.0$, $p = 0.2$), but only a nonsignificant trend compared to H ($T = 2.4$, $p = 0.08$). There was no difference in responses between G and H ($T = 0.6$, $p = 0.93$).

Therefore, in contrast to chimpanzees [32], but similar to rhesus monkeys [24], jackdaws were sensitive to eye movements and cross-distal pointing cues in this cooperative task. However, although they were highly sensitive to an unfamiliar human's direction of attention in the conflict situation described above, the jackdaws did not respond to the person's direction of attention in the cooperative context, again like the rhesus monkeys [24]. These findings suggest that the jackdaws' response may depend on the context in which cues were displayed; only the active communicatory cues may be perceived as relevant in the cooperative situation. Parallels to both communicatory cues may be found in the interaction of bonding partners, e.g., beak pointing and mutual gaze; jackdaw partners use their eyes and beaks to actively direct each others' attention to objects [15, 30].

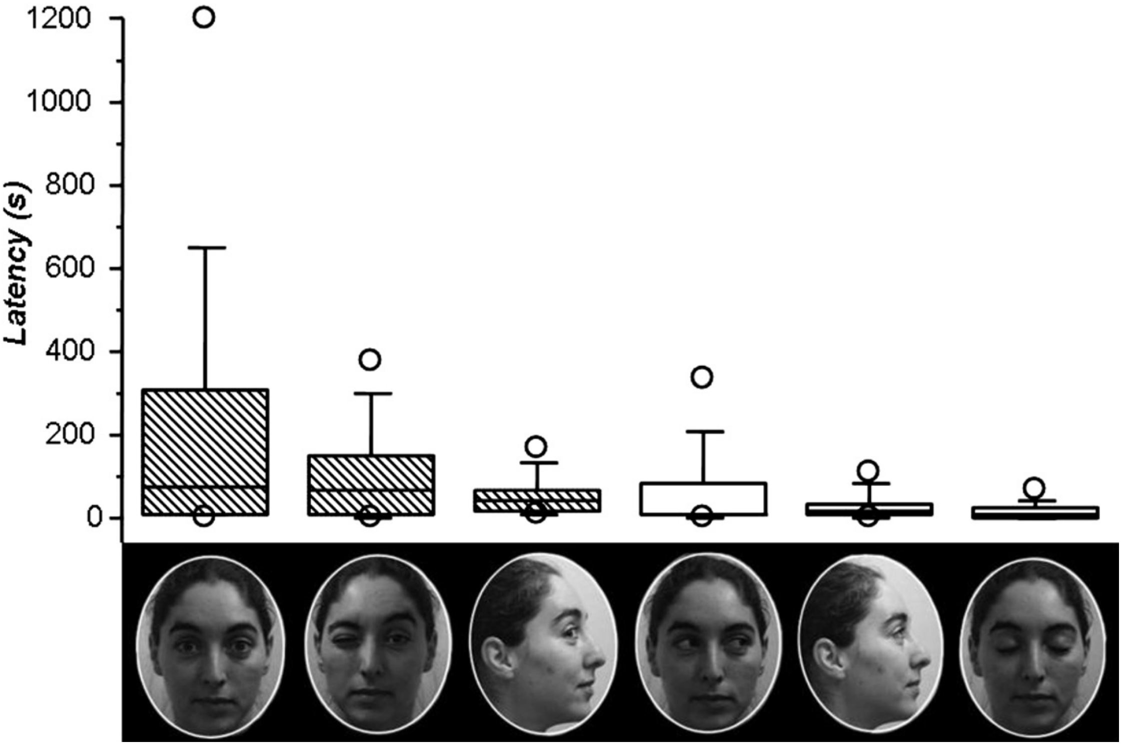

Figure 2. The Jackdaws' Response to Six Digitally Presented Attentional States of an Unfamiliar Human's Face

Box plots displaying median latency (s) to take the food in the presence of an unfamiliar person displaying different attentional states (F, O, PG, G, P, and C) presented on a TFT monitor. Whiskers designate the 90% and 10% confidence intervals. Open circles denote outliers. The hatched boxes denote the "attention toward" conditions, whereas the white boxes designate the "attention away" conditions.

The experiments, taken together, suggest that jackdaws, compared to chimpanzees [33, 34], are highly sensitive to the focus of human eyes and their communicatory function. This sensitivity to eyes could be a predisposition evolved in response to both competitive and cooperative interactions with conspecifics, i.e., determining the attentional focus of competitors and close-range communication and coordination with their partner, a vital skill for this long-term pair-bonded corvid. It could also been affected by the hand-raising history of the subjects, i.e., an intense socialization with human caregivers during a vital stage of their development, which may have enhanced their sensitivity to human expressions and gestures, as in enculturated apes [35]. Future research is necessary to assess the importance of attentional focus and direct eye contact between conspecifics during avian communication.

Experimental Procedures

Experiment 1

The subjects were ten hand-raised group-housed jackdaws. They were tested individually in a side compartment visually blocked off from their housing aviary. An unfamiliar (H1, experiment 1a) or an familiar (H2, experiment 1b) human stood 1.25 m from a 1.45-meter-high feeding pit, which was fixed at the end of a 1.50-meter-long horizontal perch (Figure S1 available online). The bird could move freely in the test compartment or settle down on a perch that was 2 m from the ground and approximately 2.5 m from H.

Once the subject had settled down after a habituation period, H moved into position and assumed one of five attentional states with the same neutral facial expression and body oriented toward the feeding pit, and then remained as motionless as possible throughout the trial. For three conditions (facing [F], eyes closed [C], and glancing [G]), H faced the food item on the feeding pit, which was approximately at chest height. For the profile (P) condition, H's face (with the eyes facing forward) was averted at a 90° angle from the food, whereas in the back (B) condition, the whole body was rotated 180° away from the food. Subjects were tested once in each of the five conditions consecutively, separated by 3 min intervals. The sequence of conditions was pseudorandomized between the birds to control for any order effects. We measured the birds' latency to take the food (a giant mealworm) from the moment it was placed onto the feeding pit and H had assumed the relevant posture. Maximum trial duration was 20 min. This practical upper limit was set to avoid ceiling effects because we knew from previous work with jackdaws that if individuals did not approach within 20 min, they were not likely to approach during the following hour, thereby rendering latency scores insensitive. When this upper limit was exceeded the trial was terminated and scored as 1200 s. If a subject exceeded the upper limit more than once, it was excluded from the analysis.

The effects of condition, order, and subject were assessed with a General Linear Model (GLM). Tukey tests were used to compare differences between individual conditions. Before the experiment, the F and B conditions were designated as the two extreme baseline conditions against which all other comparisons would be made. Alpha was set at 0.05 and all results are given two-tailed.

Experiment 2

In experiment 2, six attentional states (facing [F], one eye open one eye closed [O], glancing [G], profile glancing [PG], profile [P] and eyes closed [C]) were presented as digital images of a life-sized unfamiliar H's face, on a TFT monitor fitted inside a box (1.20 m × 1.45 m × 0.90 m), with an oval opening on the front side at a height of 1.10 m. This represented a more realistic, thus more threatening, situation for the cavity-breeding jackdaws than an open screen with a disembodied face. A wooden perch with a feeding pit attached to it at 1.30 m from the box protruded from under the oval opening (Figure S2). To reveal the stimulus, the experimenter (E) lifted an opaque wooden screen that covered the face in the opening, placed a mealworm on the feeding pit as quickly as possible, and withdrew.

The experimental procedure, scoring, and statistical analysis was very similar to experiment 1; however, an additional analysis (one-way ANOVA)

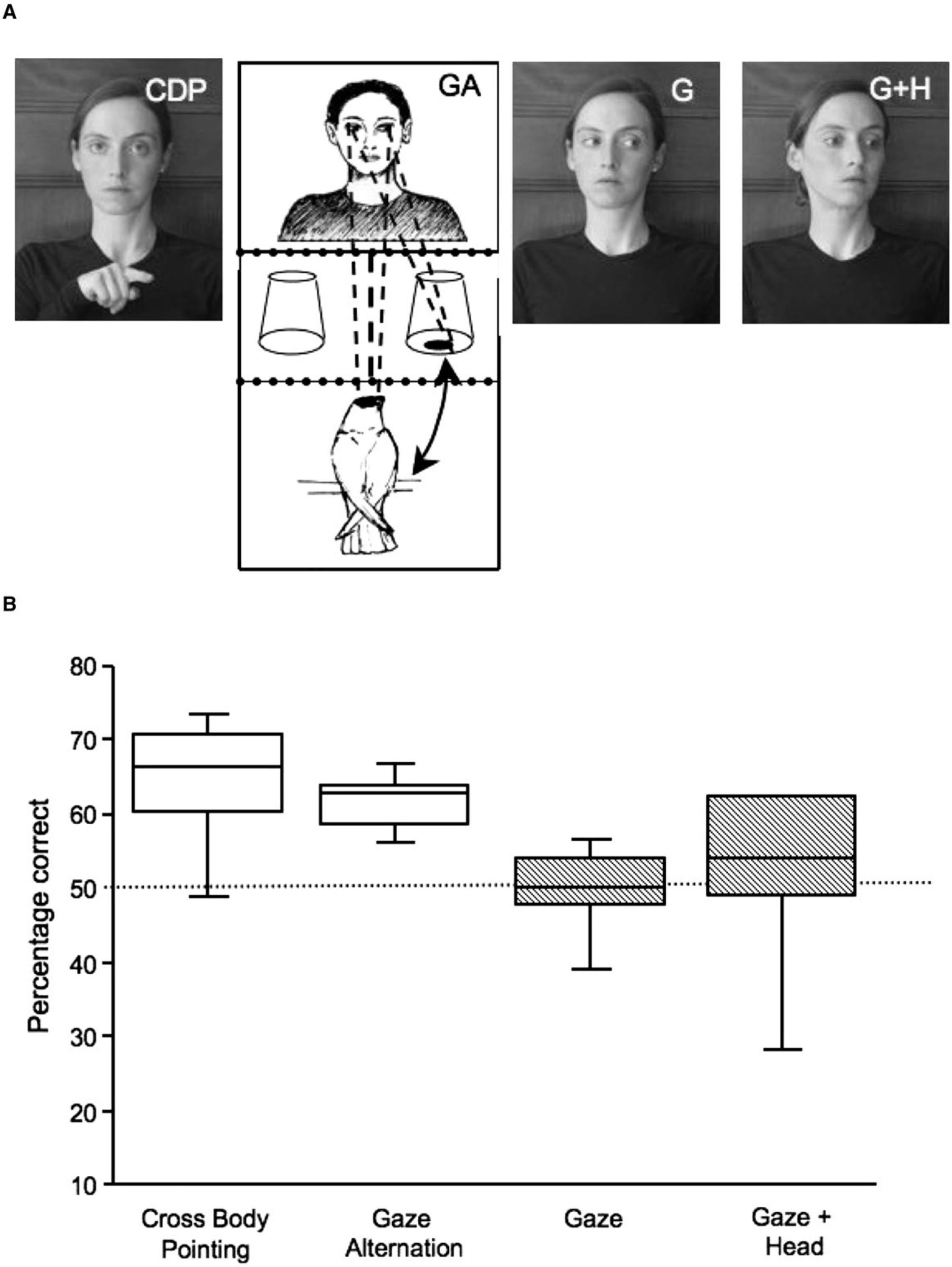

Figure 3. The Jackdaws' Responses to Human Communicative and Attentional Cues in an Object Choice Task

(A) Photographs of four social cues used in experiment 3 (CDP, GA, H, and G).

(B) Box plots displaying the median percentage correct performance in choosing the box containing the hidden food across the four conditions; communicative cues (CDP and GA) are designated by white boxes and attentional cues (G + H) are designated by hatched boxes. Whiskers designate the 90% and 10% confidence intervals.

was performed to compare attentional and inattentional states. In this analysis, the three attentional states (F, PG, and O) were grouped together and compared to the grouped inattentional states (C, G, and P). Alpha was set at 0.05 and all results are given two-tailed.

Experiment 3

Subjects were nine of the jackdaws tested in the previous experiments. The experiment was conducted in a test apparatus consisting of three compartments (Figure 3A). The subject was placed into compartment A from which it could see into the other two compartments, B and C. The middle compartment B was split into two parallel passages, each of which contained one of two identical opaque containers. E moved inside compartment C so that the subject could see her head and shoulders during presentation of the different social cues.

In a series of training trials preceding the test trials, the subjects had consistently retrieved food from the baited container at which the E had tapped (see Supplemental Data). Four conditions (social cues) were presented (Figure 3A): two static attentional cues, i.e., head + eye gaze (H) and eye gaze (G), and two communicatory cues, i.e., gaze alternation (GA; E moved their eyes between the subject and the baited container repeatedly) and cross-distal pointing (CDP; see Supplemental Data for detailed descriptions). The subject watched E while assuming that the respective posture after baiting had been completed. E then remained motionless in that pose, facing forward (except for the eye movements in GA) with a neutral facial expression until the subject made its choice.

The subjects received a total of 24 trials per condition, presented as three blocks of eight trials per condition in a predetermined sequence (CFP, G, H, and GA; see Supplemental Data for details). The percentage number of correct responses to each cue type was compared with a GLM, with subjects, cue type, and trial as factors. Alpha was set at 0.05 and all results are given two-tailed.

All experiments were approved by the Department of Zoology Animal Management Committee, University of Cambridge, and UK Home Office guidelines on the use of animals in research.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, two figures, and one table and can be found with this article online at http://www.current-biology.com/supplemental/S0960-9822(09)00879-3.

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